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Systematics and stratigraphical range of the hegetotheriids *Hegetotheriopsis sulcatus* and *Prohegetotherium sculptum* (Mammalia: Notoungulata)

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Hegetotheriidae is one of the most advanced clades within the endemic South American placental Order Notoungulata. The species *Hegetotheriopsis sulcatus* Kramarz & Paz, 2013 differs from all other known hegetotheriids in having a peculiar combination of cranial and dental features, some of them shared with Archaeohyracidae (sister group of Hegetotheriidae). A previous cladistic analysis supported *H. sulcatus* as the earliest diverging hegetotheriid. Nevertheless, a more recent analysis, based on a different data matrix, concluded that this species is an advanced form within the family, with the little-known *Prohegetotherium sculptum* Ameghino, 1897 (late Oligocene) being the most basal taxon. Here we present a revision of the concept and the content of *P. sculptum* based on a re-examination of the type specimens. We find that this material exhibits several dental and cranial characters not recognized in all previous studies; we conclude that no specimen other than the types can be assigned to *P. sculptum*, and that all the synonymies previously proposed (i.e. *P. shumwayi* and *P. crassus*) are unfounded. A new cladistic analysis, combining characters from the two aforementioned analyses, confirms the position of *H. sulcatus* as the earliest diverging hegetotheriid. The taxon was originally described based on remains from early Miocene deposits in central and northern Patagonia (Sarmiento, Chichinales and Cerro Bandera formations). Here we report new material from the late Oligocene of Cabeza Blanca (central Patagonia), and reassign other material previously attributed to *Prohegetotherium* from presumably equivalent levels at Quebrada Fiera (central West Argentina). These remains extend the occurrence of *H. sulcatus* back to the late Oligocene, and fill an important gap of the early record of Hegetotheriidae.

Keywords: Notoungulata; Hegetotheriidae; Miocene; Oligocene; Argentina; systematics

Introduction

Hegetotheriidae represents a very advanced group within the Order Notoungulata, the most diverse clade of endemic South American ungulates. This group was already diverse in the late Oligocene (Deseadan South American Land Mammal Age, SALMA), and they remained conspicuous components of terrestrial mammalian assemblages up to the Pleistocene (Loomis 1914; Cerdeño & Bond 1998). The hegetotheriids were small- to medium-sized animals, some having a gliriform appearance, with enlarged incisors and hypselodont cheek teeth. Currently, 11 nominal genera are recognized, grouped within two subfamilies – Hegetotheriinae Ameghino, 1894 and Pachyrukhinae Kraglievich, 1934 – although the monophyly of the former is still under debate (Croft & Anaya 2006; Billet *et al*. 2009; Reguero & Prevosti 2010; Kramarz & Paz 2013; Cerdeño & Reguero 2015).

The hegetotheriid species *Hegetotheriopsis sulcatus* was described by Kramarz & Paz (2013) based on a skull fragment and partial mandibles with dentition derived from early Miocene (Colhuehuapian SALMA) deposits of the Sarmiento Formation exposed at Bryn Gwyn, in central Patagonia, Argentina (Fig. 1). This species exhibits a unique combination of cranial and dental characters, some of them previously known for the Archaeohyracidae notoungulates (sister group of Hegetotheriidae), and others that typify the Hegetotheriidae. Based on a set of characters selected by Billet *et al*. (2009), Kramarz & Paz (2013) concluded that *H. sulcatus* is the earliest diverging hegetotheriid so far known.

