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Re-assessment of the Oligocene genera *Prosotherium* and *Propachyrucos* (Hegetotheriidae, Notoungulata)

Réévaluation des genres oligocènes Prosotherium *et* Propachyrucos *(Hegetotheriidae, Notoungulata)*

Federico Damián Seoane [a,*], Esperanza Cerdeño [b], Hayley Singleton [c]

[a] *Universidad de Buenos Aires, CONICET, Instituto de Estudios Andinos Don Pablo Groeber (IDEAN), Departamento de Geología, Facultad de Ciencias Exactas y Naturales, Ricardo Güiraldes 2160, C1428EGA Buenos Aires, Argentina*
[b] *Paleontología, Instituto de Nivología, Glaciología y Ciencias Ambientales; Centro Científico Tecnológico-CONICET-Mendoza, Avda. Ruiz Leal s/n, 5500 Mendoza, Argentina*
[c] *Amherst College, Beneski Museum of Natural History, 220 South Pleasant Street, 01002 Amherst, MA, USA*

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ABSTRACT

Several systematic revisions of the Hegetotheriidae have been published in the last twenty years, but some important taxonomic work remains limited to unpublished studies. In one such thesis, the late Oligocene genera *Prosotherium* and *Propachyrucos* were revised, so that *Prosotherium garzoni* and *Propachyrucos smithwoodwardi* were considered the only valid species for each genus. Later authors loosely accepted these informal revisions, but recent phylogenetic coding has yet to accurately reflect these revisions, with character states often at odds with the known material for these genera. This study re-examines most of the fossil material assigned to *Propachyrucos* and *Prosotherium*, including both published and unpublished fossils, and contributes to a better understanding of the systematics, taxonomic diversity and early morphological evolution of the pachyrukhines. We conclude that *Prosotherium garzoni* and *Propachyrucos smithwoodwardi* are indeed the only valid species for each genus, confirming the influential but unpublished revisions that have become widely accepted. The known material for these species is clarified to aid future phylogenetic studies. At the same time, *Propachyrucos aequilatus* and *Pr. robustus* are herein considered *nomina dubia*. Additionally, Miocene species originally ascribed to *Propachyrucos*, along with unpublished material loosely assigned to the same genus, are here synonymized with other genera. Finally, several fossils previously recognized as *Prosotherium* sp. are here recognized as *P. garzoni*.

Mots-clés :
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Typotheria
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RÉSUMÉ

Au cours des vingt dernières années, des révisions systématiques de plusieurs genres d'Hegetotheriidae ont été publiées, mais quelques autres sont restées inédites. C'est le cas d'une thèse de doctorat où les genres *Prosotherium* et *Propachyrucos* de l'Oligocène supérieur ont été étudiés et plusieurs synonymies ont été proposées. Néanmoins, des auteurs ultérieurs ont accepté ces synonymies informelles, ce qui a conduit à considérer *Propachyrucos smithwoodwardi* et *Prosotherium garzoni* comme les seules espèces

* Corresponding author.
E-mail addresses: fseoane@gl.fcen.uba.ar (F.D. Seoane), espe@mendoza-conicet.gob.ar (E. Cerdeño), hsingleton@amherst.edu (H. Singleton).

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valables pour les genres respectifs. Les analyses phylogénétiques d'Hegetotheriidae ont codifié certains caractères pour ces taxons, mais ils ne correspondaient pas au matériel fossile connu pour chaque espèce. Nous avons réétudié la plupart des matériaux attribués à *Propachyrucos* et *Prosotherium*, y compris des restes inédits. Nos résultats indiquent que *Prosotherium garzoni* et *Propachyrucos smithwoodwardi* sont vraiment les seules espèces valables pour chaque genre. En même temps, *Propachyrucos aequilatus* and *Pr. robustus* sont ici considérés comme *nomina dubia*. En outre, les espèces du Miocène précédemment attribuées à *Propachyrucos*, ainsi que le matériel non publié intitulé *Propachyrucos* sp., ont été synonymisés avec d'autres genres. Enfin, le matériel identifié comme *Prosotherium* sp. a été reconnu comme *P. garzoni*.

1. Introduction

South American native ungulates were widespread throughout the Cenozoic. Among them, the order Notoungulata was the most abundant and diversified (Carrillo and Asher, 2017; Cifelli, 1993; Giannini and García López, 2014; Gomes Rodrigues et al., 2018; Sosa and García López, 2018). Within this order, the family Hegetotheriidae is one of the most derived clades, characterised by hypertrophied, euhypsodont, and procumbent first incisors, lower molariforms with a deep labial groove, P2–M3 imbricated, and loss of ectoloph plications on upper molars (Cerdeño and Reguero, 2015; Cifelli, 1993; Kramarz and Paz, 2013; Seoane and Cerdeño, 2019). Hegetotheriidae currently comprises 11 genera distributed in two subfamilies: Hegetotheriinae, which most recent phylogenetic analyses have recognized as paraphyletic (with the exception of Billet, 2011 and Seoane et al., 2017), and Pachyrukhinae, a well-established monophyletic group (Cerdeño and Reguero, 2015; Croft and Anaya, 2006; Kramarz and Bond, 2017; Reguero and Prevosti, 2010; Billet, 2011; Seoane and Cerdeño, 2019).

In 1897, Ameghino differentiated the genus *Propachyrucos* from other hegetotheriids based on the presence of the complete lower dental series, with i1–3 developed and not as different in size as in other species, along with the canine developed. In the same work, the author defined the genus *Prosotherium*, recognized by the presence of large upper and lower diastemata between the external incisor (I1/i2) and the premolar (P1/p2), along with the presence of a mesiolabial (parastylar) groove in upper premolars and a deep lingual groove in upper molars. Ameghino (1897) originally identified two species of *Propachyrucos* differentiated only by size: the smaller *Pr. smithwoodwardi* and the larger *Pr. crassus*. In turn, the author defined three species of *Prosotherium*, differentiated by their size and upper molar morphology: *P. garzoni*, *P. triangulidens* and *P. robustum*. Later, Ameghino (1901) erected one more species for each genus: *Propachyrucos aequilatus*, intermediate in size between the other species and with different morphology of the trigonid, and *Prosotherium quartum*, representing the largest species of *Prosotherium* and with the p1 present (a tooth that was absent from the material then ascribed to *P. garzoni*).

Despite the fact that several species were later created, i.e. *Propachyrucos depressus* Roth, 1899, *Propachyrucos medianus* Roth, 1899, *Propachyrucos robustus* Roth, 1899, *Propachyrucos schiaffinoi* Kraglievich, 1932, *Propachyrucos ameghinorum* Simpson, 1945, and *Propachyrucos simpsoni* Chaffee, 1952, several studies reduced the diversity of the genera *Prosotherium* and *Propachyrucos* (Loomis, 1914; Reguero, 1999; Reguero and Cerdeño, 2005; see Table 1). However, the study that proposed more synonymies to consider only one species in each genus — *Prosotherium garzoni* and *Propachyrucos smithwoodwardi* — was an unpublished Ph.D. dissertation (Reguero, 1999), although posterior studies considered those results as valid (Cerdeño and Reguero, 2015; Kramarz and Bond, 2017; Reguero et al., 2007; Seoane et al., 2017). In turn, the three species of *Propachyrucos* defined by Roth (1899) were transferred to the genus *Pachyrukhos* by Pascual et al. (1978) without any systematic discussion (see Vera, 2019 and Section 3.2.1). *Propachyrucos schiaffinoi* was transferred to *Prohegetotherium* by Reguero and Cerdeño (2005) and validated by Cerdeño and Reguero (2015), and the same authors synonymized *Propachyrucos crassus* with *Prohegetotherium sculptum* (based on Reguero, 1999). *Propachyrucos aequilatus* was synonymized with *Propachyrucos smithwoodwardi* by Reguero (1999), whereas *Prosotherium quartum* and *Prosotherium robustum* were synonymized with *Prosotherium triangulidens* by Loomis (1914); Reguero (1999) defended this synonymy, and also synonymized *Prosotherium triangulidens*, *Propachyrucos ameghinorum* and *Propachyrucos simpsoni* with *Prosotherium garzoni*.

If the mentioned systematic proposals are considered, *Pr. smithwoodwardi* would be only known by few mandibular fragments, while *P. garzoni* would be known from an almost complete skeleton (Reguero, 1999; Simpson, 1945) and several cranial and mandibular fragments (Ameghino, 1897, 1901; Chaffee, 1952; Loomis, 1914). However, nearly all the phylogenetic analyses of the last 15 years have continued scoring *Pr. smithwoodwardi* for both cranial and postcranial characters (Cerdeño and Reguero, 2015; Croft and Anaya, 2006; Kramarz and Bond, 2017; Reguero and Cerdeño, 2005; Seoane et al., 2017). Most of the phylogenies previous to the Reguero's thesis (1999) used to code the genus *Propachyrucos* as a terminal unit (Cerdeño and Bond, 1998, Cifelli, 1993), encompassing the specimens referred as *Pr. smithwoodwardi*, *Pr. aequilatus*, *Pr. simpsoni* and *Pr. ameghinorum*, so they scored both cranial and

Table 1
Summary of the synonymies proposed by different authors. Hm., *Hemihegetotherium*; P., *Prosotherium*; Pa., *Pachyrukhos*; Ph., *Prohegetotherium*; Pr., *Propachyrucos*.
Tableau 1
Résumé des synonymes proposés par différents auteurs. Hm., *Hemihegetotherium* ; P., *Prosotherium* ; Pa., *Pachyrukhos* ; Ph., *Prohegetotherium* ; Pr., *Propachyrucos*.

Taxon	Loomis, 1914	Pascual et al., 1978; Kramarz et al., 2011	Reguero, 1999	Reguero and Cerdeño, 2005	Kramarz and Bond, 2017	Vera, 2019	This paper
P. robustum	*P. triangulidens*		*P. garzoni*				*P. garzoni*
P. quartum	*P. triangulidens*		*P. garzoni*				*P. garzoni*
P. triangulidens			*P. garzoni*				*P. garzoni*
Pr. depressus		*Pa. depressus*					*Pachyrukhos* sp.
Pr. medianus		*Pa. medianus*					*Pachyrukhos* sp.
Pr. robustus		*Pa. robustus*				*Hm.* cf. *tantillum*	*Nomen dubium*
Pr. ameghinorum			*P. garzoni*				*P. garzoni*
Pr. simpsoni			*P. garzoni*				*P. garzoni*
cf. *Pr. smithwoodwardi*							*P. garzoni*
Pr. aequilatus			*Pr. smithwoodwardi*				*Nomen dubium*
Pr. crassus			*Ph. sculptum*	*Ph. sculptum*	Genus indet., valid species		Genus indet., valid species
Pr? schiaffinoi			*Ph. schiaffinoi*	*Ph. schiaffinoi*			*Ph. schiaffinoi*
Pr. sp.: MLP 12-2889a							*Pa. moyani*
MLP 61-IV11-146							Interatheriidae cf. *Protypotherium*
MLP 59-II-26-91							*Pachyrukhos* sp.
MLP 61-IV-11-147–152							
MLP 61-IV-11-147–152							
MLP 61-IV-11-163–166							
MLP 61-IV-11-186–192							
MLP 61-IV-11-207							
MLP 61-IV-11-316–317							

postcranial characters. As most of the authors considered valid the results of the thesis, they scored only *Pr. smithwoodwardi* as a terminal unit, but dragged the previous scoring (Cerdeño and Reguero, 2015; Kramarz and Bond, 2017; Seoane et al., 2017). The recent phylogenetic study of hegetotheriids by Seoane and Cerdeño (2019) highlighted this incongruence and only the type materials of *Pr. smithwoodwardi* and *P. garzoni* were used in their analyses to codify these taxa. Now, the present contribution provides a detailed revision of most remains previously assigned to *Propachyrucos* and *Prosotherium* in order to discuss the proposed synonymies, confidently establish the differences between these taxa and their specific diversity, and aid future taxonomic and phylogenetic analyses of the Hegetotheriidae. In addition, we provide an evaluation of the geographic dispersion of each genus.

