

SYSTEMATIC DESCRIPTION OF THREE NEW MAMMALS (NOTOUNGULATA AND RODENTIA) FROM THE EARLY MIOCENE CERRO BANDERA FORMATION, NORTHERN PATAGONIA, ARGENTINA

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Abstract. The Cerro Bandera Formation is a mostly pyroclastic continental unit exposed in isolated areas of east-central Neuquén Province, northwestern Patagonia. Several mammals from these deposits were previously reported and support a Colhuehuapian age (early Miocene) for these levels. New findings reveal that this unit bears a much more diverse assemblage and calls into question this age assessment. Here we describe three new species. *Protypotherium sinclairi* sp. nov. (Notoungulata, Interatheriidae) is similar in size to the Santacrucian *Protypotherium australe* Ameghino, but differs from all the species of the genus by having less reduced p3–p4 talonids. *Doryperimys olsacheri* gen. et sp. nov. (Rodentia, Neopiblemidae) has hypselodont, prismatic cheek teeth that combine features of species of *Perimys* Ameghino and *Scotamys antiquus* Loomis. The systematic position of *Leucokephalos maior* sp. nov. within Caviomorpha is still uncertain, but it is definitively allied to the Deseadan *Leucokephalos zeffiaae* Vucetich, Dozo, Arnal, and Pérez in sharing rooted cheek teeth with an almost identical early occlusal simplification that resembles the 8-shaped configuration of some early octodontoids and putative chinchilloids. The three species co-occur at a single fossil locality and stratigraphic level on the northeastern slope of Barda Negra; *P. sinclairi* and *D. olsacheri* are also recorded in other levels exposed in different isolated outcrops of the Cerro Bandera Formation. *Doryperimys olsacheri*—like other previously described rodents from this unit—is unknown in other presumably coeval mammal associations, but the biochronological and paleobiogeographic meaning of this assemblage is still under study.

Key words. Notoungulata. Caviomorpha. Systematics. Cerro Bandera. Early Miocene. Neuquén. Patagonia.

Resumen. DESCRIPCIÓN SISTEMÁTICA DE TRES NUEVOS MAMÍFEROS (NOTOUNGULATA Y RODENTIA) DEL MIOCENO TEMPRANO DE LA FORMACIÓN CERRO BANDERA, NORTE DE PATAGONIA, ARGENTINA. La Formación Cerro Bandera es una unidad continental mayormente piroclástica expuesta en áreas aisladas en el centro-Este de la Provincia de Neuquén, Noroeste de Patagonia. Varios mamíferos de estos depósitos fueron reportados previamente sustentando una Edad Colhuehuapense (Mioceno temprano) para estos niveles. Nuevos hallazgos revelan que esta unidad porta una asociación mucho más diversa y cuestionan esta edad. Aquí se describen tres nuevas especies. *Protypotherium sinclairi* sp. nov. (Notoungulata, Interatheriidae) es similar en tamaño a *Protypotherium australe* Ameghino (Santacrucense), pero difiere de todas las especies del género por tener los talónidos de p3–p4 menos reducidos. *Doryperimys olsacheri* gen. et sp. nov. (Rodentia, Neopiblemidae) tiene molariformes hipselodontes, prismáticos, con caracteres combinados de las especies de *Perimys* Ameghino y de *Scotamys antiquus* Loomis. La posición sistemática de *Leucokephalos maior* sp. nov. dentro de los Caviomorpha aún es incierta, pero está definitivamente relacionado a *Leucokephalos zeffiaae* Vucetich, Dozo, Arnal, and Pérez (Deseadense) por compartir molariformes radiculados con una casi idéntica simplificación oclusal temprana que recuerda a la configuración en forma de ocho de algunos octodontoides tempranos y supuestos chinchilloideos. Las tres especies ocurren positivamente en la misma localidad y nivel estratigráfico en el faldeo nororiental de la Barda Negra; *P. sinclairi* y *D. olsacheri* también se registran en otros niveles expuestos en diferentes afloramientos aislados de la Formación Cerro Bandera. *Doryperimys olsacheri*, así como otros roedores de esta unidad previamente descritos, es desconocido en otras asociaciones de mamíferos presumiblemente coetáneas, pero el significado biocronológico y paleobiogeográfico de esta asociación aún está bajo estudio.

Palabras clave. Notoungulata. Caviomorpha. Sistemática. Cerro Bandera. Mioceno temprano. Neuquén. Patagonia.

THE Cerro Bandera Formation is a Cenozoic continental sedimentary succession exposed in isolated areas of east-central Neuquén Province, northwestern Patagonia (Fig. 1).

These outcrops represent the relicts of an old alluvial infilling developed in small local valleys eroded into Late Cretaceous and Paleocene rocks (Leanza and Hugo, 1997;

Kramarz *et al.*, 2005). This unit yielded a diverse mammal assemblage and a few bird remains (Kramarz *et al.*, 2005). Based upon the presumed correlation with the nearby Chichinales Formation suggested by Leanza and Hugo (1997) and the occurrence of some particular mammal taxa (e.g., *Cramauchenia normalis* Ameghino, 1902; *Proaditherium* cf. *P. muensteri* Ameghino, 1902; *Eosteiomys* Ameghino, 1902; *Caviocricetus lucasi* Vucetich and Verzi, 1996), Kramarz *et al.* (2005) concluded that the fossil-bearing deposits of the Cerro Bandera Formation correlate with the Lower Faunal Zone in the Colhue Huapi Member of the Sarmiento Formation at Gran Barranca (south of Colhue Huapi Lake, central Patagonia), dated at 21.1–20.1 Ma (Dunn *et al.*, 2013), the type section for the Colhuehuapian

South American Land Mammal Age (SALMA).

Additional taxa in new localities of the Cerro Bandera Formation were further reported by Kramarz (2005), Kramarz and Bond (2011), Kramarz and Paz (2013), and Kramarz *et al.* (2011, 2012), but were not fully described or investigated.

The aim of this contribution is to describe new mammal taxa from the Cerro Bandera Formation, based on recently collected specimens and/or previously reported specimens (Kramarz *et al.*, 2005) that still lack formal naming. These descriptions expand knowledge of the mammal diversity preserved in this unit allowing for further discussion of its correlation with other early Miocene mammal-bearing deposits in South America.