More recently, Cerdeño & Reguero (2015) performed a new cladistic analysis of Hegetotheriidae based on the data matrix of Croft & Anaya (2006), and concluded that *H. sulcatus* is closely related to the species of the late-diverging *Hemihegetotherium* Rovereto, 1914 (middle–late Miocene), and that the Oligocene species
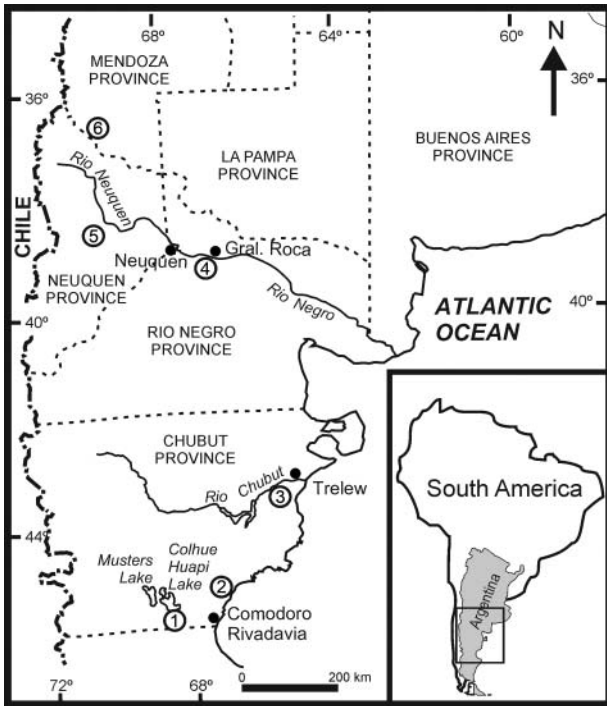

Figure 1. Location map showing the fossil localities mentioned in the text: 1, Gran Barranca of Colhue Huapi Lake (Colhue Huapi Member of the Sarmiento Formation); 2, Cabeza Blanca (Sarmiento Formation); 3, Bryn Gwyn, southern cliffs of Río Chubut (Trelew member of the Sarmiento Formation); 4, Paso Córdoba (Chichinales Formation); 5, Barda Negra (Cerro Bandera Formation); 6, Quebrada Fiera (Agua de la Piedra Formation).

Prohegetotherium sculptum Ameghino, 1897 occupies the most basal position among hegetotheriids. The latter, type species of the genus, is based on rather fragmentary materials whose diagnostic characters were not re-examined exhaustively. Despite the poor knowledge of this species, many specialists working on hegetotheriid systematics have proposed synonymies, referred new and more complete specimens, and transferred other species to the genus *Prohegetotherium* (e.g. Loomis 1914; Chaffee 1952; Reguero 1999; Reguero & Cerdeño 2005; Cerdeño & Reguero 2015).

The aim of this contribution is to revise the phylogenetic affinities of *Hemihegetotherium sulcatus*. This revision involves a review of the concept and content of *Prohegetotherium sculptum*. Additionally, we report new materials attributable to *H. sulcatus*, and propose a taxonomic re-assignment of some late Oligocene hegetotheriid material, leading to a reassessment of the stratigraphical and chronological distribution of this species.

Institutional abbreviations
AMNH: American Museum of Natural History, New York, USA; **FMNH**: Field Museum of Natural History,

Chicago, USA; **MACN**: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Ciudad Autónoma de Buenos Aires, Argentina; **MCNAM-PV**: Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano', Vertebrate Paleontology Collection, Mendoza, Argentina; **MLP**: Museo de La Plata, La Plata, Buenos Aires, Argentina; **MOZ-PV**: Colección de Paleovertebrados, Museo Provincial de Ciencias Naturales 'Dr. Prof. Juan A. Olsacher', Zapala, Neuquén, Argentina.

Anatomical abbreviations
C/c, upper/lower canine; **P/p**, upper/lower premolar; **M/m**, upper/lower molar.

Systematic palaeontology

Order **Notoungulata** Roth, 1903
Family **Hegetotheriidae** Ameghino, 1894
Genus *Prohegetotherium* Ameghino, 1897

Type species. *Prohegetotherium sculptum* Ameghino, 1897.

Included species. The type species and *P. novum* (Bordas, 1939).