2. Materials and methods

The studied materials consist of craniodental elements identified as belonging to *Propachyrucos* and *Prosotherium* within the paleontological collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN, Buenos Aires, Argentina), Museo de La Plata (MLP, La Plata, Argentina), Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano' (MCNAM, Mendoza, Argentina), Museo Paleontológico "Egidio Feruglio" (MPEF, Trelew, Argentina), American Museum of Natural History (AMNH, New York, USA) and Beneski Museum of Natural History at Amherst (ACM, Massachusetts, USA), including unpublished specimens housed in the MLP and MPEF. The type specimens of each species and most of the referred materials, as well as other species used for comparison, were revised and are detailed in Suppl. App. 1.1. Unfortunately, we could not examine the holotype of *Propachyrucos ameghinorum* stored in the AMNH, and its comparison is only based on published descriptions. Catalogue numbers for MACN specimens are those corresponding to the present inventory, except for some materials previously published (Cerdeño and Reguero, 2015; Kramarz and Bond, 2017; Reguero and Cerdeño, 2005) with numbers provided by Patterson (1952) in an unpublished catalogue. In such a case and following the MACN curator's suggestions, we use the old informal numbers (e.g., MACN A 52-451).

To avoid confusions through the text, abbreviations of generic names are *P.* for *Prosotherium* and *Pr.* for *Propachyrucos*.

Taxonomic results are based on morphological and morphometric comparisons of the revised specimens. The dimensions were taken with a Vernier caliper with 0.01 mm of error. Terminology and measurements follow Kramarz and Paz (2013), Cerdeño and Reguero (2015), Cerdeño et al. (2017) and Seoane and Cerdeño (2019). We provide statistical analyses of the studied samples, using PAST3 software (Hammer et al., 2001). Even though the samples are small, we have performed some statistical analyses in order to check to what extent they support the taxonomic interpretations for each genus. In all cases, we performed a one-way ANOVA for the pool sample of one tooth (one ANOVA for the p2, one ANOVA for the p3, etc.; see Suppl. App. 1.2) and all the assumptions were met (Levene's test and Shapiro-Wilk's test). We used as independent variable (or factor) the different species and as dependent (or explicative) variable the size of the teeth. The p value was set to 0.05.

3. Systematic palaeontology

Order **Notoungulata** Roth, 1903
Suborder **Typotheria** Zittel, 1893
Family **Hegetotheriidae** Ameghino, 1894
Subfamily **Pachyrukhinae** Kraglievich, 1934
(Diagnosis in Cerdeño and Bond, 1998)

3.1. Genus ***Prosotherium*** *Ameghino, 1897*

1897 *Prosotherium* Ameghino: 426 (original description).

1945 *Propachyrucos* (*partim, non* Ameghino): Simpson: 551.

1952 *Propachyrucos* (*partim, non* Ameghino): Chaffee: 524

2015 *Propachyrucos* (*partim, non* Ameghino): Cerdeño and Reguero: fig. 8A–H.

Type species. *Prosotherium garzoni* Ameghino, 1897.

Included species. The type only.

Emended diagnosis (amended after Reguero, 1999). Around 20–30% larger than *Propachyrucos*, *Pachyrukhos* Ameghino, 1897, *Paedotherium* Burmeister, 1888, and *Tremacyllus* Ameghino, 1891. Slightly smaller than *Medistylus* Stirton, 1952. Adult without I2–C/i3–p1, generating great diastemata (I1–P1 and i2–p2), as deciduous teeth (DI2–DC/di3–dp1) are not replaced. Short and robust process of the maxilla anteriorly directed, lateral to the infraorbital foramen, which is sharp and long in *Pachyrukhos*, *Paedotherium*, and *Tremacyllus*, very reduced in *Medistylus* and absent in Hegetotheriinae. Upper premolars with paracone fold and parastylar groove developed but variable. Upper molars with a deep lingual groove like *Medistylus* but differing from this genus by the absence of mesostyle. Horizontal ramus of the mandible higher than in *Propachyrucos*, *Pachyrukhos*, *Tremacyllus* and *Paedotherium*, but similar to *Hegetotherium*, *Hemihegetotherium torresi* and *Hemihegetotherium tantillum*, and lower than in *Hemihegetotherium achataleptum* and *Hemihegetotherium trilobus*; anterior labial foramen below the canine, and posterior labial mental foramen below the p3 or p4, preceded by a long groove that could present multiple small foramina and reaches the level of the p2 or p1. Proportion i2/i1 around to 2/3 and i2 less developed than in *Propachyrucos*, but similar to all other species of Hegetotheriidae. Lower p2 with rounded trigonid, larger than talonid; p3–4 with more angular trigonids, and trigonid usually larger than talonid.

Occurrence. Sarmiento Formation, Chubut Province, and Agua de la Piedra Formation, Mendoza Province, Argentina. Late Oligocene, Deseadan SALMA.

Remarks. Ameghino (1897) characterized *Prosotherium* by the presence of upper and lower diastemata (between

I1–P1 and between i2–p2); absence of i3–c–p1; triangular upper premolars and bilobed molars with a deep lingual groove in the middle of the lingual face. He described three species: *P. garzoni* (Fig. 1A–F), *P. robustum* (Fig. 1G–H), and *P. triangulidens* (Fig. 1I–J). In 1901, the author defined a fourth species, *P. quartum* (Fig. 1K–N), from a single mandibular fragment, which had four lower premolars (p1–4).

Loomis (1914) studied the fauna from Cabeza Blanca (near Chico River, Chubut Province; Sarmiento Formation) and reported several specimens of *Prosotherium*, currently stored in the ACM (Suppl. App. 1.1). Years later, Chaffee (1952) studied the fauna from Scarritt Pocket (Chubut Province) and described a single specimen of *Prosotherium*, stored in the AMNH (Suppl. App. 1.1). Both Loomis (1914) and Chaffee (1952) as well as Simpson (1945) proposed that *Prosotherium* and *Propachyrucos* could be synonymous, as the difference between them might be considered interspecific variation, but continued describing them as separate genera. Later, Reguero (1999) concluded that both genera are valid, but he established several synonymies of species within each genus and of some species of *Propachyrucos* with those of *Prosotherium* (see below). However, because of the fact that Reguero's (1999) work is an unpublished thesis, the nomenclatural acts erected there are not available (ICZN, 1999, art. 8 and 11) and are further discussed here.

3.1.1. ***Prosotherium garzoni*** *Ameghino, 1897*

(Figs. 1–2)

1897 *Prosotherium garzoni* Ameghino: 426 (original description), Fig. 12.

1897 *Prosotherium triangulidens* Ameghino: 427 (original description); regarded as synonymy herein.

1897 *Prosotherium robustum* Ameghino: 427 (original description); regarded as synonymy herein.

1901 *Prosotherium quartum* Ameghino: 371 (original description); regarded as synonymy herein.

1945 *Propachyrucos ameghinorum* Simpson: 551 (original description), fig. 1 and plate 1; regarded as synonymy herein.

1952 *Propachyrucos simpsoni* Chaffee: 524 (original description), plate 17, figs. 1–2; regarded as synonymy herein.

2015 *Propachyrucos* cf. *Pr. smithwoodwardi* Cerdeño and Reguero: fig. 8A–H; regarded as synonymy herein.

Lectotype. MACN A 52-455, fragment of skull with right and left I1, right P1–2, and left P1–3, M1–3 (Fig. 1A–B). This specimen was informally proposed as lectotype by Patterson (1952) and Reguero (1999).

Paralectotype. MACN A 52-456, left mandibular fragment with p2–4 and m2–3 (Fig. 1C–F).

Diagnosis. As for the genus.

Occurrence. Sarmiento Formation, Chubut Province; Agua de la Piedra Formation, Mendoza Province. Late Oligocene, Deseadan SALMA, Argentina.

Referred material in this study. From Agua de la Piedra Formation, Mendoza Province: 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; MCNAM-PV 4190, right mandibular fragment with p3–m2; MCNAM-PV 4711, right mandibular fragment with p2–4; MLP 79-XII-18-38, left maxillary fragment with P1–2; MLP 93-XI-21-54 g, right M1 or M2. From Sarmiento Formation, Chubut Province: AMNH 29574 (holotype of *Pr. ameghinorum*), nearly complete skeleton; AMNH 29604 (holotype of *Pr. simpsoni*), mandibular fragment with complete left and right i1–m3, including alveoli of di3–dc–dp1; MACN A 52-462 (lectotype of *P. quartum*, see comments below about it), left mandibular fragment with alveoli of i1–2, di3–dc–dp1, and p2–3 (p2 partially preserved inside the alveolus); MACN A 52-464 (holotype of *P. triangulidens*), fragment of palate with left P1–M3; MACN A 52-465 (holotype of *P. robustum*), fragment of palate with right P1–M3; MPEF 5753, mandibular fragment with symphysis and alveoli of both i1–2 and dp1, right p2–m3 and left p2; MPEF 5754, left mandibular fragment with p2–4; MPEF 5755, right mandibular fragment with p2–p4; MPEF 5761, set including probably right P4, two right M1 or M2, three right p3 or p4, and three right m1 or m2.

Remarks. Ameghino (1897) described *Prosotherium garzoni* based on a fragment of skull and a left mandibular ramus (MACN A 52-455–456; Fig. 1A–F). The author illustrated the palate as having both complete dental series (Ameghino, 1897, fig. 12), but currently this specimen has only the right P1–2, isolated in a separate fragment, and the left P4 is missing. Ameghino (1897) differentiated this species for the presence of a mesiolabial (parastylar) groove in the upper premolars and of a deep lingual groove in the upper molars, along with large upper and lower diastemata. In the same work, Ameghino (1897) described two other species, *P. robustum* (Fig. 1G–H) and *P. triangulidens* (Fig. 1I–J) based only on upper teeth. The author differentiated *P. robustum* for the larger size, the rectangular morphology of the P1, with a groove in the lingual face, and by the absence of the mesiolabial groove in the premolars; in turn, he differentiated *P. triangulidens* by the triangular morphology of the premolars with an almost transversally implantation, and the absence of the mesiolabial groove in the premolars. Later, Ameghino (1901) based *P. quartum* on a mandibular fragment without preserved teeth (Fig. 1K–N), characterised by bearing p1 (alveolus), and upper teeth with labial groove. As the latter are now lost, we here designate the mandibular fragment as a lectotype. This mandibular fragment is catalogued as MACN A 52-462, but it was erroneously labelled as MACN A 52-467, which corresponds to M1 or M2 referred to *P. triangulidens*. Loomis (1914) considered the difference in size between *P. triangulidens* and *P. robustum* as insufficient grounds for being recognized as different species, and so he synonymized the two. With regard to *P. quartum*, Loomis stated that the presence of the p1 was not a distinctive characteristic, because it is present in *P. garzoni* as well; he