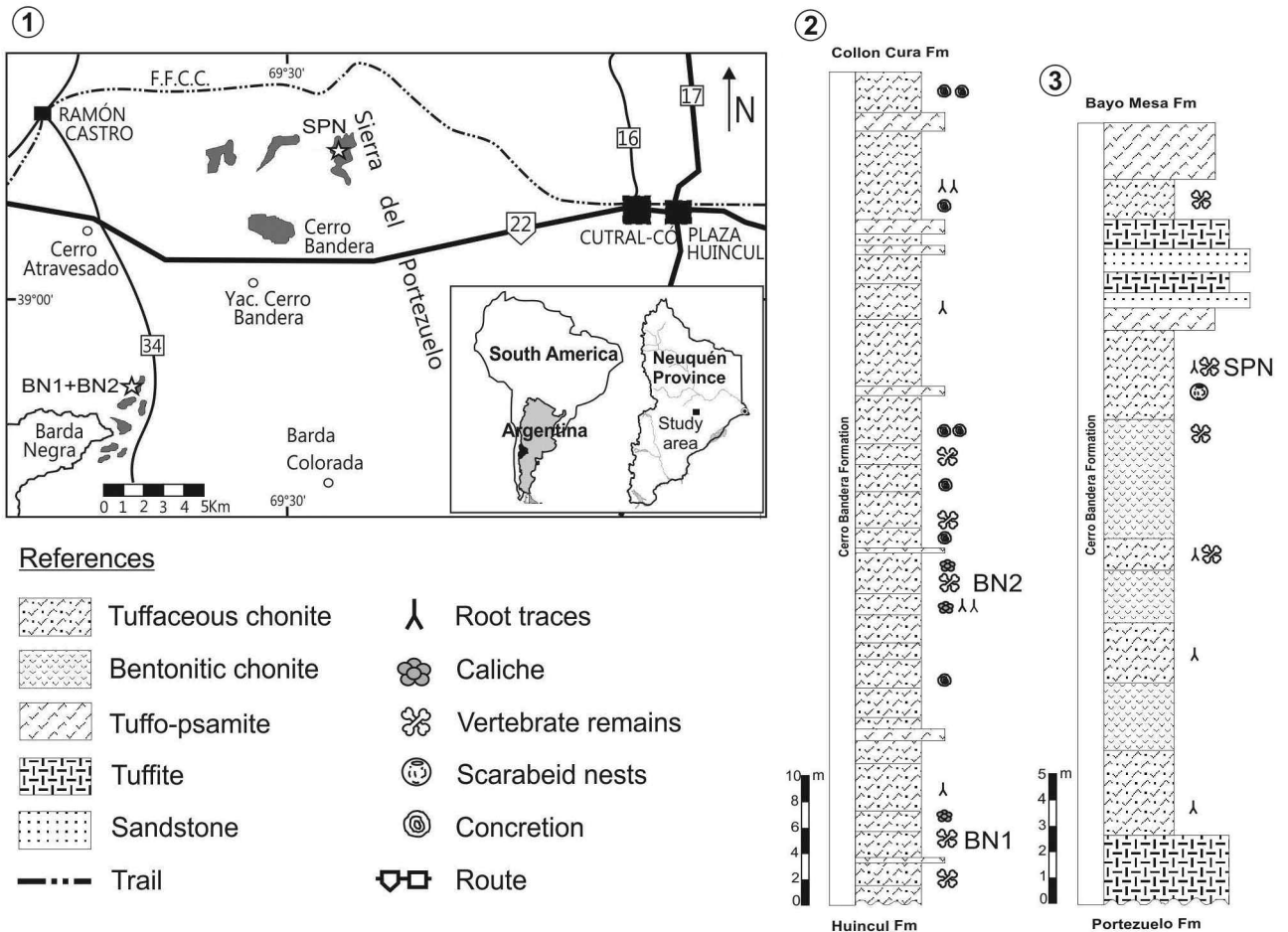


Figure 1. Geographic and stratigraphic provenance of the specimens described in this paper. 1, Geographic location of the exposures of the Cerro Bandera Formation (grey areas) in central Neuquén Province. White stars show the location of the fossil localities. 2, Stratigraphic section of the Cerro Bandera Formation on the northeastern slope of Barda Negra showing the stratigraphic position of the mammal-bearing horizons exposed at BN1 and BN2. 3, Stratigraphic section of the Cerro Bandera Formation at the northwestern slope of Sierra del Portezuelo Norte showing the stratigraphic position of the mammal-bearing horizon exposed at SPN. Modified from Kramarz *et al.* (2005, 2011).

Institutional abbreviations. MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Buenos Aires, Argentina; MLP, Museo de La Plata, Buenos Aires, Argentina; MOZ-PV, Colección de Paleovertebrados, Museo Provincial de Ciencias Naturales "Dr. Prof. Juan A. Olsacher", Zapala, Neuquén, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; PVPH, Colección Paleontología de Vertebrados, Museo Municipal Carmen Funes, Plaza Huincul, Neuquén, Argentina.

GEOLOGICAL SETTING AND FOSSIL LOCALITIES

The Cerro Bandera Formation is 45 m-thick and consists of pyroclastic deposits showing evidence of fluvial reworking and/or pedogenesis, alternating with primary fall-out pyroclastic deposits, with abundant bentonitic horizons in the lower section and scant intercalated sandstones in the upper section. The abundant tuffaceous and tuffitic contents would have originated from discontinuous ash fall derived from Andean or sub-Andean volcanic centers. The origin of these deposits is associated with a fluvial environment in an intermontane foreland basin; lacustrine deposits accumulated in the central, topographically lower areas of the paleovalleys, whereas paleosols accumulated in the marginal, higher areas. This depositional system resulted in marked lateral facies variations among the currently isolated exposures (Leanza and Hugo, 1997; Kramarz *et al.*, 2005).

Several isolated outcrops of the Cerro Bandera Formation bearing vertebrate remains were identified in east-central Neuquén Province (Fig. 1). The fossils studied herein are derived from exposures located along the northeastern slope of Barda Negra and the northwestern slope of Sierra del Portezuelo Norte. In Barda Negra Locality 1 (Loc. BN1, Fig. 1.1) (39° 02' 06.3" S; 69° 40' 54.3" W), mammal remains come from whitish-greyish tuffaceous horizons, about six meters from the base of the stratigraphic section exposed in the area (Fig. 1.2). A second site at Barda Negra (Locality BN2) (39° 02' 09.4" S; 69° 40' 47.6" W) is represented by similar rocks located nearly 25 m from the exposed base (Fig. 1.2). In Sierra del Portezuelo Norte (Loc. SPN, Fig. 1.1) (38° 52' 52" S; 69° 28' 22" W), the level bearing the remains described herein is a pedogenized tuffaceous chonite (*sensu* Teruggi *et al.*, 1978) with poorly preserved scarabeid nests, about 21 m from the base of the

stratigraphic section exposed in the area (Fig. 1.3).

SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903

Family INTERATHERIIDAE Ameghino, 1887a

Genus *Protypotherium* Ameghino, 1885

Type species. *Protypotherium antiquum* Ameghino, 1885.

Included species. *P. attenuatum* Ameghino, 1887a; *P. praeutilum* Ameghino, 1887a; *P. australe* Ameghino, 1887b; *P. diastematum* (Ameghino, 1891); *P. distinctum* Cabrera and Kraglievich, 1931; and *P. minutus* Cabrera and Kraglievich, 1931.

Chronological and geographic distribution. Early-late Miocene, Patagonia (Chile and Argentina), central Argentina, and Bolivia (Ameghino, 1885, 1887a; Cione *et al.*, 2000; Flynn *et al.*, 2002, 2008; Croft *et al.*, 2009).

Protypotherium sinclairi sp. nov.

Figure 2, Table 1

1984 *Protypotherium* sp.; Vucetich and Bond, p. 105.

2005 *Protypotherium* sp.; Kramarz *et al.*, p. 282, fig. 4A.

Holotype. PVPH 352, partial right mandibular ramus with i2–m2 (Loc. SPN).

Etymology. After the paleontologist William J. Sinclair, in recognition of his substantial contributions to the knowledge of Miocene typotheres systematics.

Referred specimens and provenance. MOZ-PV 899, right mandibular fragment with p3–p4 (Loc. BN1); MOZ-PV 1034, left mandibular fragment with p2–p3 (Loc. BN2); MLP 75-II-5-8, right mandibular fragment with p2–m3 (see discussion below).

Diagnosis. Interatheriid with talonids of p3–p4 shorter (mesiodistally) than the trigonid, as in all species of *Protypotherium* and *Miocochilius anomopodus* Stirton, 1953, and unlike the species of *Cochilius* Ameghino, 1902 and *Interatherium* Ameghino, 1887b. Differs from *M. anomopodus* by lacking diastemata between c, p1, and p2. Differs from all the species of *Protypotherium* by having a more elongate p2 with more pronounced labial and lingual flexids, and transversely larger p3–p4 talonids that are almost as wide as the trigonids. Size similar to *P. australe*, larger than *P. praeutilum* and much larger than *P. attenuatum*.

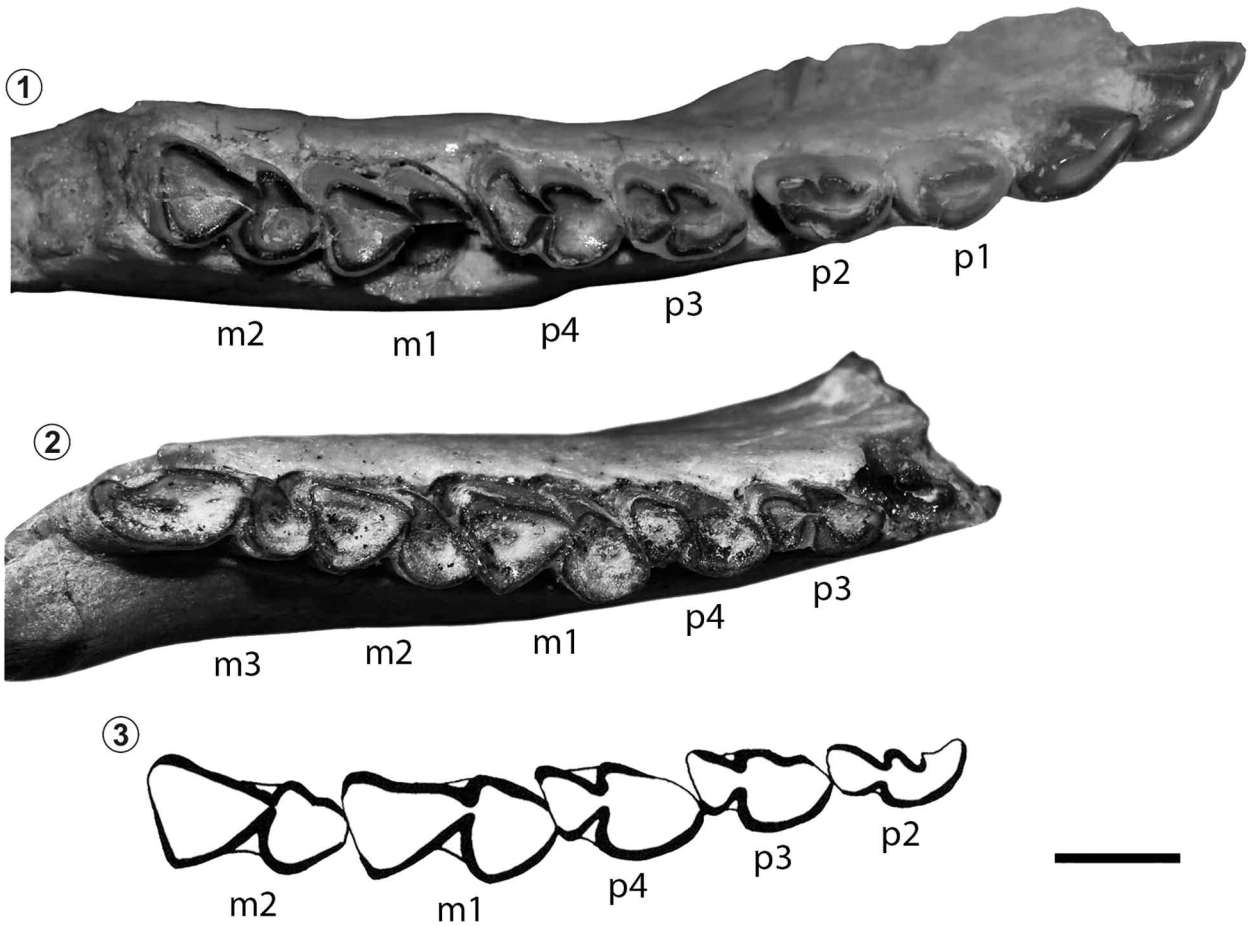


Figure 2. Comparison of lower dentitions of *Protypotherium sinclairi* sp. nov. and *Protypotherium australe* Ameghino. 1, *Protypotherium sinclairi* sp. nov., VVPH 352 (holotype), right mandibular ramus with i2–m2 in occlusal view; 2, MLP 75-II-5-8, right mandibular ramus with p3–m3 in occlusal view; 3, *Protypotherium australe*, schematic occlusal view of the p2–m2 series (modified from Tauber, 1996). Abbreviations: m, lower molar; p, lower premolar. Scale bar= 5 mm.