Distribution. Late Oligocene–early Miocene; central Patagonia and west central Argentina.

Prohegetotherium sculptum Ameghino, 1897
(Fig. 2A–D)

Material. Lectotype: MACN A 52-443, left maxillary fragment with the alveolus for the canine and P1–P3 (Fig. 2A, B). Paralectotype: MACN A 52-444, left portion of maxillary with incomplete P3–M3, and part of nasals and frontals (Fig. 2C, D).

Revised diagnosis. Upper canine not reduced and implanted anterolabial to the P1, as in *Hemihegetotherium*. P1 not much reduced, being nearly 33% smaller than P2, subtriangular in cross section with a very pronounced parastylar projection. Well-developed parastylar sulcus on P1 and P2. Crest on the maxillary extending lateral to the infraorbital foramen.

Description. The maxillary MACN A 52-443 (lectotype) (Fig. 2A, B) preserves three prismatic, hypselodont cheek teeth and an alveolus in front of the mesialmost tooth. The preserved anterior margin of the maxillary immediately in front of the alveolus corresponds to the suture with the premaxillary (Fig. 2B). Therefore, the alveolus belongs to the canine. The alveolus is somewhat triangular in outline, longer labially than lingually and wider mesially than distally. The alveolus for the canine is placed anterolabial to the P1, so that the distal half overlaps the anterolabial
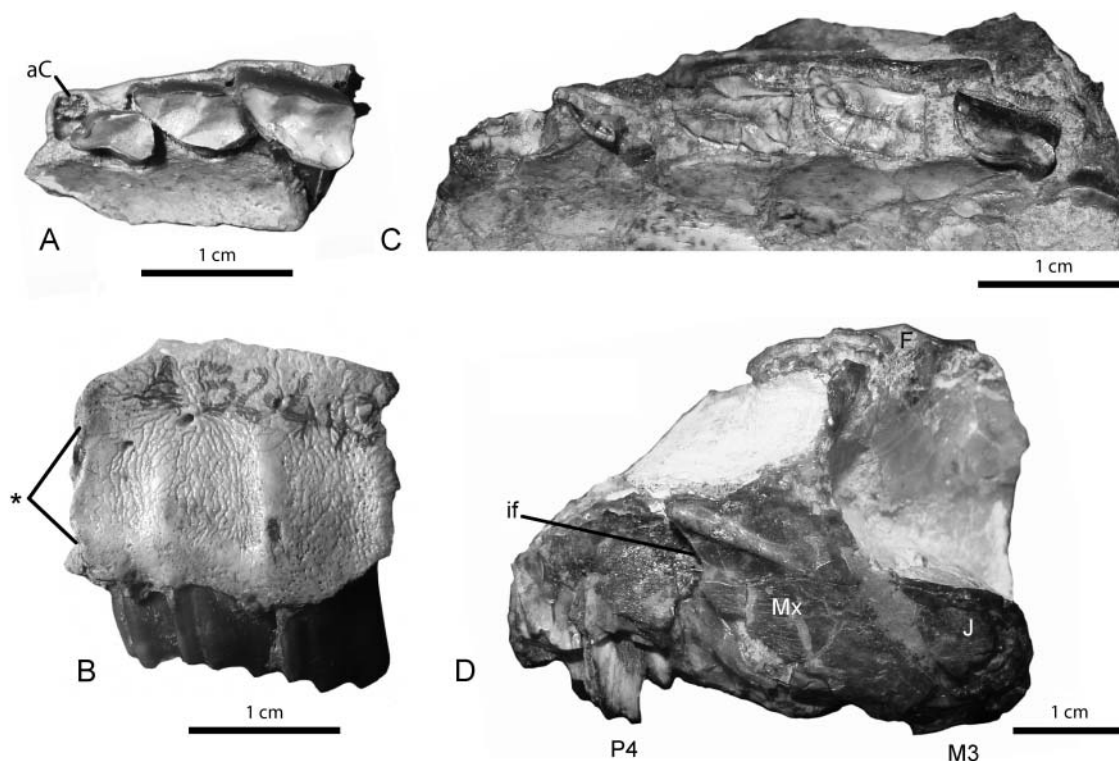
Figure 2. Type specimens of *Prohegetotherium sculptum* Ameghino, 1897. **A, B,** MACN A 52-443 (lectotype), left maxillary fragment with the alveolus for the canine and P1–P3; **A,** occlusal view; **B,** lateral view. **C, D,** MACN A 52-444 (paralectotype), left maxillary with P3–M3; **C,** palatal view; **D,** lateral view. Abbreviations: aC, alveolus for the upper canine; F, frontal; if, infraortbital foramen; Mx, maxillary; *, contact with the premaxillary.