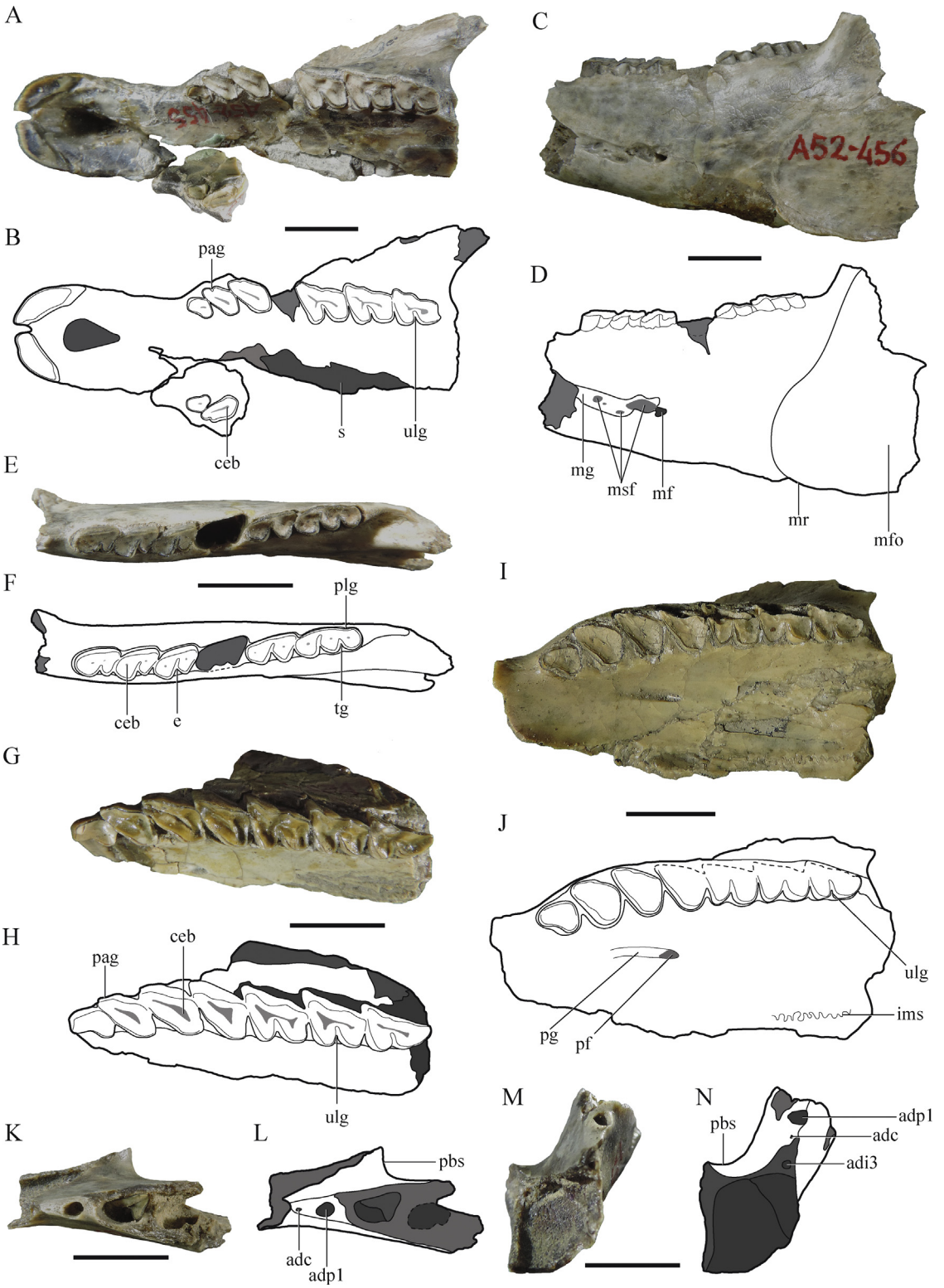


Fig. 1. *Prosotherium garzoni*. A, B, original and schematic drawing of MACN A 52-455 (lectotype of *P. garzoni*) in ventral view, cranial fragment with left I1, P1–3, M1–3 and right I1, P1–2; C, D, E, F, original and schematic drawing of MACN A 52-456 (paralectotype of *P. garzoni*), left mandibular fragment with p2–m3 (except m1) in lateral (C, D) and occlusal (E, F) views; G, H, original and schematic drawing of MACN A 52-465 (holotype of *P. robustum*) in ventral view, cranial fragment with right (seen as left) P1–M3; I, J, original and schematic drawing of MACN A 52-464 (holotype of *P. triangulidens*) in ventral view, palatal fragment with left P1–M3; K, L, M, N, original and schematic drawing of MACN A 52-462 (lectotype of *P. quartum*), left mandibular fragment with alveoli of i1–2, di3, dc, dp1, p2–3, in occlusal (K, L) and anterodorsal (M, N) views. Abbreviations: adc: alveolus of deciduous canine; adi3;

synonymized *P. quartum* with *P. triangulidens* because of their similar size (Table 1).

When Simpson (1945) described *Propachyrucos ameghinorum* AMNH 29574, a nearly complete skeleton from Scarritt Pocket (Chubut Province), he based his conclusions only on the presence of a complete dental series, but indicated that the skull was almost equal to that of *Prosotherium* (Simpson, 1945, p. 553). Strikingly, Simpson did not compare this specimen with the type of *P. garzoni* or with the data published by Loomis (1914). From the same locality, Chaffee (1952, Plate 17, fig. 3) later assigned the specimen AMNH 29608 (maxillary and mandibular fragments; see Suppl. App. 1.1 on interpretation of lower teeth) to *P. garzoni*, after having compared it with the specimen AMNH 14154 of this species (Loomis, 1914). At the same time, Chaffee (1952) described *Propachyrucos simpsoni* based on an almost complete lower jaw with both left and right i1–m3.

In his influential but unpublished study of Oligocene typotheres, Reguero (1999) recognized the validity of both *Prosotherium* and *Propachyrucos*. He synonymized *Prosotherium triangulidens*, *P. robustum*, and *P. quartum* with *P. garzoni*, arguing that their differences in size were insufficient for establishing different species. Reguero (1999) also synonymized *Propachyrucos simpsoni* and *Pr. ameghinorum* with *Prosotherium garzoni*. He stated that, aside from a small difference in size, the dental morphology of *Pr. ameghinorum* (AMNH 29574; see Section 3.2) is very similar to that of *P. garzoni*. In addition, he considered *Pr. simpsoni* (AMNH 29604; see Section 3.2) as synonymous with *P. garzoni* based on the presence of poorly developed canine and p1 (herein interpreted as dc and dp1), the similar size, the lingual face of the m2–3 straighter than in *Propachyrucos smithwoodwardi*, and the trigonid of p3–4 larger than the talonid.

Over the last twenty years, several studies have accepted Reguero's (1999) interpretation, so that *Pr. ameghinorum*, *Pr. simpsoni* and *P. triangulidens* have disappeared from the literature (e.g., Cerdeño and Reguero, 2015; Kramarz and Bond, 2017; Reguero and Cerdeño, 2005; Seoane et al., 2017). Recently, Cerdeño and Reguero (2015) assigned several specimens from Quebrada Fiera (Mendoza Province) to *Propachyrucos* cf. *Pr. smithwoodwardi*. These authors only compared these new materials to *Pr. smithwoodwardi* and *P. garzoni*, implicitly accepting the synonymies proposed by Reguero (1999). However, as Reguero's (1999) nomenclatural acts remain unpublished and unofficial (see Section 3.1), only the synonymies of *P. robustum* and *P. quartum* with *P. triangulidens* proposed by Loomis (1914) are at present formally valid.

Discussion. After revising the type material, we have found some minor differences in the premolars of these specimens. In *Prosotherium garzoni*, the P2–3 (P4 is missing) have a well-developed parastylar groove and the lingual face of P1 is straight to slightly concave (Fig. 1A–B). The parastylar groove is also present in the type of *P. robustum* (Fig. 1G–H), but shallower, and the lingual face of the P1 is concave. In turn, the type of *P. triangulidens* (Fig. 1I–J) lacks the parastylar groove, and the lingual face of the P1 is concave. This variability is also seen among other specimens referred to *Prosotherium*: ACM 3731 (Fig. 2A–B) has the P1 with straight to slightly convex lingual face, and P2–4 lack the parastylar groove; MACN A 52-458 shows the P1 with concave lingual face and P2–3 without parastylar groove; MACN A 52-468 has lost the P1, but the parastylar groove is barely visible on the P2–3 (little worn, representing a young individual). The type specimens of *P. garzoni* and *P. robustum*, MACN A 52-455 and MACN A 52-465, respectively, are also relatively young individuals, as they preserve remnants of the central fossettes. This feature is not observable in the type of *P. triangulidens*, MACN A 52-464 (Fig. 1I–J), because teeth are broken at the alveolar level, where premolars appear to be shorter and wider; this condition is explained by the change of the crown shape that occurs with ontogeny, as it has been observed in other hegetotheriids (e.g., Sostillo et al., 2018; Vera and Ercoli, 2018), as well as in mesotheriids (Billet et al., 2008; Cerdeño and Schmidt, 2013; Gomes Rodrigues et al., 2017).

Ameghino (1901) differentiated *P. quartum* from *P. garzoni* by the fact that the former is larger and possesses p1. Both Loomis (1914) and Reguero (1999) recognized the presence of p1 in specimens of *P. garzoni*, which we here re-interpret as dp1. We suggest that the presence of this tooth (along with di3 and dc) varies with ontogeny. For example, the specimen MACN A 52-461, which represents an early ontogenetic stage, bears the right p2 without wear inside the alveolus and p3 is little worn and retains a small fossettid and a posterolingual groove. In addition, this specimen has three small alveoli between i2 and p2, which we herein interpret as for di3, dc, and dp1, respectively (Fig. 2C–D; Suppl. App. 1.2; see also Reguero, 1999). The condition in MACN A 52-461 (p3 more worn than

alveolus of deciduous i3; adp1: alveolus of deciduous p1; ceb: centred enamel band; e: ectoflexid; ims: intermaxillary suture; mf: mental foramen; mfo: masseteric fossa; mg: mandibular groove; mr: mandibular ridge; msf: multiple small foramina; pag: parastylar (mesiolabial) groove; pbs: posterior border of the symphysis; pf: palatine foramen; pg: palatine groove; plg: posterior lingual groove; s: sediment; tg: talonid groove; ulg: upper lingual groove. The scale bar equals 1 cm.

Fig. 1. *Prosotherium garzoni*. A, B, original et dessin schématique de MACN A 52-455 (lectotype de *P. garzoni*) en vue ventrale, fragment crânien avec I1, P1–3, M1–3 gauches et I1, P1–2 droits ; C, D, E, F, original et dessin schématique de MACN A 52-456 (paralectotype de *P. garzoni*), fragment mandibulaire gauche avec p2–m3 (sauf m1) en vues latérale (C, D) et occlusale (E, F) ; G, H, original et dessin schématique de MACN A 52-465 (holotype de P. *robustum*) en vue ventrale, fragment crânien avec P1–M3 droites (vue de gauche) ; I, J, original et dessin schématique de MACN A 52-464 (holotype de *P. triangulidens*) en vue ventrale, fragment palatin avec P1–M3 gauches ; K, L, M, N, original et dessin schématique de MACN A 52-462 (lectotype de *P. quartum*), fragment mandibulaire gauche avec les alvéoles de i1–2, di3, dc, dp1, p2–3, en vues occlusale (K, L) et antéro-dorsale (M, N). Abréviations : adc : alvéole de dc ; adi3 ; alvéole de di3 ; adp1 : alvéole de dp1 ; ceb : bande d'émail centrée ; e : ectoflexide ; ims : suture intermaxillaire ; mf : foramen mentonnier ; mfo : fossette massétérique ; mg : sillon mandibulaire ; mr : crête mandibulaire ; msf : petits foramina ; pag : sillon parastylaire (mésiolabial) ; pbs : bord postérieur de la symphyse ; pf : foramen palatin ; pg : sillon palatin ; plg : sillon lingual postérieur ; s : sédiment ; tg : sillon du talonide ; ulg : sillon lingual supérieur. La barre d'échelle est égale à 1 cm.