TABLE 1. Dental measurements (in mm) of *Protypotherium sinclairi* sp. nov.

	i2		i3		c		p1		p2		p3		p4			m1			m2			i2-m2 length
	L	W	L	W	L	W	L	W	L	W	L	TalW	TriW	L	TalW	TriW	L	TalW	TriW	L	TalW	
PVPH 352	3.2	2.3	5.3	2.5	5.4	2.4	5.1	3.1	5.7	3.3	5.3	3.4	2.9	6.3	3.8	3.8	6.7*	4.4	6.9	4.3	4.5	46.1
MOZ-PV 899											5.2	3.3	2.7	5.7	3.2	3.1						
MOZ-PV 1034									4.1	2.5	5.6	2.8	2.6									
MLP 75-II-5-8											5.2	2.9	2.6	5.4	3.7	3	7.5	3.9	4.2	7.1	3.8	3.8

Abbreviations: c, lower canine; i, lower incisor; L, total preserved length; m, lower molar; p, lower premolar; TalW, talonid width; TriW, trigonid width; W, maximum preserved width; * approximate.

Discussion

The features of the lower premolars mentioned in the diagnosis are clearly distinct from those of other interthere

species and are constant among the referred specimens. Contrarily, other characters of the incisors, molars and mandible seem to vary greatly among specimens referred

to this and other species of *Protypotherium*. Further comparisons could eventually support the inclusion of additional characters in the diagnosis.

The taxonomic status of the numerous species of *Protypotherium* and other interatheriines was discussed by Sinclair (1909) and later by Tauber (1996) (see Tab. 2), although a few species based on materials that cannot be compared with *P. sinclairi* (i.e., upper cheek teeth) remain unresolved and deserve the following comments.

Protypotherium diversidens Ameghino, 1891, is based on a juvenile maxillary with the deciduous premolars and M1–M2 (MACN A 4052). The size of the preserved M1 (length= 5.7 mm, width= 3.4 mm) is very similar to that of *P. attenuatum* (see Tauber, 1996, p. 22), much smaller than in *P. australe*, and consequently also smaller than the inferred size of *P. sinclairi*. Tentatively, we herein propose *P. diver-*

sidents as a junior synonym of *P. attenuatum*.

Protypotherium diastematum is based on a palate (MACN A 4044) with a small diastema between P1 and P2 (Ameghino, 1891). We found a similar condition in specimens referred to other species, but the actual distribution, variability and systematic relevance of this feature is still uncertain for us, and thus we prefer to keep *P. diastematum* as a valid species for the time being. The size of *P. diastematum* (M1–M3 length= 18.8 mm) is definitively smaller than in *P. australe* (see Sinclair, 1909, p. 35), and therefore smaller than *P. sinclairi*.

Protypotherium martini Lane, 1927, is also based on a maxilla. According to Lane (1927) it differs from other species of *Protypotherium* by having more elongated upper cheek teeth. However, the type of *Protypotherium compressidens* Ameghino, 1891 (MACN A 4029–4030), inter-

TABLE 2. Species of *Protypotherium* and their corresponding synonyms.

Species	Synonyms	Source	Age
<i>P. antiquum</i> Ameghino, 1885	–		Huayquerian or Chasicooan
<i>P. distinctum</i> Cabrera and Kraglievich, 1931	–		Chasicooan
<i>P. minutus</i> Cabrera and Kraglievich, 1931	–		Chasicooan
<i>P. australe</i> Ameghino, 1887b	<i>P. palmidens</i> (Ameghino, 1889)	Sinclair, 1909	Santacrucian
	<i>P. furculosus</i> (Ameghino, 1891)	Sinclair, 1909	Santacrucian
	<i>P. distortus</i> (Ameghino, 1891)	Sinclair, 1909	Santacrucian
	<i>P. altus</i> (Ameghino, 1891)	Sinclair, 1909	Santacrucian
	<i>P. lineare</i> Ameghino, 1894	Sinclair, 1909	Santacrucian
<i>P. praerutilum</i> Ameghino, 1887a	<i>P. claudum</i> Ameghino, 1889	Tauber, 1996	Santacrucian
	<i>P. compressidens</i> Ameghino, 1891	Sinclair, 1909	Santacrucian
	<i>P. convexidens</i> Ameghino, 1891	Sinclair, 1909	Santacrucian
	<i>P. leptocephalus</i> (Ameghino, 1891)	Sinclair, 1909	Santacrucian
<i>P. attenuatum</i> Ameghino, 1887a	<i>P. martini</i> Lane, 1927	This paper	Santacrucian
	<i>P. globossum</i> Ameghino, 1891	Sinclair, 1909	Santacrucian
	<i>P. icochiloides</i> (Ameghino, 1894)	Sinclair, 1909	Santacrucian
	<i>P. rectus</i> (Ameghino, 1891)	Sinclair, 1909	Santacrucian
	<i>P. diversidens</i> Ameghino, 1891	This paper	Santacrucian
<i>P. diastematum</i> Ameghino, 1891	–		Santacrucian
<i>P. sinclairi</i> sp. nov.	–	This paper	Colhuehuapian?
<i>P. minor</i> Bordas, 1939	<i>Cochilius minor</i> (Bordas, 1939)	This paper	Colhuehuapian

preted by Sinclair (1909) and by Tauber (1996) as a junior synonym of *P. praerutilum*, has even more elongated upper cheek teeth. Consequently, *P. martini* should be considered a junior synonym of *P. praerutilum*. Alternatively, *P. compressidens* and *P. martini* could be united in a separate species in which the lower premolars (preserved in the holotype of *P. compressidens*) differ definitively from those of *P. sinclairi* (i.e., talonids more reduced transversely).

Protypotherium minor Bordas, 1939, based on a partial skull with dentition (MACN Pv 11742), is the only species of *Protypotherium* described from deposits bearing Colhuehuapian mammals. The upper premolars of the type and only known specimen are clearly bilobed with no reduction of the anterior lobe, a feature that characterizes species of *Protypotherium*. Therefore, *P. minor* is more properly referable to the genus *Cochilius*.