portion of the premolar. The P1 is subtriangular in cross section, is longer labially than lingually, and bears a conspicuous parastylar lobe projecting mesially (instead of mesiolabially). The mesiolingual face is strongly concave. A well-marked parastylar sulcus demarcates the parastylar lobe from the labial wall of the tooth. The P2 is almost 50% larger than the P1 (see Supplemental Appendix 1). The crown is widest distally and tapers mesially to a pointed parastylar lobe, projected mesiolabially. The parastylar sulcus is much more moderate than in P1, and the mesiolingual face is convex. The P3 is as the P2, but slightly wider distally, with less-pointed parastylar lobe and less-pronounced parastylar sulcus.

MACN A 52-444 (paralectotype) preserves part of the P3–M3 series (Fig. 2C). Except in the M3, the apical portion of the crowns is eroded, as well as the bony alveolar borders, and thus irregular cross sections of the teeth are preserved. The P3 and P4 are very badly preserved; at least the P4 seems to be similar to the molars but proportionally shorter (mesiodistally) (Supplemental Appendix 1). The M1 and M2 are roughly trapezoidal, longer than wide, with the mesial wall forming a continuous curve with the lingual wall. The distal wall is transverse. The parastylar sulcus is inconspicuous. The labial wall bears a slight undulation. The deep furrow on the external wall mentioned by Loomis (1914) is nonexistent.

The M3 is smaller than the M2 (Supplemental Appendix 1), the parastylar region is less prominent, and the labial undulation is more marked. The lingual wall has a superficial sulcus, and the distal wall is slightly notched.

In both the lectotype and the paralectotype, all the teeth have a thin layer of cement (width *c*. 6% of the maximum width of M1) on the lingual wall and on the lingual portion of the mesial wall. The layer of cement on the lingual wall of the M3 of the paralectotype is somewhat broader than in the other teeth, but in all cases the layer is thinner than the enamel on the same portion of the tooth.

The nature of the 'reptile-like' sculptures on the maxillaries, the frontals and the nasals is controversial. The grooves forming this sculpture are mainly organized radially from a set of tiny vascular foramina, especially in the lectotype (Fig. 2B). In some specimens of *Hegetotherium* (e.g. MACN A 631), the rostral portion of the maxillaries shows a similar arrangement of vascular grooves in front of the infraorbital foramen, but much more superficial than in *P. sculptum*. Therefore, the sculptures could be the result of a natural condition accentuated by weathering and/or other taphonomic factors, as proposed by Loomis (1914), and would have no diagnostic value. Another remarkable feature preserved in the paralectotype is the presence of a sharp crest on the maxillary, anterior to the orbital margin (Fig. 2D). This crest projects anteriorly,

beyond the posterior (lateral) border of the infraorbital foramen, and forms a laminar extension that partially conceals the foramen in lateral view. No hegetotheriine has a comparable structure. However, it strongly resembles the spine-like anterior projection of the maxillary, lateral to the infraorbital foramen, which characterizes pachyrukhine hegetotheriids (see Billet 2011).