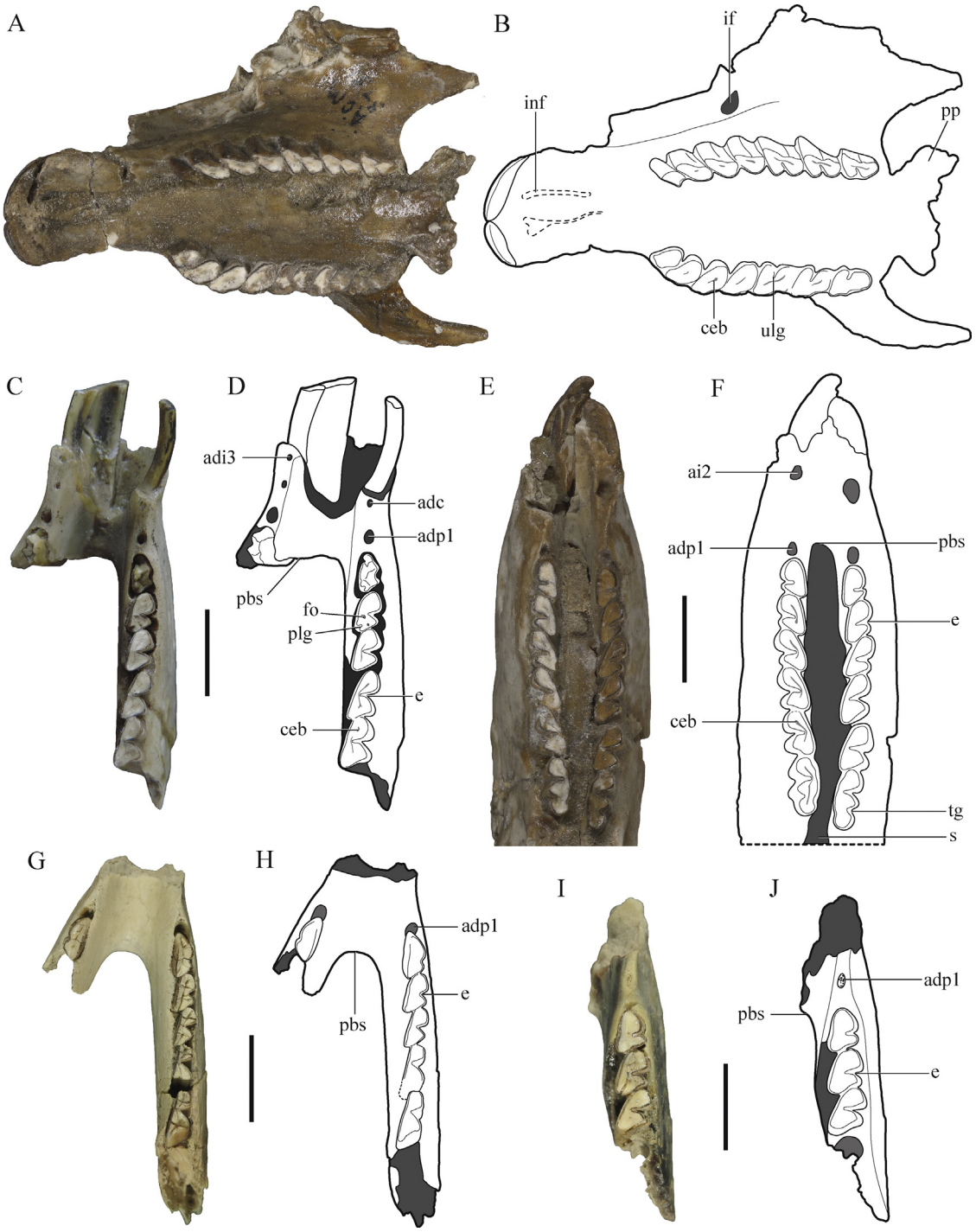


Fig. 2. Cranial and mandibular specimens of *Prosotherium garzoni* at different ontogenetic stages (see text). A, B, original and schematic drawing of ACM 3731 in ventral view, with both I1–M3 series; C, D, original and schematic drawing of MACN A 52-461 in occlusal view, with left i1–2, alveoli of deciduous i3–c–p1 and p2 without wear, and right alveolus of i1, i2, alveoli of deciduous c–p1, p2 erupting and p3–m2; E, F, original and schematic drawing of ACM 3731 in occlusal view, with both i1, alveoli of i2 and deciduous p1 and p2–m3; G, H, original and schematic drawing of MPEF 5753 in occlusal view, with both alveoli of deciduous p1, left p2 and right p2–m2; I, J, original and schematic drawing of MPEF 5755 in occlusal view, with right alveolus od deciduous p1 and p2–4. Abbreviations: adc: alveolus of deciduous canine; adi3; alveolus of deciduous i3; adp1: alveolus of deciduous p1; ai2: alveolus of i2; ceb: centred enamel band; e: ectoflexid; fo: fossettid; if: infraorbital foramen; inf: incisor foramina; pbs: posterior border of the symphysis; plg: posterior lingual groove; pp: palatine projection; s: sediment; tg: talonid groove; ulg: upper lingual groove. The scale bar equals 1 cm.

Fig. 2. Spécimens crâniens et mandibulaires de *Prosotherium garzoni* à différents stades ontogénétiques (voir texte). A, B, original et dessin schématique d'ACM 3731 en vue ventrale, avec les deux séries I1–M3 ; C, D, original et dessin schématique de MACN A 52-461 en vue occlusale, avec i1–2, alvéoles

p2) allows us to infer that the erupting sequence occurred posteriorly–anteriorly, as established for *Paedotherium* and contrary to *Tremacyllus* (Cerdeño et al., 2017; Sostillo et al., 2018), although Vera and Ercoli (2018) established the opposite for one specimen of *Tremacyllus*. The lectotype of *P. quartum* MACN A 52-462 represents a later ontogenetic stage, in which the alveoli of di3–dc–dp1 are closing (Fig. 1K–N), as these teeth would not have replacement; the p2 is broken in the alveolus and we cannot infer to what extent it was erupted. Other specimens such as ACM 3731 (Fig. 2E–F) and MPEF 5753 (Fig. 2G–H) represent the following ontogenetic stage, where there is no trace of the alveolus of the canine (although that region is not well preserved), and the p2 is in use. The next stage is represented by MACN A 52-459 and MPEF 5755 (Fig. 2I–J), in which the alveolus of dp1 is almost resorbed, as Gomes Rodrigues et al. (2017) showed for the mesotheriine *Typotheriopsis* (but see Cerdeño and Schmidt, 2013 about the interpretation of deciduous dentition — DP2/dp3 — in mesotheriines). The paralectotype MACN A 52-456, in which there is no trace of the dp1 alveolus, appears to represent the latest ontogenetic stage of the materials we examined (Fig. 1E–F). In terms of size, we do not find differences to justify the specific differentiation of *P. quartum*; the dimensions of the alveolus of p2 are similar to the measurements of this tooth in the pool sample of *P. garzoni* (Suppl. App. 1.3).

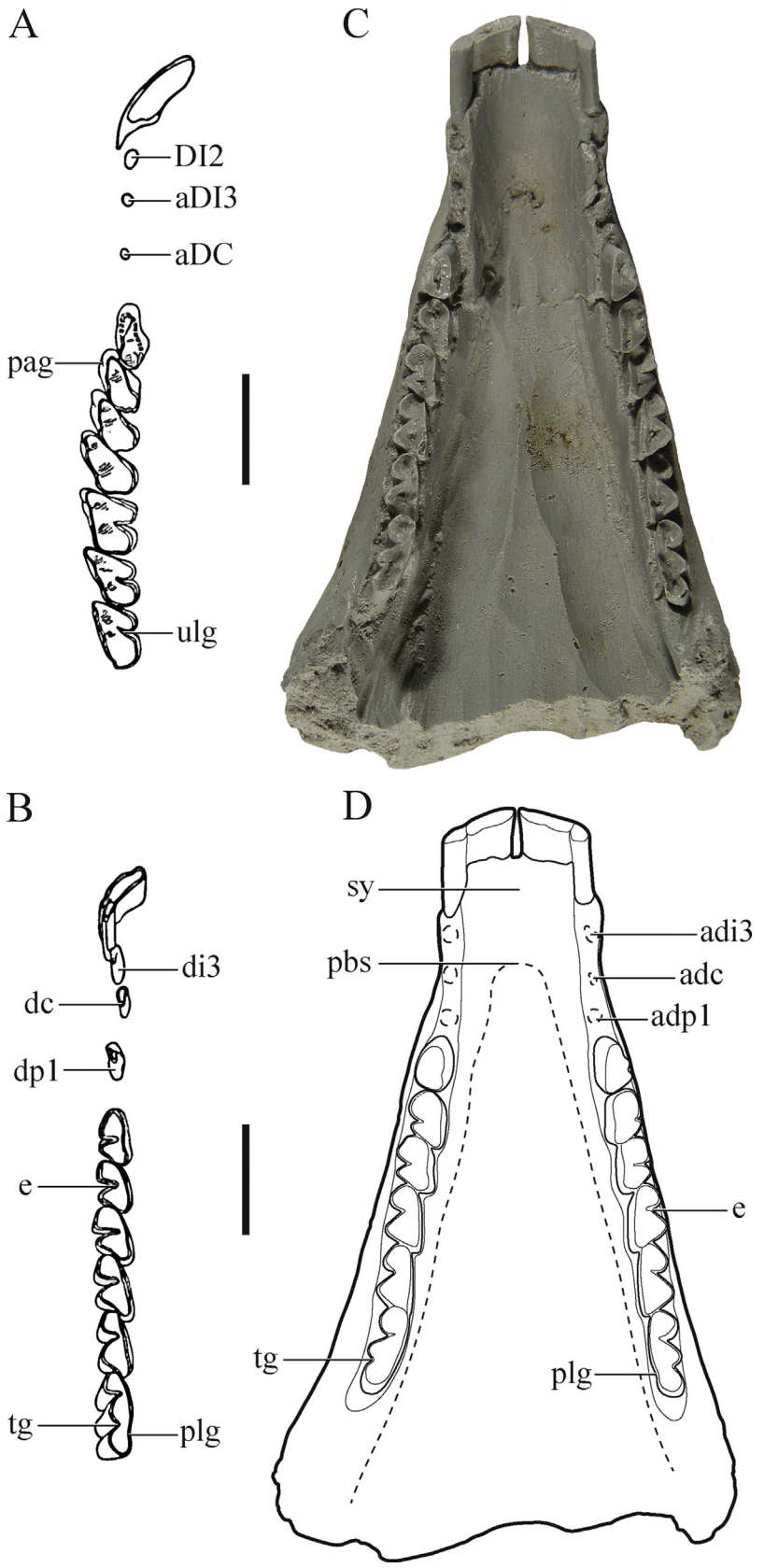
Based on dental measurements and on the observed ontogenetic stages, we agree with Loomis (1914) and Reguero (1999), and consider *P. triangulidens*, *P. robustum*, and *P. quartum* as junior synonyms of *P. garzoni* (Table 1).

In reference to *Propachyrucos ameghinorum*, Simpson (1945, p. 553) recognized the similarity of its skull to that of *Prosotherium*. In addition, he superficially compared the postcrania with the specimens of *Prosotherium* collected by Loomis, but he did not consider the published measurements (Loomis, 1914, p. 70). After Simpson (1945), the holotype of *Pr. ameghinorum*, AMNH 29574, bears I3 and C represented by tiny alveoli, and he proposed that the teeth were probably lost in the lifetime; the alveolus of I2 is a little larger and the author stated that this tooth would be small but functional. In turn, the preserved i3–c–p1 are small, cylindrical and procumbent teeth. Comparing with *P. garzoni*, *Pr. ameghinorum* AMNH 29574 shares the presence of parastylar groove in upper premolars, upper molars with deep lingual groove, some vestigial anterior teeth with diastemata between them and similar size (Simpson, 1945, fig. 1; Fig. 3A–B, Suppl. App. 1.2–3). These similarities lead us to reinterpret these anterior teeth in AMNH 29574 as deciduous: DI2–DI3–DC and di3–dc–dp1, contrary to Simpson (1945). The P1 has the lingual face concave like the holotypes of *P. robustum* and *P. triangulidens* (Fig. 1G–J). The P2–4 have a shallow groove between parastyle and paracone like the holotype of *P. robustum* (Fig. 1G–H). The di3–dc–dp1 are more procumbent than the corresponding teeth in *Propachyrucos* (see Section 3.2). In addition, the lengths of i1–m3 and p2–m3 in *Pr. ameghinorum* is 53.1 mm and 30.9 mm, respectively (Simpson, 1945, table 1), closer to those in *P. garzoni* ACM 3137 (53 mm and 33.2 mm, respectively) and MACN A 52-456 (p2–m3, 30.1 mm; Fig. 1C–D) than to those in *Pr. smithwoodwardi* MACN A 52-451 (41 mm and 23.5 mm, respectively) (Ameghino, 1897, p. 425, and see Section 3.2).

In summary, when we compare *Pr. ameghinorum*, *Pr. smithwoodwardi* and *P. garzoni*, we find that the features present in *Pr. ameghinorum* are the same as in the juvenile specimens of *P. garzoni*, most notably including the di3–dc–dp1 separated by diastemata, the presence of the parastylar groove in upper premolars and lingual groove in upper molars, the concave lingual face of P1, and their similarity in size. While all these characteristics support synonymizing *Pr. ameghinorum* with *P. garzoni*, it should be noted that we did not directly examine the holotype of *Pr. ameghinorum* (AMNH 29574). Accordingly, we could not corroborate the presence of the mental foramina in AMNH 29574 (and Simpson [1945] did not describe the mandible). This characteristic foramen is present in several mandibular fragments assigned to *Prosotherium*, as MACN A 52-456, 52-459, 52-461, ACM3731, MPEF 5753, 5754, 5755, although, in MACN A 52-459 and MPEF 5755, the foramen is not as well preserved as in the paralectotype MACN A 52-456.