In the holotype of *Protypotherium claudum* Ameghino, 1889 (MACN A 551), interpreted as a junior synonym of *P. australe* by Tauber (1996), the talonids of p3–p4 are almost as wide as the trigonids, as in *P. sinclairi*. However, the premolars are vaguely molariform, structurally very different from those of *P. sinclairi* and other recognized species: the lingual column of the metaconid is much less prominent, the talonids are much shorter distolingually, the p3 lacks a lingual flexid, and the p4 lingual flexid is much more superficial. *Protypotherium claudum* is positively distinct from *P. sinclairi*, either as a separate species or as a synonym of *P. australe*.

The premolar morphology of MLP 75-II-5-8 (Fig. 2.2), here referred to *P. sinclairi*, is definitively closer to that of the holotype than to any other currently known specimen of *Protypotherium*. It comes from the Sarmiento Formation exposed along the southern cliffs of the Chubut River at Bryn Gwyn, in central Patagonia. The bearing horizon, which also provided the holotype of *Gaimanomys alwinea* Vucetich and Bond, 1984, is a light grey sandstone near the top of the Sarmiento Formation (Trelew Member), overlying beds bearing Colhuehuapian mammals and underlying the marine Gaiman Formation. This finding documents that *P. sinclairi* had a wide distribution in Patagonia.

Specimen PVPH 351 from the Cerro Bandera Formation (Loc. SPN) was listed by Kramarz *et al.* (2005) as co-specific with the specimen herein selected as holotype of *P. sinclairi* and was interpreted as having deciduous premolars.

Nevertheless, a further analysis revealed that at least the p3 and p4 of PVPH 351 are rootless (i.e., they are not deciduous) and do not show the reduced talonids typical of *Protypotherium*. Therefore, this specimen could more likely belong to some species of *Cochilius*.

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Family NEOEPIBLEMIDAE Kraglievich, 1926

Genus *Doryperimys* gen. nov.

Type species. *Doryperimys olsacheri* sp. nov.

Etymology. *Dory*, from the Greek “spear,” in relation to the spear-like cross section of the cheek teeth, and *Perimys* Ameghino, 1887a, an early Miocene chinchilloid.

Chronological and geographic distribution. Early Miocene, Colhuehuapian? SALMA; Neuquén Province, Argentina.

Diagnosis. Small neoeplemid, size similar to adult specimens of *Perimys incavatus* Ameghino, 1902, with hypselodont, biprismatic cheek teeth (triprismatic in M3), with wide interprismatic cement. Differs from species of *Perimys* by having the following combination of characters: cheek teeth formed by comparatively broader prisms; labial apices of the lower cheek tooth prisms much sharper (more lanceolate occlusal contour); posterior prism of m1–m2 much more extended lingually than the anterior one; lingual flexid more penetrating in m1 than in m3 (in contrast to species of *Perimys*); enamel remnant covering the labialmost portion of the anterior wall of the lower molars and the lingualmost portion of the posterior wall of the upper ones.

Doryperimys olsacheri sp. nov.

Figure 3, Table 3

Holotype. MOZ-PV 955, a right mandibular fragment with p4–m3 (Loc. BN1).

Hypodigm. The holotype and the following specimens: MOZ-PV 956, right maxillary fragment with M1–M2 (Loc. BN1); MOZ-PV 957, right mandibular fragment with erupting p4, m1–m2 (Loc. BN1); MOZ-PV 958, partial left m1 or m2 (Loc. BN1); MOZ-PV 959, left m1 or m2 (Loc. BN1); MOZ-PV 960, right m1 or m2 (Loc. BN1); MOZ-PV 961, left p4 (Loc. BN1); MOZ-PV 962, right M1 or M2 (Loc. BN1); MOZ-PV 963, right

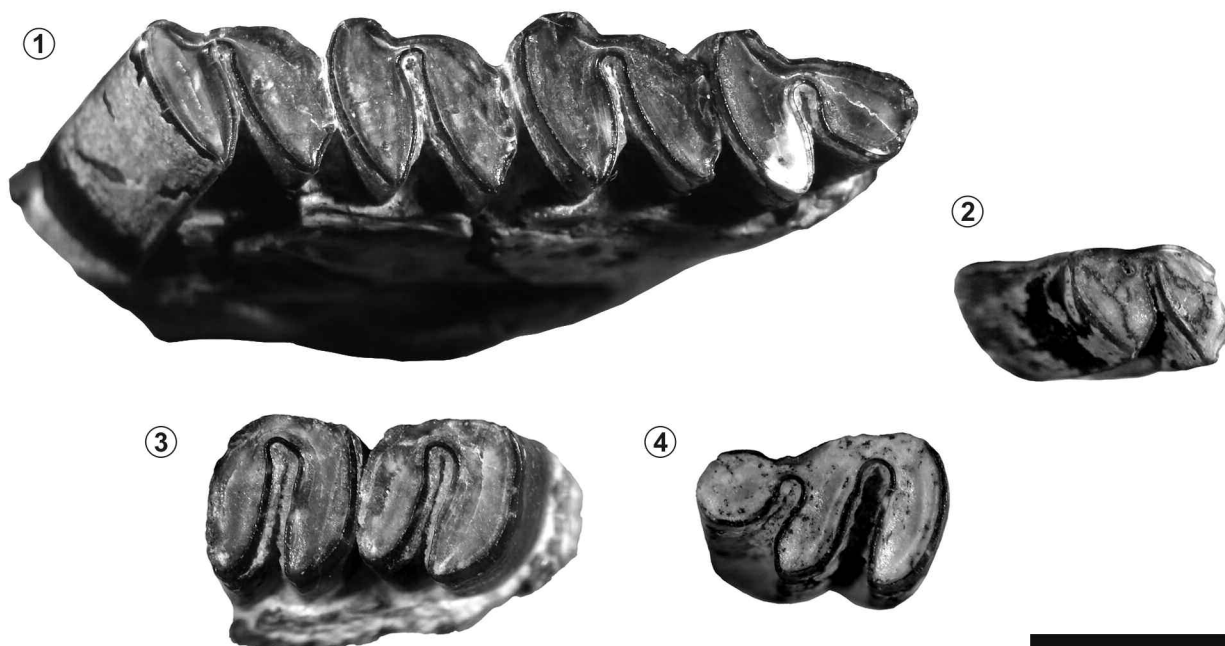


Figure 3. *Doryperimys olsacheri* sp. nov. 1, MOZ-PV 955 (holotype), right p4–m3 in occlusal view; 2, MOZ-PV 1047, right m3 in occlusal view; 3, MOZ-PV 956, right M1–M2 in occlusal view; 4, MOZ-PV 988, right M3 in occlusal view. Scale bar= 5 mm.