In sum, the most distinct features of the dentition of the types of *P. sculptum* are those of the premolars and the unusual location of the alveolus for the canine. The molars, in contrast, show no particular differences with those of other hegetotherines such as *Hegetotherium mirabile*, *Sallatherium altiplanense* and '*Prohegetotherium*' *schiaffinoi*. The differential features of the cheek teeth and of the preserved parts of the skull lead us to propose the revised diagnosis for *P. sculptum* given above.

Remarks. Florentino Ameghino erected this species in 1897 based on the two syntypes indicated above, probably from the Deseadan locality Cabeza Blanca in central Patagonia (Fig. 1). Ameghino did not provide a detailed description, but remarked that in this species the upper premolars have an anterolabial sulcus (parastylar sulcus in the current dental terminology) and a well-developed canine, unlike in the better known genus *Hegetotherium* (Early Miocene). Ameghino did not refer lower teeth to *P. sculptum*. He also remarked on the presence of a conspicuous sculpture on the preserved bones (Fig. 2B; see also Ameghino 1897, fig. 10), that he compared with some reptiles. This feature obviously inspired the specific epithet.

Loomis (1914) wrote that *Prohegetotherium sculptum* is characterized by the presence of a deep external furrow on the upper molars, and interpreted the sculpture of the cranial bones as a result of weathering. He also erected the species *P. shumwayi*, smaller than *P. sculptum*, based on a right maxillary fragment with four cheek teeth (see Loomis 1914, fig. 29), interpreted as P2–M1, from Cabeza Blanca.

Chaffee (1952) assigned to *Prohegetotherium sculptum* a mandible with complete dentition (AMNH 29605, from the Deseadan Scarrit Pocket locality in central Patagonia), essentially because, unlike in *Hegetotherium*, the lower canine is not reduced, in concordance with the condition mentioned by Ameghino (1897) in the upper canine of the syntype.

MacFadden *et al.* (1985) referred to *Prohegetotherium* all the specimens of Hegetotheriidae from the late Oligocene locality Salla in Bolivia. These specimens represent two species, the larger close in size to *P. sculptum*.

Reguero & Cerdeño (2005) formally designated MACN A 52-443 as the lectotype of *Prohegetotherium sculptum*, and MACN A 52-444 as the paralectotype. They stated that the former preserves the alveolus for the canine, P1–P3, and the latter preserves P3–M2. They proposed a formal diagnosis for the genus *Prohegetotherium*, and a revised diagnosis for *P. sculptum*, the latter based entirely on characters not preserved in the syntypes. These authors interpreted the sculpture on the cranial bones of the syntypes as not being diagnostic features, following Loomis (1914). They synonymized *P. sculptum* with *P. shumwayi* and with *Propachyrucos crassus* Ameghino, 1897 (based on partial mandibles). Additionally, they referred to *P. sculptum* several specimens with upper and/or lower dentition, besides the mandible AMNH 29605 described by Chaffee (1952). All the referred specimens came from the Deseadan of central Patagonia, except for one from Quebrada Fiera (Mendoza Province, western Argentina; Fig. 1). Moreover, Reguero & Cerdeño (2005) transferred *Propachyrucos*? *schiaffinoi* Kraglievich, 1932 (from Uruguay) to *Prohegetotherium* (as a senior synonym of *Ethegotherium carettei* (Minoprio, 1947)), and assigned all the Bolivian specimens to this species or to a new genus, *Sallatherium*.

Cerdeño *et al*. (2010) reassigned to the archaeohyracid *Archaeohyrax suniensis* the only Quebrada Fiera specimen listed as *Prohegetotherium sculptum* by Reguero & Cerdeño (2005).

More recently, Cerdeño & Reguero (2015, fig. 2E) figured the lectotype of *Prohegetotherium sculptum* (MACN A 52-443) as preserving P2–P4, contrary to all previous statements and without justification. They figured the paralectotype as preserving P3–M3, but in the table of measurements they also included the size of a nonexistent P2. They erected a new species of *Prohegetotherium*, *P. malalhuense*, from Quebrada Fiera, and identified as *Prohegetotherium* cf. *sculptum* four isolated cheek teeth from the same locality.