As said above, Reguero (1999) also synonymized *Propachyrucos simpsoni* with *P. garzoni*. Chaffee (1952) described the species from a mandibular fragment with left and right i1–m3, but alveoli of i3–c–p1 (AMNH 29604), and as a *confer* referred material he assigned a mandibular fragment with left and right i1–2, p1, dp2–4 and m1 (AMNH 29620). The type of *Pr. simpsoni* AMNH 29604 (Chaffee, 1952, Plate 17, figs. 1–2; Fig. 3C–D) shares with *P. garzoni* the i1–2 clearly procumbent, reduced alveoli of i3–c–p1, the robustness of the dentary, and the morphology of the p3–4, in which the talonid is smaller than the trigonid (Fig. 3C–D; Chaffee, 1952), while in *Propachyrucos* the lobes are similar in size (Table 2). In addition, *Pr. simpsoni* and *P. garzoni* are similar in size (L i1–m3, 53 mm and L p2–m3, 32.1 mm in *Pr. simpsoni*; L i1–m3, 53 mm and 33.2 mm in *P. garzoni* ACM 3731; see also Suppl. App. 1.4). The reduced alveoli in AMNH 29604 are herein reinterpreted as for deciduous teeth, di3–dc–dp1, as in the case of *Pr. ameghinorum*, which adds to the other mentioned similarities between *Pr. simpsoni* and *P. garzoni*; the interpretation of alveoli for deciduous teeth is congruent with the presence of a remnant of central enamel in the occlusal face of the teeth (Chaffee, 1952, Plate 17, figs. 1–2), which indicates a still young individual.

des dents de lait di3–dc–dp1 et p2 sans usure gauches, et alvéole du i1, i2, alvéoles de dc–dp1, p2 en éruption et p3–m2 droites ; E, F, original et dessin schématique d'ACM 3731 en vue occlusale, avec i1, les alvéoles de i2 et des dents de lait dp1 et p2–m3 ; G, H, original et dessin schématique de MPEF 5753 en vue occlusale, avec les alvéoles des dp1, p2 gauche et p2–m2 droites ; I, J, original et dessin schématique de MPEF 5755 en vue occlusale, avec l'alvéole droite des dents de lait dp1 et p2–4 droites. Abréviations : adc : alvéole de dc ; adi3 ; alvéole de di3 ; adp1 : alvéole de dp1 ; ai2 : alvéole de i2 ; ceb : bande d'émail centrée ; e : ectoflexide ; fo : fossettide ; if : foramen infraorbital ; inf : foramen incisif ; pbs : bord postérieur de la symphyse ; plg : sillon lingual postérieur ; pp : projection palatine ; s : sédiment ; tg : sillon du talonide ; ulg : sillon lingual supérieur. La barre d'échelle est égale à 1 cm.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Concerning AMNH 29620, we have doubts about Chaffee's (1952) interpretation of dp2–4, because they are high (described as deep in the mandible almost reaching the bottom) and without roots or sign of permanent teeth below them; besides, the supposed dp2 (Chaffee, 1952: fig. 4) does not show a morphology of p2 (the trigonid would be longer, the ectoflexid shallower and lingual face straighter); this illustration is more compatible with a p4–m3 series, in which m2 is barely worn and m3 is erupting; however, as we have not revised this specimen, we cannot check this possibility and the relative position of these teeth in the preserved mandible and with respect to the supposed p1 (Chaffee described the latter as bilobed, so it could really correspond to p2 or p3, but not to p1, which is elliptic in Hegetotheriidae). So, we base our conclusions on *Pr. simpsoni* only on the type AMNH 29604, keeping in mind that AMNH 29620 could have been wrongly described.

To test whether differences in size between the synonymized species *Pr. ameghinorum*, *Pr. simpsoni*, *P. garzoni*, and *Propachyrucos smithwoodwardi* are significant, we performed one ANOVA for each tooth position and Tukey's multiple comparison test (see Section 2 and Suppl. App. 1.2 for details). The analyses revealed that *Pr. smithwoodwardi* is significantly different from *Pr. ameghinorum*, *Pr. simpsoni*, and *P. garzoni* in all teeth (p2, p3, p4, m1 and m2). In addition, when we compare the length of the series i1–m3 and p2–m3, we find that *Pr. smithwoodwardi* is significantly smaller (near 20%) than the other three species (which, in turn, are very similar to each other; see absolute values above). On the other hand, the analyses show that *Pr. ameghinorum* is significantly different from *P. simpsoni* in the p2 and significantly different from *P. garzoni* in the m1 and m2 (Suppl. App. 1.2). As a whole and considering that differences between *Pr. simpsoni* with *P. garzoni* are not significant, the statistical analyses support the synonymy between *Pr. ameghinorum* and the two latter species, being separated from *Pr. smithwoodwardi*.

Based on the previous comparisons and discussion, we formally propose the synonymy of *Pr. ameghinorum*, *Pr. simpsoni* and *P. garzoni*, supporting Reguero's (1999) interpretation, with priority of name for *P. garzoni* (Table 1).

A few additional comments should be made regarding the specimens from the Agua de la Piedra Formation (Quebrada Fiera, Mendoza Province, Argentina) identified by Cerdeño and Reguero (2015) as *Propachyrucos* cf. *Pr. smithwoodwardi*. The authors justified this assignment mainly because of the lesser development of the paracone fold of the upper molars with respect to *P. garzoni*. Also, they referred several mandibular fragments with premolars with long and more or less labially rounded trigonids, together with short and triangular talonids, and m1–2 showing rounded trigonid and triangular to trapezoidal talonid. Despite the fact that the authors did not compare directly with the type material of *P. garzoni*, they found that the sample of Quebrada Fiera showed some features more similar to *P. garzoni* and others more similar to *Pr. smithwoodwardi*, and even the size showed some variation with respect to *Pr. smithwoodwardi* (e.g., MCNAM PV 3960 being larger). However, the authors stated that these differences were not sufficient to recognize two pachyrukhine taxa with certainty. The present revision of this material confirms that it corresponds to a single taxon, but also reveals that the upper dentition matches that of *P. garzoni*, whereas the upper dentition is unknown for *Pr. smithwoodwardi* (see below); therefore, we consider that all specimens from Quebrada Fiera referred to as *Propachyrucos* cf. *Pr. smithwoodwardi* (Cerdeño and Reguero, 2015) instead belong to *Prosotherium garzoni* (Table 1).

3.2. Genus ***Propachyrucos*** *Ameghino, 1897*

1897 *Propachyrucos* Ameghino: 425 (original description).

Type species. *Propachyrucos smithwoodwardi* Ameghino, 1897.

Included species. The type only.

Emended diagnosis (after Ameghino, 1897 **and** Reguero, 1999**).** Nearly 20% smaller than *Prosotherium*, similar in size to *Pachyrukhos* and *Paedotherium*, but nearly 30% larger than *Tremacyllus*. Horizontal mandibular ramus shallow and with constant height, in contrast to the other genera, in which the height increases backward; labial mental foramen below the canine and a small second foramen below the p4. Differs from *Pachyrukhos*, *Tremacyllus* and *Paedotherium* by the complete dental series. Lower i1–c procumbent, but not as much as in the other genera. Differs from *Hegetotherium*, *Pachyrukhos*, *Paedotherium*, *Prosotherium*, and *Tremacyllus* by the lack of diastemata between the anterior teeth. Lower p2 with trigonid larger than talonid; p3 with trigonid slightly larger than talonid; and p4 with trigonid slightly smaller than talonid.

Occurrence. Sarmiento Formation, late Oligocene, Deseadan SALMA. Chubut Province, Argentina.

Remarks. Ameghino (1897) defined the genus *Propachyrucos* as larger than *Pachyrukhos*, with complete

Fig. 3. Cranial and mandibular specimens of *Prosotherium garzoni*. A, B, scheme of AMNH 29574 (holotype of *Propachyrucos ameghinorum*) in occlusal view, upper right I1, DI2–3–DC and P1–M3 (A); scheme lower left i1–2, di3–dc–dp1 and p1–m3 (B); C, D, original (cast) and schematic drawing of AMNH 29604 (holotype of *Propachyrucos simpsoni*) in occlusal view, with both i1–2, alveoli of di3–dc–dp1, and p2–m3. Abbreviations: aDC/adc: alveolus of upper/lower deciduous canine; aDI/adi: alveolus of upper/lower deciduous incisor; adp1: alveolus of deciduous p1; e: ectoflexid; pag: parastylar (mesiolabial) groove; pbs: posterior border of the symphysis; plg: posterior lingual groove; sy: symphysis; tg: talonid groove; ulg: upper lingual groove. A–B modified from Simpson (1945, fig. 1). The scale bar equals 1 cm.

Fig. 3. Spécimens crâniens et mandibulaires de *Prosotherium garzoni*. A, B, schéma d'AMNH 29574 (holotype de *Propachyrucos ameghinorum*) en vue occlusale, I1, DI2–3–DC et P1–M3 droites (A) i1–2, di3–dc–dp1 et p1–m3 gauches (B) ; C, D, original (moule) et dessin schématique d'AMNH 29604 (holotype de *Propachyrucos simpsoni*) en vue occlusale, avec 1–2, alvéoles des di3–dc–dp1 et p2–m3 droites et gauches. Abréviations : aDC/adc : alvéole des canines de lait supérieure/inférieure ; aDi/adi : alvéole des incisives de lait supérieure/inférieure ; adp1 : alvéole de dp1 ; e : ectoflexide ; pag : sillon parastylaire (mésiolabial) ; pbs : bord postérieur de la symphyse ; plg : sillon lingual postérieur ; sy : symphyse ; tg : sillon du taloniде ; ulg : sillon lingual supérieur. A–B modifié d'après Simpson (1945, fig. 1). La barre d'échelle est égale à 1 cm.

Table 2
Length of the trigonid and talonid of the main specimens studied in this article. Measurements in mm. Abbreviations: l: left; r: right. *See Table 1 for the present interpretation of these taxa.
Tableau 2
Longueur des trigonide et talonide des principaux spécimens étudiés dans cet article. Mesures en mm. Abréviations : l : gauche; r : gauche. *Voir Tableau 1 pour la présente interprétation de ces taxons.

	Specimen	Tooth	Trigonid	Talonid
Propachyrucos smithwoodwardi	MACN A 52-451	p3	1.9	1.6
		p4	1.9	2
		m1	2	2.5
		m2	2.3	2.4
	MACN A 52-452	p3	2	1.6
		p4	1.7	2
		m1	1.9	2.4
		m2	1.9	2.5
'*Propachyrucos aequilatus*'*	MACN A 52-454	p4	2.7	2.1
		m1	2.6	2.5
		m2	2.6	2.6
'*Propachyrucos*' *crassus**	MACN A 52-448	p3	3.2	3.6
'*Propachyrucos depressus*'*	MLP 12-2915a	p3 l	2	2.1
		p4 l	1.8	2.1
		m1 r	1.7	1.9
		m2 r	1.6	1.8
'*Propachyrucos medianus*'*	MLP 12-3160	p3	1.7	2.4
		p4	1.9	2.4
'*Propachyrucos robustus*'*	MLP 12-3161	m1	3.1	4.4
'*Propachyrucos simpsoni*'*	AMNH 29604 left	p3	2.5	2
		p4	2.4	2.3
		m1	2.7	2.8
		m2	2.8	2.8
	AMNH 29604 right	p3	2.6	1.9
		p4	2.6	2.2
		m1	2.4	3.1
		m2	2.4	3.5
Propachyrucos sp.*	MLP 12-2889a	m1	1.6	2.5
		m2	1.7	2.5
	MLP 59-II-26-91	p4	1.8	2.4
	MLP 61-IV-11-186	p4	1.6	1.9
		m1	1.7	2
		m2	1.6	2.1
	MLP 61-IV-11-192	p4	1.65	2.05
		m1	1.8	2.3
	MLP 61-IV-11-207	p3	2	1.8
		p4	1.8	2.1
Prosotherium garzoni	AMC 3731 left	p3	3.1	2.3
		p4	3.2	2.5
		m1	3.4	2.8
		m2	3.6	2.7
	AMC 3731 right	p3	3.15	2.35
		p4	3.2	2.4
		m1	3.65	2.75
		m2	3.4	3.1
	AMNH 14154	p3	2.5	2
		p4	2.6	2.3
		m1	2.8	–
	MACN A 52-456	p3	2.7	1.9
		p4	3	2.4
		m2	2.6	2.9
	MACN A 52-459	p3	2.7	2.6
		p4	2.8	2.6
		m1	3	3
		m2	2.85	3.05
	MACN A 52-460	p3	2.7	1.9
		p4	2.7	2.1
		m1	2.8	2.8
		m2	2.95	2.65
	MACN A 52-461	p3	2.65	2.15
		p4	2.7	2.3
		m1	3.05	3.05
		m2	3	3.1

Table 2 (*Continued*)

	Specimen	Tooth	Trigonid	Talonid
Prosotherium sp.	MPEF-PV 5753	p3	2.3	2.1
		p4	2.25	2.45
		m2	3.2	2.4
	MPEF-PV 5754	p3	2.7	2.2
		p4	2.9	2.3
	MPEF-PV 5755	p3	2.8	2.7
		p4	2.85	2.75
	MPEF-PV 5761	p3	2.75	2.25
	(set of teeth)	p3	2.6	2.3
		p3	2.8	2.3
		m1	2.9	3.2
		m1	3	3.2
		m1	2.9	3.2