TABLE 3. Dental measurements (in mm) of *Doryperimys olsacheri* gen. et sp. nov.

	p4			m1			m2			m1 or m2			m3			p4-m3 length
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	
MOZ-PV 955	5.2	2.3	4	5.1	3.6	4.4	5	4	4.5				5.1	3.8	3.9	20.1
MOZ-PV 959										4.4	3.6	3.5				
MOZ-PV 961	3.8	2.1	3.1													
MOZ-PV 1407													3.9	3.1	3	
MOZ-PV 957							3.9	3	3.1							
MOZ-PV 987										4.8	4	4				
MOZ-PV 960										5	3.5	3.5				
MOZ-PV 1046													4.8	4.3	3.8	
MOZ-PV 984	4.1		3.3	4.4	3.3	3.9										
				M1			M2			M1 or M2			M3			
				L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	3W
MOZ-PV 956				4	4	3.6	3.7	4.1	4.1							
MOZ-PV 962										3.8	4.1	3.6				
MOZ-PV 988													6.3	3.9	3.6	1.9
MOZ-PV 963															3.3	1.8

Abbreviations: AW, anterior prism maximum preserved width; L, total preserved length; m, lower molar; M, upper molar; p, lower premolar; PW, posterior prism maximum preserved width; 3W, third prism of M3 maximum preserved width.

M3 (Loc. BN1); MOZ-PV 984, right mandibular fragment with p4–m2 (Loc. BN2); MOZ-PV 986, right m1 or m2 (Loc. BN2); MOZ-PV 987, left m1 or m2 (Loc. BN2); MOZ-PV 988, isolated right M3 (Loc. BN2); MOZ-PV 989, left M3 (Loc. BN2); MOZ-PV 1046, left m1 or m2 (Loc. BN1); MOZ-PV 1047, right m3? (juvenile) (Loc. BN1).

Etymology. In acknowledgement of the Museum “Dr. Prof. Juan A. Olsacher” of Zapala, Neuquén, whose staff collaborated kindly with our project during field trips to Cenozoic localities in Neuquén Province.

Diagnosis. As for the genus.

Description and comparisons. All cheek teeth (Fig. 3.1–4) are hypselodont (high crowned and rootless), biprismatic (triprismatic on M3), with a thin isthmus (labial in the uppers, lingual in the lowers) connecting the prisms. Cement fills the lingual (and narrowest) portion of the interprismatic spaces (hypoflexid), and partially covers the labial portion of their internal walls. A thin layer of cement also irregularly covers the external walls of the crowns.

The prisms of the lower molars (Fig. 3.1–2) have convex anterior and posterior walls, sharp labial apices and rounded lingual sides. Thus, the occlusal outline is strongly spear-like or lanceolate, with the main transverse diameter somewhat oblique anterolabial–posterolingually. The posterior prism extends further lingually than the anterior one, and thus the lingual wall of each tooth is inflected in front of the lingual aspect of the posterior prism. This inflection is more pronounced on m1 than on m3. Enamel surrounds the crown, except for: a) a thin vertical band on the lingual tip of the posterior prisms, and b) the central part of the anterior wall of the anterior prisms, where the crown contacts the preceding tooth. Interestingly, there is a vestige of enamel covering on the labialmost part of the anterior wall, absent in all species of *Perimys* and in *Scotamys antiquus* Loomis, 1914. A probable m3, MOZ-PV 1047 (Fig. 3.2), preserves a small, rounded enamel lake on the lingual portion of the posterior prism, posterior to the hypoflexus, very likely corresponding to the metafossettid. Unlike in the holotype and other specimens lacking enamel lakes, the lingual inflection in this tooth is inconspicuous on the occlusal surface but much more pronounced when viewed from the base. Therefore, the lingual inflection is not homologous with the metaflexid, but rather is a secondary inflection of the lingual wall that becomes deeper with age,

as in species of *Perimys* (Kramarz, 2002, p. 173). The p4 (Fig. 3.1) is essentially as the molars, but the anterior prism is irregularly rhomboidal, much shorter transversely than the posterior prism. The labial portions of the internal walls of the hypoflexid are more divergent than in the molars. The enamel is absent in a thin vertical band on the anterior aspect of the anterior prism.

No upper premolar has been recovered. In the upper molars referred to this species (Fig. 3.3), the lingual apices are less sharp, and the internal walls of the hypoflexus are less divergent than in the lower ones. Thus, the lanceolate outline of the prisms is less pronounced, but more than in upper molars of species of *Perimys*. The enamel is much reduced or absent on the entire labial wall and on the posterior wall of the posterior prism, except on its lingualmost portion. The M3 tentatively referred to this species (Fig. 3.4) is typically triprismatic, as in all species of *Perimys*, but the two anterior prisms are vaguely lanceolate, less than in M1 and M2, but definitively more than in M3 of *Perimys*. The third prism is sub-circular in outline and transversely very short (nearly 50% of the transverse extension of the second prism). The isthmus connecting the second and third prisms is comparatively broader. Enamel is absent from the labial aspect of the two anterior prisms and the isthmus connecting them, as well as on the posterior wall of the third prism; therefore, the single enamel band on the labial wall of the tooth is comparatively broader than in all the species of *Perimys*.

The mandibular portion preserved in the holotype shows similar anatomy to that of *Perimys*: The diastema in front of the p4 is lower than the alveolar line, the mental foramen opens laterally, the notch for the tendon of the *masseter medialis pars infraorbitalis* is below m1 and continuous with the masseteric crest, the alveolus for the incisor runs medial to the tooth row, and its bottom is below m1–m2.

Discussion

Perimys, with 21 described species, was among the most abundant and diverse caviomorph rodents during Colhuehuapian and Santacrucian times. According to Scott (1905, p. 433), *Perimys* “...includes a surprising number of species, which, in size, range from very small animals to the largest rodents yet found in the [Santa Cruz] formation.” Taxonomic identification of these species is extremely difficult because

the characters supporting the nominal species (mostly dental characters) are usually inconsistently distributed within a given sample. Recent revisions concluded that such characters represent different ontogenetic stages and/or mere individual variation within very few taxa (Kramarz, 2002; Vucetich *et al.*, 2010). *Doryperimys olsacheri* shares with species of *Perimys* the well defined lingual flexids on the lower molars, a distinct third lobe on M3, and a short lower incisor. However, *D. olsacheri* is clearly distinct from all species of *Perimys* by having less reduced enamel (*e.g.*, on the labial tip of the anterior wall of the anterior prism) and, particularly, by the lanceolate cross section of the prisms. In fact, the general appearance of the cheek teeth series of the holotype superficially resembles that of some basal cavioids (*i.e.*, “eocardiids”). Nevertheless, in “eocardiids” the prisms are mainly transverse instead of oblique, and the enamel is not reduced on the anterior wall of the lower molars (nor the posterior wall of the upper ones). Other distinct features are suggestively shared with the Deseadan (late Oligocene) *S. antiquus*: hypoflexid narrower lingually than labially, posterior prism of lower molars transversely wider than the anterior prism, third lobe of M3 much narrower than the anterior prisms, and cement filling only the internal part of the interprismatic spaces. Owing to this particular combination of characters, we prefer herein to erect a new genus to include this new species instead of assigning it to *Perimys* (or *Scotamys*), although assessment of the systematic meaning of all these characters is pending further cladistic analysis.