Material identifiable as *Prohegetotherium sculptum*. The only dental element shared by the two syntypes is the P3. In the paralectotype, this tooth is badly preserved, but at least the preserved occlusal outline and the size of the preserved part of the crown (Supplemental Appendix 1) do not differ significantly from the P3 of the lectotype, thus supporting the conspecificity of the syntypes.

The most conspicuous dental feature preserved in the lectotype of *Prohegetotherium sculptum* is the location of the alveolus for the canine, labial to and partially overlapping the parastylar region of the P1. This condition strongly resembles that observed in species of *Hemihegetotherium* (Rovereto 1914; Croft & Anaya 2006) and in the holotype of '*Hegetotherium*' *novum* Bordas, 1939 (early Miocene), but is absent in all the remaining known hegetotheriids, including the specimens referred to *P. sculptum* by Reguero & Cerdeño (2005) preserving the upper canine (or its alveolus).

Prohegetotherium shumwayi Loomis, 1914 was interpreted as junior synonym of *P. sculptum* by Reguero & Cerdeño (2005). We have not examined the type and only known specimen at hand, but according to the figure and the dental measurements given by Loomis (1914), the P3 is nearly 18% shorter and 30% narrower than in the

lectotype of *P. sculptum* (see Supplemental Appendix 1), and the P2–P3 length is 33% shorter. Similarly, the M1 is 20% shorter and 36% narrower than in the paralectotype of *P. sculptum* (Supplemental Appendix 1). These quantitative differences are similar to or even larger than differences between *P. sculptum* and *P. schiaffinoi* and among species of *Hemihegetotherium* (Croft & Anaya 2006). Moreover, the P2 and P3 are more trapezoidal in occlusal outline than in *P. sculptum*. Consequently, there is no good evidence supporting the synonymy proposed by Reguero & Cerdeño (2005).

Cerdeño & Reguero (2015, fig. 2A–D) described as *Prohegetotherium* cf. *sculptum* three isolated upper premolars from Quebrada Fiera. These teeth have a less prominent parastylar lobe and much less marked parastylar sulcus than in the lectotype. The teeth interpreted as P3 are shorter and wider than the P3 of the lectotype; the one interpreted as a probable P4 is larger than the P4 of the paralectotype (Supplemental Appendix 1). The taxonomic position of these specimens is uncertain, but they are unlikely to be conspecific with the types of *P. sculptum*.

Concerning the lower dentition, a labial displacement of the p1 is expected to be associated with a labial displacement of the upper canine observed in the lectotype of *P. sculptum* (Fig. 2A), as this occurs in species of *Hemihegetotherium*. However, no specimen preserving the lower dentition that has been referred to *P. sculptum* in previous works shows this feature. The Mandible AMNH 29605, referred to *P. sculptum* by Chaffee (1952, pl. 16, figs 2, 3) has the canine and the p1 in line with the tooth row. Interestingly, in the three syntypes of *Propachyrucos crassus* (MACN A 52-448, 52-449 and 52-450), considered a synonym of *P. sculptum* by Reguero & Cerdeño (2005), the p1 (or its alveolus) is set lingual to the subsequent lower teeth (see Fig. 3), contrary to what is seen in *Hemihegetotherium*. Therefore, *P. crassus* is unlikely to represent the lower dentition of *P. sculptum*. Alternatively, the types of *P. crassus* and *P. sculptum* could represent the lower and upper dentition of the same species, in which the occlusal relationship between C1 and p1 is unique among hegetotheriids, and probably among notoungulates. Consequently, we prefer provisionally to

Figure 3. *Propachyrucos crassus* Ameghino, 1897, MACN A 52-448 (syntype), right mandibular fragment with p1–p3, in occlusal view. Note the position of the p1, implanted in the dentary lingual to the p2.

keep *P. crassus* as a separate species of uncertain generic position. Therefore, we conclude that all the specimens referred to *P. sculptum* in previous studies are either not conspecific with the type specimens or cannot be confidently assigned to this species.