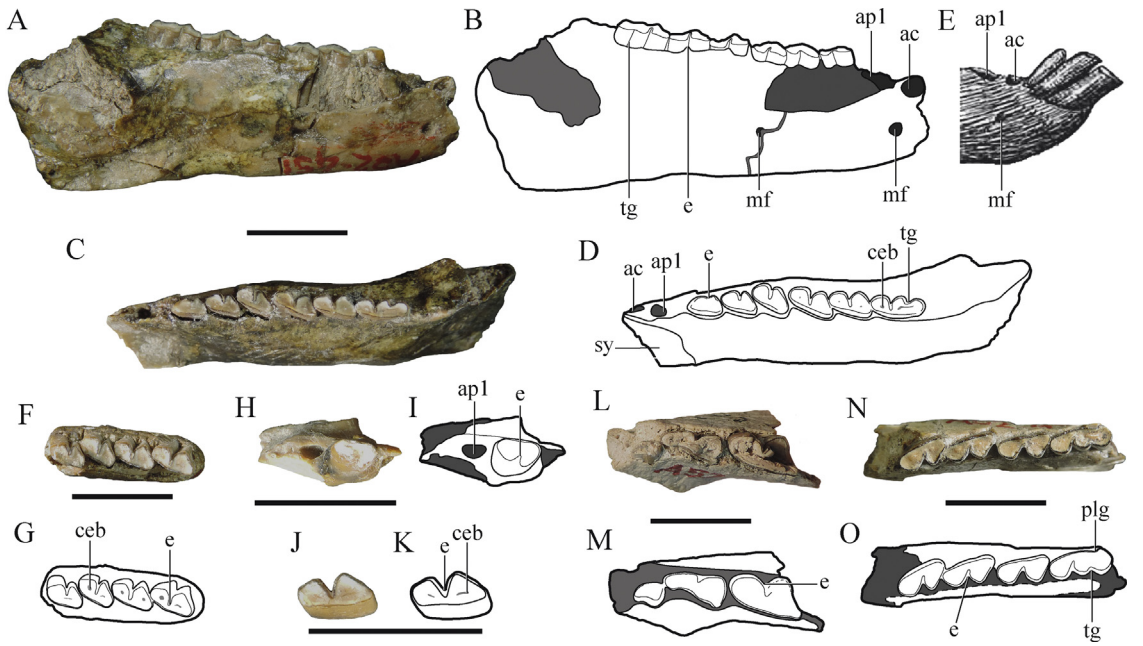

Fig. 4. Specimens formerly identified as *Propachyrucos* by Ameghino (1897, 1901). A, B, C, D, *Propachyrucos smithwoodwardi*, original and schematic drawings of MACN A 52-451 (holotype), with right alveoli of c–p1 and p2–m3 in lateral (A, B) and occlusal (C, D) views; E, *Propachyrucos smithwoodwardi*, anterior lower dentition of MACN A 52-451 (holotype) modified after Ameghino (1897); F, G, *Propachyrucos smithwoodwardi*, original and schematic drawing of MACN A 52-452, with left p3–m2 (see as right) in occlusal view; H, I, J, K, *Propachyrucos smithwoodwardi*, original and schematic drawings of MACN A 52-453, with left alveolus of p1 and p2 (H, I,) and right m2 (J, K) in occlusal view; L, M, "*Propachyrucos*" *crassus*, original and schematic drawing of MACN A 52-448 (lectotype) in occlusal view, with right p1–3; N, O, "*Propachyrucos aequilatus*", original and schematic drawing of MACN A 52-454 (holotype) in occlusal view, with left p4–m3; Abbreviations: ac: alveolus of canine; ap: alveolus of premolar; ceb: centred enamel band; e: ectoflexid; en: entoflexid; inf: incisive foramen; mf: mental foramen; pf: palatine foramen; plg: posterior lingual groove; plp: posterolingual projection; sy: symphysis; tg: talonid groove. The scale bar equals 1 cm.

Fig. 4. Spécimens anciennement identifiés comme *Propachyrucos* par Ameghino (1897, 1901). A, B, C, D, *Propachyrucos smithwoodwardi*, originaux et dessins schématiques de MACN A 52-451 (holotype), avec alvéoles droites de c–p1 et p2–m3 en vues latérale (A, B) et occlusale (C, D) ; E, *Propachyrucos smithwoodwardi*, dentition inférieure antérieure de MACN A 52-451 (holotype) modifié d'après Ameghino (1897) ; F, G, *Propachyrucos smithwoodwardi*, original et dessin schématique de MACN A 52-452, avec p3–m2 gauches (à l'envers par rapport à l'original) en vue occlusale ; H, I, J, K, *Propachyrucos smithwoodwardi*, originaux et dessins schématiques de MACN A 52-453, avec les alvéoles gauches de p1 et p2 (H, I) et droite de m2 (J, K) en vue occlusale ; L, M, "*Propachyrucos*" *crassus*, original et dessin schématique de MACN A 52-448 (lectotype) en vue occlusale, avec p1–3 droites ; N, O, "*Propachyrucos aequilatus*", original et dessin schématique de MACN A 52-454 (holotype) en vue occlusale, avec p4–m3 gauches ; Abréviations : ac : alvéole de canine ; ap : alvéole de la prémolaire ; ceb : bande d'émail centrée ; e : ectoflexide ; en : entoflexide ; inf : foramen incisif ; mf : foramen mentonnier ; pf : foramen palatin ; plg : sillon lingual postérieur ; plp : projection postérolinguale ; sy : symphyse ; tg : sillon du talonide. La barre d'échelle est égale à 1 cm.

dental series and incisors not reduced. Initially, the author identified two species differentiated by size, *Pr. smithwoodwardi* (Fig. 4A–K) smaller than *Pr. crassus* (Fig. 4L–M), both described on the basis of a few mandibular fragments. Subsequently, Ameghino (1901) described *Pr. aequilatus* (Fig. 4N–O), which had an intermediate size and trigonid as large as the talonid in p4–m2, instead of smaller as it is in *Pr. smithwoodwardi* and *Pr. crassus* (see Table 2).

Roth (1899) proposed the same generic name, *Propachyrucos*, for three new species (*Pr. depressus* — Fig. 5 A–F —, *Pr. medianus* — Fig. 5G–J —, and *Pr. robustus* — Fig. 5K–L) from the Collón Curá

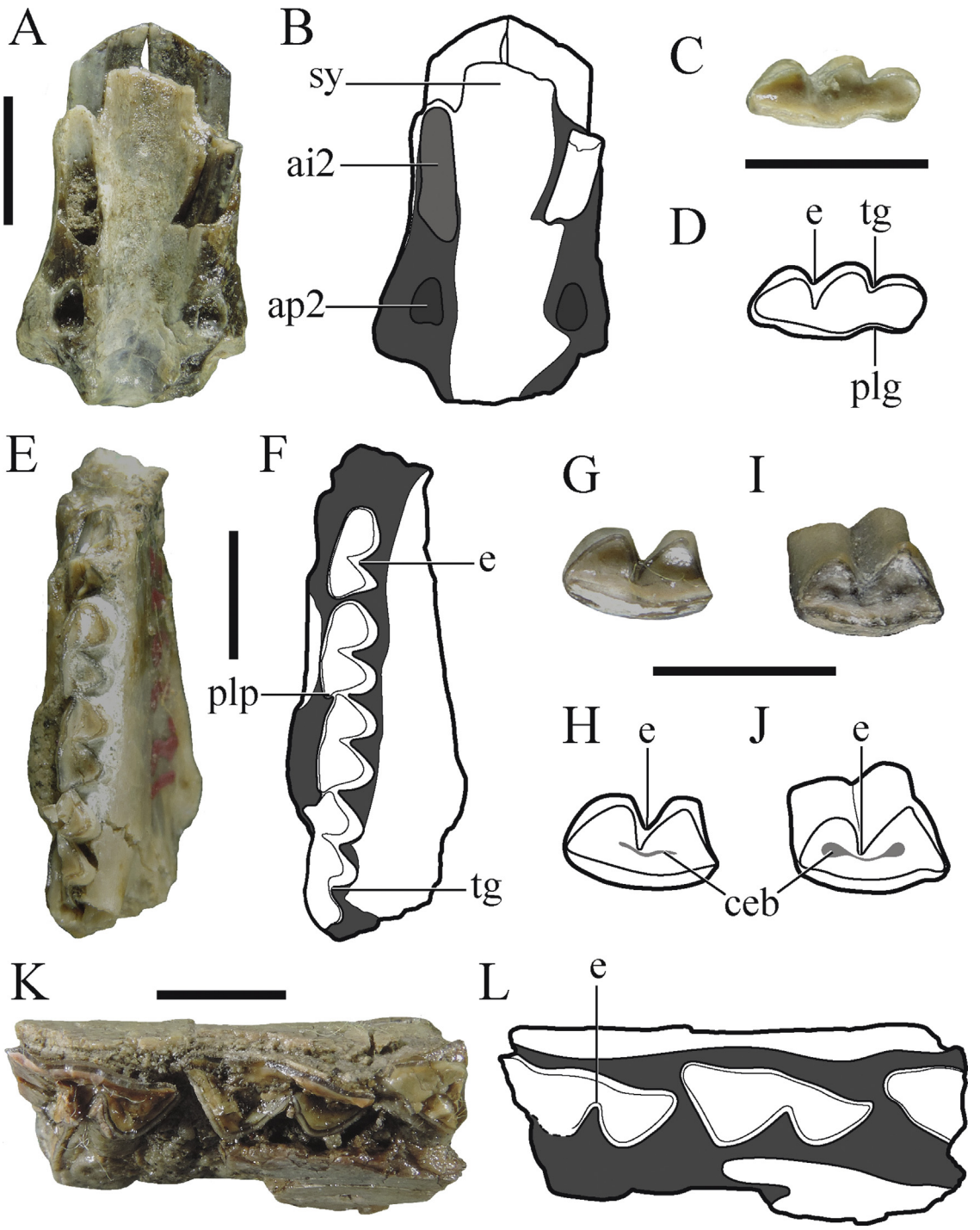

Fig. 5. Specimens formerly identified as *Propachyrucos* by Roth (1899). A, B, C, D, E, F, *Pachyrukhos* sp., original and schematic drawings of MLP 12-2915a (syntypes of *Propachyrucos depressus*), symphysis with right i1–2 and alveolus of p2 and left i1 and alveoli of i2 and p2 (A, B), right m3 (C, D), right mandibular fragment with p4–m3 (E, F) in occlusal view; G, H, I, J, *Pachyrukhos* sp., original and schematic drawings of MLP 12-3160 (holotype of *Pr. medianus*), right p3 (G, H) and p4 (I, J) in occlusal view; K, L, *nomen dubium*, original and schematic drawing of MLP 12-3161 (holotype of *Pr. robustus*), right mandibular fragment with p4–m2 in occlusal view. Abbreviations: ai: alveolus of incisor; ap: alveolus of premolar; ceb: centred enamel band; e: ectoflexid; plg: posterior lingual groove; plp: posterolingual projection; sy: symphysis; tg: talonid groove. The scale bar equals 0.5 cm.

Fig. 5. Spécimens anciennement identifiés comme *Propachyrucos* par Roth (1899). A, B, C, D, E, F, *Pachyrukhos* sp., originaux et dessins schématiques de MLP 12-2915a (syntypes de *Propachyrucos depressus*), symphyse avec i1–2 et alvéole de p2 droites et i1, alvéole de i2 et p2 gauches (A, B), m3 droite (C, D), fragment mandibulaire droit avec p4–m3 (E, F), tout en vue occlusale ; G, H, I, J, *Pachyrukhos* sp., originaux et dessins schématiques de MLP 12-3160 (holotype de *Pr. medianus*), p3 (G, H) et p4 (I, J) droits en vue occlusale ; K, L, *nomen dubium*, original et dessin schématique de MLP 12-3161 (holotype de *Pr. robustus*), fragment mandibulaire droit avec p4–m2 en vue occlusale. Abréviations : ai : alvéole de l'incisive ; ap : alvéole de la prémolaire ; ceb : bande

Formation (Colloncuran SALMA, early middle Miocene) of Río Negro Province, but the author acknowledged in a footnote (Roth, 1899, p. 176) the previous definition by Ameghino (1897), confirming the correct allocation of the three species in the same genus. Loomis (1914) only mentioned and rewrote Ameghino's (1897, 1901) descriptions of *Pr. smithwoodwardi* and *Pr. aequilatus* (he excluded *Pr. crassus*), and ignored the species described by Roth (1899). Later, Roth's species were included in the genus *Pachyrukhos* by Pascual et al. (1978), without any taxonomic discussion. This unjustified interpretation was followed by other authors (e.g., Kramarz et al., 2011; López et al., 2018), likely based on the stratigraphic provenance of these species, where *Pachyrukhos* was found (see Seoane and Cerdeño, 2019; Vera, 2019). However, Mones (1986) had listed these species as belonging to *Propachyrucos*. We discuss here the generic ascription of these species (see below).