CAVIOMORPHA incertae sedis

Genus *Leucokephalos* Vucetich, Dozo, Arnal, and Pérez, 2014

Type species. *Leucokephalos zeffiae* Vucetich, Dozo, Arnal, and Pérez, 2014.

Chronological and geographic distribution. Late Oligocene–early Miocene. Chubut and Neuquén provinces, Argentina.

Leucokephalos maior sp. nov.

Figure 4, Table 4

Holotype. MOZ-PV 969, partial left mandible with i, p4–m2 (Loc BN1).

Etymology. From Latin *maior*= greater, in reference to its size larger than the type species.

Diagnosis. Nearly 35% larger than the type species. Metalophulid II of p4 more curved, labial apex of hypoconid on p4–m3 sharper.

Description and comparisons. The cheek teeth are rooted. The preserved portions of the crowns are longer than high (Fig. 4.2), suggesting that the teeth were moderately worn and relatively low-crowned with very ephemeral fossettids, rather than very worn and high-crowned with relatively persistent fossettids. The occlusal surfaces are almost flat (not terraced), although on the p4 the occlusal plane of the trigonid is somewhat higher than the talonid (Fig. 4.2), very likely due to differential wear. The enamel covering is uniform around the crowns.

The p4 (Fig. 4.1) is longer than wide, proportionally longer than in the type species. On the trigonid, a small, ovoid anterofossetid separates the transverse metalophulid I from the metalophulid II, which curves forward to

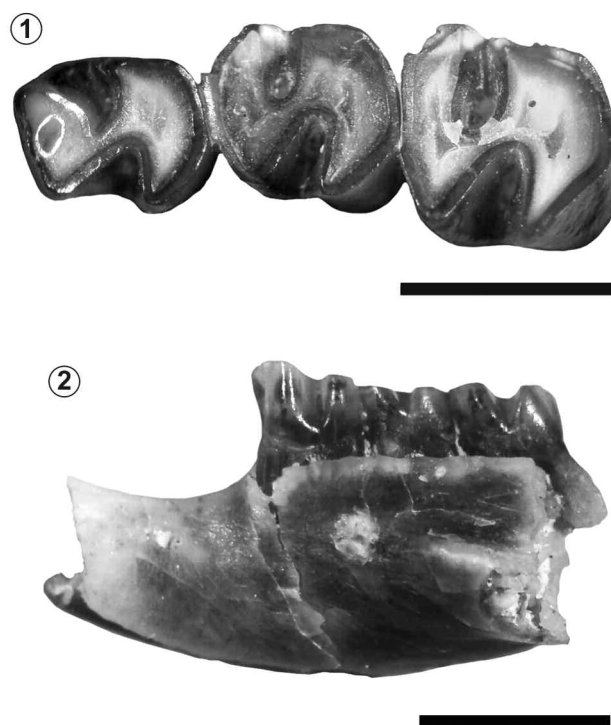


Figure 4. *Leucokephalos maior* sp. nov., MOZ-PV 969, holotype. 1, left p4–m2 in occlusal view; 2, left mandible in lateral view. Scale bar= 3 mm in 1, 5 mm in 2.

TABLE 4. Compared dental measurements (in mm) of *Leucokephalos* spp.

		p4			m1			m2		
		L	AW	PW	L	AW	PW	L	AW	PW
<i>Leucokephalos maior</i> sp. nov.	MPEF-PV 583	2.55	1.70	2.1	2.55	2.28	2.42	2.95	2.88	2.62
<i>Leucokephalos zeffiae</i> Vucetich et al. 2014	MOZ-PV 969 (Holotype)	1.81	1.55	1.70	1.88	1.66	1.70	2.03	2.15	2.07

Abbreviations: AW, anterior preserved width; L, total preserved length; m, lower molar; p, lower premolar; PW, posterior preserved width.

contact the metaconid. In the holotype of *L. zeffiae* and some referred specimens (Vucetich *et al.*, 2014: figs. 5F–H), the metalophulid II is indistinct, but according to the geometry of the lingual flexid, this lophid seems to be straighter than in *L. maior*, whereas in the less worn specimen referred to *L. zeffiae* by Vucetich *et al.* (2014) (MPEF PV 585, Vucetich *et al.*, 2014: fig. 5E), the metalophulid II points to the entoconid and does not contact the metaconid. The talonid is a simple lobe, wider than the trigonid, with a straight lingual wall and a sharp labial apex. There is a small anterior projection of the lingual wall of the talonid, suggesting the presence of a moderate anterior arm of the entoconid. This structure is not discernible in the holotype of *L. zeffiae*, but is visible in the referred specimen, MPEF PV 586 (see Vucetich *et al.*, 2014: fig. 5F). The ectolophid is thin and oblique, connecting the protoconid with the central portion of the talonid. The lingual flexid (mesoflexid?) and the hypoflexid are subtriangular and penetrate almost up to the midpoint of the transverse diameter of the crown.

The m1 (Fig. 4.1) is sub-rounded in occlusal view due to the markedly convex anterior and posterior walls. The only features preserved on the occlusal surface are a very penetrating hypoflexid (also reaching the middle of the transverse diameter) and a transverse lingual flexid on the anterior half of the crown (anterior to the hypoflexid). The resulting occlusal design is vaguely octodontiform, as in the m1 of MPEF PV 584, referred to *L. zeffiae* by Vucetich *et al.* (2014: fig. 5G).

The m2 (Fig. 4.1) is larger and proportionally wider than m1, the anterior wall of the crown is less convex, and the lingual flexid is proportionally larger. This tooth is remarkably

similar to the m2 of the holotype of *L. zeffiae*. It differs only by having a sharper labial tip of the hypoconid, a little more penetrating hypoflexid, and more constrained lingual exit of the lingual valley.