Distribution. According to the taxonomic conclusions reached above, *Prohegetotherium sculptum* is only known from the Deseadan levels of the Sarmiento Formation exposed at the Cabeza Blanca locality in Chubut Province, central Patagonia.

<div style="text-align:center">

Genus *Hegetotheriopsis* Kramarz & Paz, 2013
Hegetotheriopsis sulcatus Kramarz & Paz, 2013
(Fig. 4A–C)

</div>

2015 *Prohegetotherium* sp. Cerdeño & Reguero: 676.

Material. Holotype: MACN Pv CH2015, left portion of rostrum and palate with P1–M3. Newly referred material: MCNAM-PV 3984, isolated left M1 or M2, MCNAM-PV 4620, isolated right m3, late Oligocene (Deseadan SALMA), Agua de la Piedra Formation, Quebrada Fiera, Mendoza Province; MACN PV CH2137, right mandibular fragment with p2–p4, late Oligocene (Deseadan SALMA), Sarmiento Formation, Cabeza Blanca, Chubut Province. See Kramarz & Paz (2013) for previously referred material.

Remarks. Cerdeño & Reguero (2015) described the isolated M1 or M2 MCNAM-PV 3984 as *Prohegetotherium* sp. and compared it with '*P*'. *schiaffinoi* and indirectly with *P. sculptum*. We find that this tooth (Fig. 4A) agrees with *Hegetotheriopsis sulcatus* but differs from *Prohegetotherium* and from all other hegetotheriids by having a very conspicuous vertical sulcus on the lingual wall. The parastyle points more labially than in the holotype of *P. sulcatus*, but similar to some referred specimens (e.g. MOZ-PV-1036) from the Cerro Bandera Formation in Neuquén Province (Kramarz & Paz 2013). The size is somewhat larger (15–20%) than in the M1 and M2 of *P. sculptum* and *H. sulcatus* (Supplemental Appendix 1), and much larger than in *Sallatherium altiplanense* and other species referred to *Prohegetotherium* by Cerdeño & Reguero (2015).

Cerdeño & Reguero (2015) admitted that the isolated m3 MCNAM-PV 4620 is similar to the m3 of *Hegetotheriopsis sulcatus*, except by being slightly larger, but referred it tentatively to *Prohegetotherium* without further comparisons. In fact, this tooth (Fig. 4B) compares well with the only known m3 of *H. sulcatus* (MACN Pv CH2014; Kramarz & Paz 2013, fig. 3). It is nearly 20% longer and 14% wider than in *H. sulcatus*, but is similarly larger than the m3 of all the specimens referred to *P. sculptum* by Reguero & Cerdeño (2005) (see Supplemental Appendix 1), and even much larger than the m3 of

Figure 4. *Hegetotheriopsis sulcatus* Kramarz & Paz, 2013, late Oligocene; occlusal views. **A,** MCNAM-PV 3984, isolated M1 or M2 from Quebrada Fiera (Mendoza Province); **B,** MCNAM-PV 4620, isolated m3 from Quebrada Fiera (Mendoza Province); **C,** MACN PV CH2137, right mandibular fragment with p2–p4 from Cabeza Blanca (Chubut Province).

all the specimens referred to other species of *Prohegetotherium* by Cerdeño & Reguero (2015, table 2). Here, we tentatively refer this tooth to *H. sulcatus*.

The cheek teeth of the mandibular fragment MACN PV CH2137 from Cabeza Blanca (Fig. 4C) show no particular differences in size (Supplemental Appendix 1) and morphology from those of the specimens referred to *Hegetotheriopsis sulcatus* by Kramarz & Paz (2013).