Kraglievich (1932) described the species *Propachyrucos? schiaffinoi* from a palate fragment from Fray Bentos Formation (Uruguay), but this species was later transferred to the genus *Prohegetotherium* Ameghino, 1897 by Reguero (1999), a decision followed by Reguero and Cerdeño (2005) and Cerdeño and Reguero (2015), but see Kramarz and Bond (2017) about the concept of the genus *Prohegetotherium*.

Simpson (1945, fig. 1, Plate 1) described *Propachyrucos ameghinorum* (Fig. 3A–B) from the locality of Scarritt Pocket (Chubut Province), and later Chaffee (1952) erected *Pr. simpsoni* (Fig. 3C–D) from the same locality. Both species have been discussed above and formalized as synonyms of *Prosotherium garzoni* (see Section 3.1).

Reguero (1999) informally synonymized *Propachyrucos crassus* with *Prohegetotherium sculptum* Ameghino, 1897, agreeing with Patterson's (1952) unpublished catalogue. Posteriorly, this synonymy was formalized by Reguero and Cerdeño (2005), although recently Kramarz and Bond (2017) considered it as valid species, but of uncertain generic position. Reguero (1999) also synonymized *Pr. aequilatus* with *Pr. smithwoodwardi*, which is discussed below.

In summary, the present revision and the following discussion indicate that the genus *Propachyrucos* is only conformed by *Propachyrucos smithwoodwardi*.

3.2.1. ***Propachyrucos smithwoodwardi*** *Ameghino, 1897*

(Fig. 4A–K, N–O)

1897 *Propachyrucos smithwoodwardi* Ameghino: 425 (original description), fig. 11.

Holotype. MACN A 52-451, right mandibular fragment with alveoli of c–p1 and p2–m3 (Fig. 4A–E); the anterior part figured by Ameghino (1897) is presently missing and is reproduced here (Fig. 4E) after Ameghino's illustration.

Diagnosis. As for the genus.

Occurrence. Sarmiento Formation, late Oligocene, Deseadan SALMA. Chubut Province, Argentina.

Referred material. MACN A 52-452, left mandibular fragment with p3–m2 (Fig. 4F–G); MACN A 52-453, left mandibular fragment with alveoli of c–p1 and p2, and an isolate right m1 or m2 (Fig. 4H–I, J–K, respectively).

Remarks. Ameghino (1897) characterized this species as having the complete dental series, relatively large i3 and canine (not reduced), and lower mandibular rami than in *Pachyrukhos*. The specimen MACN A 52-451 (Fig. 4A–E), though incomplete (as noted by Reguero, 1999, p. 189), matches the original illustration and description of *Pr. smithwoodwardi*, and it thus corresponds to the holotype of the species.

Following the comparisons described above, our study distinguishes *Propachyrucos smithwoodwardi* from *Prosotherium garzoni* and reassigns many species originally attributed to *Propachyrucos* to the genus *Prosotherium*. The following discussion focuses then on *Pr. smithwoodwardi*, *Pr. crassus*, whose transfer to the genus *Prohegetotherium* (Reguero and Cerdeño, 2005) has been recently rejected (Kramarz and Bond, 2017), *Pr. aequilatus*, and the species described by Roth (1899) from Colloncuran levels.

Discussion. Regarding *Propachyrucos crassus* (Fig. 4L–M), we studied all material assigned to this species (see Suppl. App. 1.1), which consists of three mandibular fragments constituting the syntypes (MACN A 52-448–52-450), which were differently interpreted. Reguero and Cerdeño (2005), based on Reguero's (1999) work, considered MACN A 52-448–52-449 as bearing c–p2 and MACN A 52–450 as p1–p2, whereas Kramarz and Bond (2017) considered MACN A 52–448 with p1–p3 and the three fragments possessing the p1 (or its alveolus) lingual to the tooth row. When we examined the lower jaws of Deseadan Hegetotheriidae, we found that all specimens present bilobed p2 and elliptical p1 without any groove (i.e. *Sallatherium altiplanense*, Reguero and Cerdeño [2005, fig. 2e]; *Pr. smithwoodwardi* [Fig. 4A–E]; *P. garzoni* [Figs. 1–3]; specimen assigned to *Prohegetotherium sculptum* by Chaffee [1952, plate 16, figs. 2–3]; *Pr. ameghinorum* [Fig. 3B]). Based on this evidence, we agree with Kramarz and Bond's (2017) interpretation and consider the first bilobed tooth as p2, so MACN A 52-458–52-459 have p1–3 and MACN A 52-450 has p1–2 (Fig. 4L–M). This established, we find that the elliptical p1 lingually placed and the bilobed p2 with long and narrow trigonid lingually concave is a combination of features unique to this taxon. However, the elliptical cross section of p1 is shared by almost all Hegetotheriidae. Besides, *Pr. crassus* can be excluded from *Propachyrucos* and *Prosotherium* based on the following features: larger size, lingual position of the p1, p2 with long and narrow trigonid, lingually concave, and p2–3 with trigonid smaller than talonid (Table 2).

d'émail centrée ; e : ectoflexide ; plg : sillon lingual postérieur ; plp : projection postérolinguale ; sy : symphyse ; tg : sillon du talonide. La barre d'échelle est égale à 0,5 cm.

On the other hand, following Kramarz and Bond's (2017) revision of *Prohegetotherium sculptum*, there is no known lower dentition of this species to compare with *Pr. crassus*, which supports their conclusion about maintaining this species of uncertain generic position, and clearly apart from *Propachyrucos*. The features of *Pr. crassus* (lingual position of p1, morphology of the p2 and general size) are shared with the specimen AMNH 29605 described by Chaffee (1952, Plate 16, fig. 2–3) as *Prohegetotherium sculptum*, and could represent the same taxon. It is evident that additional materials and the revision of all remains attributed to *Prohegetotherium sculptum* are necessary to clarify this taxonomy.

Concerning *Pr. aequilatus*, it is only known by its holotype (Ameghino, 1901), a left mandibular fragment with p4–m3 (MACN A 52-454; Fig. 4N–O; Suppl. App. 1.4). Mones (1986: p. 161) included this specimen as *Pr. smithwoodwardi*, whereas Reguero (1999) recognized it as type of *Pr. aequilatus*. The p4 has a rounded trigonid, barely larger than the triangular talonid, and a straight lingual face; m1–2 have the trigonid smaller than the talonid, and the lingual face is also straight; m3 has a deep ectoflexid and a shallow labial talonid groove; its lingual face is slightly convex, with a posterior furrow that lingually delimits the third lobe. The m1–2 differ from *Pr. smithwoodwardi*, in which the trigonid is smaller than the talonid (Table 2) and the lingual face is slightly convex; in addition, *Pr. aequilatus* is 15–20% larger and the mandibular ramus is higher than in *Pr. smithwoodwardi*. In turn, the talonid smaller than the trigonid in p4 coincides with *P. garzoni*, but the statistical analyses show *Pr. aequilatus* significantly different from both *P. garzoni* (for m1 and m2) and *Pr. smithwoodwardi* (for p4, m1 and m2) (see Suppl. App 1.2). Therefore, *Pr. aequilatus* cannot be clearly assigned to any of these species/genera and we propose to consider the name as a *nomen dubium*.

With respect to *Propachyrucos depressus*, the only specimen in the MLP collection (MLP 12-2915a, Fig. 5A–F) comprises two symphyseal fragments, one right mandibular fragment with p4–m3, one left mandibular fragment with probably p3–p4, and an isolated right m3. Due to the presence of two right m3 and two symphyses, at least two individuals are present and thus the specimens constitute syntypes, instead of the holotype of the species as mentioned by Vera (2019: fig. 4I). The original description (Roth, 1899) does not detail how many specimens the author had in hand. The symphysis fragment that preserves the anterior dentition bears the right and left i1, right i2, alveolus of left i2 and both subtriangular alveoli of a posterior tooth (likely p2), separated by a short diastema (Fig. 5A–B). The absence of i3–c–p1 and the highest degree of procumbence discard these specimens from belonging to *Propachyrucos*; their assignment to *Prosotherium* is also discarded because of their smaller size (Suppl. App. 1.3–4). The isolated m3 has the third lobe rounded (Fig. 5C–D), a characteristic of *Pachyrukhos* and different from the triangular outline in *Paedotherium* (Cerdeño and Bond, 1998; Ercoli et al., 2018). In addition, the m1–2 preserved in one mandibular fragment (Fig. 5E–F) present the posterolingual projection observed in *Pachyrukhos* (Seoane and Cerdeño, 2019), which is not present in *Paedotherium* or *Tremacyllus* (Cerdeño and Bond, 1998; Ercoli et al., 2018). Therefore, the syntypes of *Propachyrucos depressus* are herein considered as belonging to *Pachyrukhos* (Table 1 and see Suppl. App. 1.5, figure S1, for comparison with *Pachyrukhos*). Because of the missing p2 in the syntypes, we cannot ascertain to which of the two species of *Pachyrukhos* recognized by Seoane and Cerdeño (2019) it would belong, even though the Colloncuran age points to *Pachyrukhos moyani* Ameghino, 1885.

Out of the three teeth (p3, p4 and m3) described by Roth (1899) as *Propachyrucos medianus*, only the two premolars were located (MLP 12-3160; Fig. 5G–I), although Vera (2019) only illustrated one tooth as holotype and considered it m1 or m2, without performing any anatomical comparison. These teeth are similar in size to *Pachyrukhos* (Seoane and Cerdeño, 2019) and *Paedotherium* (Ercoli et al., 2018) and are slightly larger than in the holotype of *Pr. smithwoodwardi*, but smaller than *Prosotherium* (Suppl. App. 1.3–4). Their trigonids are subtriangular and smaller than the talonids (also triangular; Table 2), and the distal face is straight with a small posterolingual projection, so their morphology is closer to that of *Pachyrukhos* (Seoane and Cerdeño, 2019) than to that of *Paedotherium* (Ercoli et al., 2018), *Tremacyllus*, where the talonids are smaller than trigonids (Cerdeño and Bond, 1998; Ercoli et al., 2018), or *Propachyrucos*. Since Pascual et al.'s (1978) work, several authors accepted the transference of this species to *Pachyrukhos* (Kramarz et al., 2011; López et al., 2018; Vera, 2019). The premolars of *Pachyrukhos medianus* (MLP 12-3160) are larger than those of *Pachyrukhos moyani* and coincide with the material from the Collon Curá Formation identified as *Pachyrukhos* sp. 1 by Seoane and Cerdeño (2019).