Additionally, there are some differences between *L. zeffiae* and *L. maior* in the timing of closure and erasure of the lingual valleys. In the holotype of *L. maior*, the antero-fossettid of p4 is still present, whereas in the holotype of *L. zeffiae* and in referred specimens with comparatively less worn m1 and m2, this structure is already worn away (see Vucetich *et al.*, 2014: fig. 5E–H). These differences could be the result of the differential wear on the p4 trigonid of MOZ-PV 969 mentioned above.

The lower incisor is broken posteriorly at the level of the m2, but owing to its implantation it seems to have been long, with its posterior end reaching at least a point behind m3, as in *L. zeffiae*. Anteriorly, the tooth is broken at the level of the anterior portion of the diastema; at this point the cross section is nearly as wide (1.45 mm) as long, the distal face is convex, and the mesial one is straight.

As in the type species, the mandibular diastema is long and gently curved, the mental foramen is very large, rounded, close to the dorsal border of the diastema, and faces anteriorly, the notch for the tendon of the *masseter medialis pars infraorbitalis* is very poorly marked, and the masseteric crest rises at the level of anterior border of the m1 (Fig. 4.2). However, the mandibular ramus is proportionally more robust than in *L. zeffiae*; the masseteric crest is more salient and located higher in the mandible.

Discussion

Other Paleogene–early Neogene caviomorphs also display an 8-shaped occlusal configuration of the lower molars, at least temporarily. However, *Cephalomys* Ameghino, 1897, and *Litodontomys* Loomis, 1914, are much more hypsodont, the enamel is typically reduced on the anterior wall of the molars, and the structure of p4 is radically different. The acaremyids *Acaremys* Ameghino, 1887a and *Sciamys* Ameghino, 1887a are more hypsodont, whereas in *Galileomys* Vucetich and Kramarz, 2003, and *Platypitamyx* Wood, 1949, the crowns are terraced and neither of them acquires an 8-shaped design. In the late Miocene octodontid *Chasicomys* Pascual, 1967, the premolars are not replaced. The structure of the p4 trigonid of *L. maior* resembles that of the isolated tooth tentatively referred to *Banderomys* (Kramarz, 2005: fig. 5C), recorded in the same levels of the Cerro Bandera Formation, but this taxon has more hypsodont and larger teeth, and the molars do not acquire an 8-shaped pattern with wear. Consequently, and although some minor differences could be identified, MOZ-PV 969 is much closer to the holotype of *L. zeffiae* than to any other known taxon with 8-shaped molars, and therefore the generic assignment herein proposed is the most reasonable one with the current evidence.

CONCLUDING REMARKS

The three species here described, *Protypotherium sinclairi*, *Doryperimys olsacheri*, and *Leucokephalos maior*, broaden the knowledge on notoungulate and caviomorph rodent diversity and distribution in northern Patagonia during the early Miocene.

The type and several specimens referred to *D. olsacheri* and the type of *L. maior* come from the same level of the Cerro Bandera Formation exposed on the northeastern slope of Barda Negra (BN1). The type of *P. sinclairi* was unearthed from isolated exposures of the same unit on the northwestern slope of Sierra del Portezuelo Norte (SPN), almost 25 km from Barda Negra, and the exact correlation with BN1 is uncertain. However, at least one specimen referable to *P. sinclairi* is derived from BN1, supporting the co-occurrence of the three species.

Accepting the transference of the Colhuehuapian *Protypotherium minor* to the genus *Cochilius* here proposed, *P. sinclairi* is the only nominal species of *Protypotherium* posi-

tively recorded in pre-Santacrucian deposits. It differs from other species primarily by the lesser degree of reduction of the p3–p4 talonids. Reguero *et al.* (2003) and Reguero and Prevosti (2010) concluded that at least the reduction of the p3 talonid in *Protypotherium* and *Miocochilius* is the primitive condition among late-diverging interatheriids. However, such reduction is extreme in the late Miocene species and less pronounced in the Santacrucian species, suggesting that the condition observed in *P. sinclairi* is plesiomorphic compared with the remaining species of the genus. Thus, a revised analysis of interathere phylogeny at species level is required for a better understanding of the evolutionary meaning of this character.

Leucokephalos maior, only known by the holotype, is a small caviomorph with rooted cheek teeth with a vaguely 8-shaped occlusal design resembling that of some cephalomyids (Chinchilloidea?) and some extinct octodontoids. Its relationships with the main caviomorph clades are still uncertain, but whatever its proper systematic position, it is unambiguously close to the Cabeza Blanca species *L. zeffiae*, differing only by its larger size (see Tab. 4), some mandibular features, and minor dental details.

The chinchilloid *Doryperimys* displays a singular combination of dental characters, some shared with the species of *Perimys* and others with *Scotamys antiquus*. This taxon is unknown in other Miocene or Oligocene mammal associations, even much better sampled assemblages from southern and central Patagonia, and in those latitudinally closer and presumably coeval associations in northern Patagonia and Chile (*i.e.*, Chichinales and Laguna del Laja, see Barrio *et al.*, 1989; Kramarz *et al.*, 2004; Flynn *et al.*, 2008). The exclusive occurrence of *Doryperimys*, as well as other supposedly endemic rodents in deposits of the Cerro Bandera Formation (*i.e.*, *Garridomys* Kramarz *et al.*, 2012 and *Banderomys* Kramarz, 2005) reveals the distinctive character of this rodent assemblage.

The mammal-bearing deposits of the Cerro Bandera Formation were originally assigned to the early Miocene Colhuehuapian SALMA (Leanza and Hugo, 1997; Kramarz *et al.*, 2005). The record in these levels of additional taxa described from older mammal assemblages has cast doubts on this biochronological assessment (see Kramarz *et al.*, 2011 for a preliminary discussion). Furthermore, the known distribution of the taxa herein described provide ambiguous

biochronological interpretations: *Protypotherium* species are only known for Colhuehuapian and younger associations, whereas *Leukocephalos* was previously known for the Deseadan Cabeza Blanca fauna. Efforts to obtain absolute dates from the Cerro Bandera Formation have been unfruitful to date because all sampled horizons are extremely pedogenized and/or bear altered glass and plagioclase (Heizler, pers. comm.). A complete discussion of the chronological meaning and paleobiogeographic implications of this mammal assemblage is pending an integrative paleontological and stratigraphic study still in progress, which includes the findings reported here and numerous new fossil-mammal materials from the Cerro Bandera Formation and other Miocene deposits in northern Patagonia.

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