The holotype of *Pr. robustus*, MLP 12-3161 (Fig. 5K–L), is a right mandibular fragment with p4–m2, only the m1 complete, and all occlusally broken. Roth (1899) described them as such a partial series (p4–m2), but Vera (2019) interpreted the series m1–3 and the complete tooth as m2 (although it is included as m1 in table 2 and fig. 3B). It is not easy to determine who is right, as the last molar is posteriorly incomplete and cannot be confidently identified as the m3. The complete molar (m1 or m2) of *Pr. robustus* is 60–70% larger than those (m1 or m2) of *Propachyrucos* and *Pachyrukhos* (Suppl. App. 1.4), and therefore we agree in discarding MLP 12-3161 from these two genera. Our comparisons show that *Pr. robustus* is similar to *Hegetotherium mirabile* Ameghino, 1887 (see Seoane and Cerdeño, 2019), with which MLP 12-3161 shares a subtriangular to semicircular trigonid, smaller than the triangular talonid; deep and wide ectoflexid; and slightly convex lingual face, but lacks the posterolingual projection present on lower molars of *H. mirabile* (Seoane and Cerdeño, 2019). In turn, Vera (2019) established the affinities of MLP 12-3161 with *Hemihegetotherium*, closing it to *Hm. tantillum* Vera, 2019. However, Vera (2019) characterized the m1–2 of *Hm. tantillum* by having the convex distal face, trigonids similar in length to talonids, and medial and distal projections, but none of these characteristics is present in *Pr. robustus* MLP 12-3161. The complete molar of this specimen has the distal face straight, trigonid shorter than talonid (Table 2), and lacks the mesial and distal projections

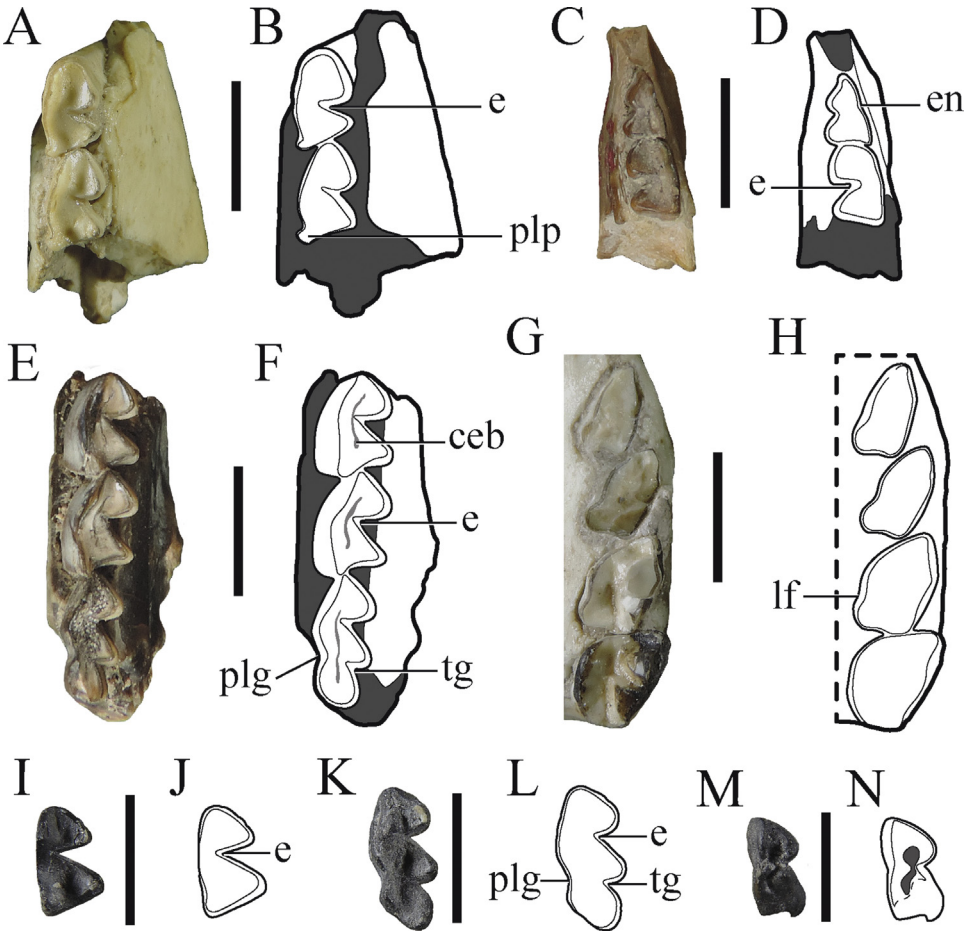

Fig. 6. Specimens labeled as *Propachyrucos* sp. in the MLP. A, B, *Pachyrukhos* sp., original and schematic drawing of MLP 61–IV–11–207, right mandibular fragment with p3–4 in occlusal view; D', E', F', G', *Pachyrukhos moyani*, original and schematic drawings of MLP 12-2889a, left mandibular fragment with p2–3 (C, D) and right mandibular fragment with m1–3 (E, F) in occlusal view; G, H, *Pachyrukhos* sp., original and schematic drawing of MLP 61–IV–11–317, left cranial fragment with P2–M1 in ventral view; I, J, K, L, M, N, *Pachyrukhos* sp., original and schematic drawings of MLP 59-II-26-91, right p4 (I, J), right m3 (K, L) and possible deciduous right premolar (M, N) in occlusal view. Abbreviations: ceb: centred enamel band; e: ectoflexid; en: entoflexid; plg: posterior lingual groove; plp: posterolingual projection; tg: talonid groove. The scale bar equals 0.5 cm.

Fig. 6. Les spécimens étiquetés comme *Propachyrucos* sp. dans le MLP. A, B, *Pachyrukhos* sp., original et dessin schématique de MLP 61-IV-11-207, fragment mandibulaire droit avec p3–4 en vue occlusale ; C, D, E, F, *Pachyrukhos moyani*, originaux et dessins schématiques de MLP 12-2889a, fragment mandibulaire gauche avec p2–3 (C, D) et fragment mandibulaire droit avec m1–3 (E, F) en vue occlusale ; G, H, *Pachyrukhos* sp., original et dessin schématique de MLP 61-IV-11-317, fragment crânien gauche avec P2–M1 en vue ventrale ; I, J, K, L, M, N, *Pachyrukhos* sp. originaux et dessins schématiques de MLP 59-II-26-91, p4 droite (I, J), m3 droite (K, L) et possible prémolaire droite [dent de lait] (M, N) en vue occlusale. Abréviations : ceb : bande d'émail centrée ; e : ectoflexide ; en : entoflexide ; plg : sillon lingual postérieur ; plp : projection postérolinguale ; tg : sillon du talonide. La barre d'échelle est égale à 0,5 cm.

(Fig. 5K–L). Hence, we consider *Propachyrucos robustus* as a *nomen dubium*, highlighting the similarity between this specimen and *H. mirabile*.

In addition to the type material of these species, we found several unpublished specimens in the MLP catalogued as *Propachyrucos* sp.: MLP 12-2889a, 59-II-26-91, 61-IV-11-139–152, 61-IV-11-163–166, 61-IV-11-186–192, 61-IV-11-207 and 61-IV-11-316–317 (Suppl. App. 1.1). Most of them share the diagnostic characters of *Pachyrukhos* (Seoane and Cerdeño, 2019): lower teeth with both lobes subtriangular and trigonid smaller than talonid, except in the p3, where the trigonid is rounded and as large as the talonid (Fig. 6A–B); p2 with reduced trigonid (when it is present) (Fig. 6C–D); m1–2 with posterolingual projection (Fig. 6E–F); m3 with wide and shallow posterolingual groove and rounded third lobe (Fig. 6E–F); upper premolars with a smooth furrow in the posterior part of the lingual face and molars without any groove (Fig. 6G–H). Based on these features, we identify MLP 12-2889a as *Pachyrukhos moyani*, and the remaining material as *Pachyrukhos* sp. The specimen MLP 61-IV-11-146 is unique in having a quadrangular trigonid that is separated from the talonid by opposite labial and lingual grooves, suggesting that this specimen belongs to Interatheriidae (cf. *Protypotherium*) rather than to Hegetotheriidae.

Most of these specimens come from El Pajarito (early Miocene, Colhuehuapian SALMA, Chubut Province; Goin et al., 2007): MLP 61-IV-11-139–152, MLP 61-IV-11-163–166, MLP 61-IV-11-186–192, MLP 61-IV-11-207 and MLP 61-IV-11-316–317. Instead, MLP 12-2889a, which

comes from the Collón Curá Formation (early middle Miocene, Neuquén Province) and MLP 59-II-26-91 comes from Laguna de La Bombilla (Chubut Province). This specimen (Fig. 6I–N) deserves a special comment. It is constituted by three isolated teeth, a right p4, a right m3, and a right incomplete unworn premolar. The p4 (Fig. 6I–J) shows the condition observed in *Pachyrukhos*, both lobes triangular and the posterior one more developed; the m3 (Fig. 6K–L) is trilobed, with the first lobe triangular and with a small mesial projection, and the third lobe rounded; the lingual face is convex, but with a shallow concavity opposite to the labial talonid groove. According to the size (Suppl. App. 1.4) and the presence of a trilobed m3 with rounded third lobe, MLP 59-II-26-91 could belong to *Propachyrucos* or to *Pachyrukhos*, but the morphology of p4 allows its assignment to *Pachyrukhos* sp. The recognition of *Pachyrukhos* at Laguna de La Bombilla sheds light on the age of this site. It was firstly interpreted as an early–middle Oligocene locality by Marshall et al. (1983), but recently Miquel and Bellosi (2010) postulated that the Sarmiento Formation outcrops at this locality, and this formation covers from middle Eocene to early Miocene (41.6–18.7 Ma) according to Ré et al. (2010). The presence of *Pachyrukhos* points to an early Miocene age for the bearing-fossil deposits at Laguna La Bombilla.

4. Conclusions

The revision of the types and most specimens assigned in previous works to *Prosotherium* and *Propachyrucos* allows us to recognize the validity of both genera, each constituted by one species. All proposed nomenclatural acts are summarized in Table 1. We recognize *Prosotherium garzoni* in the late Oligocene (Deseadan SALMA) Sarmiento Formation (Chubut Province), as well as in Agua de la Piedra Formation (Mendoza Province), represented by cranio-mandibular and postcranial elements. We confirm the synonymies proposed by Loomis (1914) and informally by Reguero (1999) of *Prosotherium robustum*, *Prosotherium quartum*, *Prosotherium triangulidens*, *Propachyrucos ameghinorum* and *Propachyrucos simpsoni* with *P. garzoni*, and add the specimens from Mendoza assigned to *Propachyrucos* cf. *Pr. smithwoodwardi* by Cerdeño and Reguero (2015). In turn, we recognize *Propachyrucos smithwoodwardi* in the Sarmiento Formation (Chubut Province), only represented by three mandibular fragments and an isolated lower tooth. This fact reveals that many cranial and postcranial characters previously coded for this species in phylogenetic analyses were erroneous. In the recent analysis by Seoane and Cerdeño (2019), only the type materials of *P. garzoni* and *Pr. smithwoodwardi* were codified. Concerning *P. garzoni*, the present revision provides new data to codify some characters considered as missing in that analysis, but they do not change the phylogenetic results (Seoane and Cerdeño, 2019). Maybe the detailed study of the skeleton AMNH 29574 of "*Pr. ameghinorum*" could complete some still missing data modifying the present phylogenetic hypothesis.

The revision of the holotype of *Propachyrucos aequilatus* (MACN A 52-454) allows differentiating it from *Pr. smithwoodwardi*, being larger, with trigonid as large as the talonid in m1–2 and the lingual face straighter, which leads us to disagree with their synonymy proposed by Reguero (1999). The p4 of MACN A 52-454 is closer to that of *P. garzoni*, but molars are significantly different from those of this species. So, we propose that *Propachyrucos aequilatus* be considered a *nomen dubium*.

Regarding *Propachyrucos crassus*, previously synonymized with *Prohegetotherium sculptum* (Reguero, 1999; Reguero and Cerdeño, 2005), we agree with Kramarz and Bond (2017) in considering it a valid species of an uncertain genus. Differences with *Propachyrucos smithwoodwardi* and *Prosotherium garzoni* allow excluding it from these genera. The need for a complete revision of the materials assigned to *Prohegetotherium sculptum* leaves open the precise taxonomic determination of *Pr. crassus*.

With respect to the Miocene species assigned to *Propachyrucos* by Roth (1899), *Pr. depressus* is recognized as *Pachyrukhos* sp.; *Pr. medianus* is larger than *Pachyrukhos moyani* and could be the same taxon as *Pachyrukhos* sp. 1 from the Collón Curá Formation described by Seoane and Cerdeño (2019); *Pr. robustus* is rejected from belonging to *Propachyrucos* or *Pachyrukhos*, presenting some similarities with *Hegetotherium*, but it is considered here as a *nomen dubium*.

The unpublished materials labelled as *Propachyrucos* sp. in the MLP collection, from El Pajarito (Chubut Province), the Collón Curá Formation (MLP 12-2889a; Neuquén Province), and Laguna de La Bombilla (MLP 59-II-26-91; Chubut Province), are mostly recognized here as belonging to *Pachyrukhos*. The specimen MLP 61-IV-11-146 from El Pajarito is removed from Hegetotheriidae and recognized as Interatheriidae. The assignment of MLP 59-II-26-91 to *Pachyrukhos* indicates an early Miocene age for the fossil-bearing deposits at Laguna La Bombilla.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://doi.dx.org/10.1016/j.crpv.2019.07.001.

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