Phylogenetic relationships

Prohegetotherium sculptum was traditionally interpreted as ancestral to *Hegetotherium* and to more advanced hegetotheriines (Loomis 1914; Simpson *et al*. 1962). Croft & Anaya (2006) performed the first cladistic analysis of Hegetotheriidae, but they analysed *Prohegetotherium* at the generic level, based on specimens from Salla currently assigned to '*P*'. *schiaffinoi* (Reguero & Cerdeño 2005). Billet *et al*. (2009) also analysed '*P*'. *schiaffinoi* as representing the genus *Prohegetotherium*. Reguero & Prevosti (2010) analysed *P. sculptum* separately from '*P*'. *schiaffinoi*, concluding that both are basal hegetotheriids.

The phylogenetic position of *Hegetotheriopsis sulcatus* was previously examined by Kramarz & Paz (2013) using a data matrix developed by Billet *et al*. (2009). This matrix was compiled for analysing the relationships among archaeohyracid, hegetotheriid and mesotheriid notoungulates. It included 39 dental and cranial characters scored in 17 ingroup taxa, of which nine terminal taxa were hegetotheriid species, genera or groups of genera. Kramarz & Paz (2013) concluded that *H. sulcatus* represents the earliest diverging hegetotheriid. Its exclusion from the clade including all the remaining hegetotheriids analysed was supported by the presence of a lingual sulcus on the upper molars and the absence of a zygomatic plate of the maxillary, which are plesiomorphies shared with the archaeohyracids. Kramarz & Paz (2013) also included *Prohegetotherium sculptum* in the analysis, represented only by the type specimens and mandible AMNH 29605 described by Chaffee (1952). This taxon was nested within the clade including the hegetotheriine hegetotheres, close to the Deseadan taxa *Sallatherium* and '*P*'. *schiaffinoi*.

Both *Prohegetotherium sculptum* and *Hegetotheriopsis sulcatus* were also included in a phylogenetic analysis recently performed by Cerdeño & Reguero (2015). This analysis was based on a data matrix modified from that of Croft & Anaya (2006), specifically intended for the study of hegetotheriid phylogeny. The resulting data matrix included 25 dental (upper and lower), cranial and postcranial characters scored in 14 ingroup taxa (mostly at the species level). Cerdeño & Reguero (2015) scored all of the 25 characters for *P. sculptum* (i.e. without missing data). The authors did not provide a list of examined specimens for the analysis, but it is clear that they scored most of the characters in *P. sculptum* using specimens referred to this species in previous studies, in addition to the syntypes. Their results supported *P. sculptum* as the most basal taxon among the Hegetotheriidae, whereas *H. sulcatus* was deeply nested higher in the tree, close to the advanced hegetotheriine *Hemihegetotherium*.

Here, we performed a new cladistic analysis based on the data matrix of Croft & Anaya (2006) extended by Cerdeño & Reguero (2015), with the addition of nine characters selected from the data matrix of Billet *et al*. (2009) that are potentially informative for Hegetotheriidae phylogeny. We also included the early Miocene '*Hegetotherium*' *novum*, interpreted as one of the earliest diverging hegetotheriids (Kramarz & Paz 2013). The genus *Hegetotherium* is represented by *H. mirabile*, the type and best-known species from the late early Miocene Santacrucian fauna (Sinclair 1909). Other species described from middle Miocene deposits (e.g. *H. andinum* Roth, 1899, *H. cerdasensis* Croft *et al*., 2016) were not considered as our analysis does not focus on the intrageneric relationships of geologically younger taxa.

The resulting matrix has 15 ingroup taxa and 34 characters (Supplemental Appendices 2 and 3). All multistate characters were treated as unordered. The scorings of some taxa were modified from previous analyses as discussed below.

In *Prohegetotherium sculptum*, all characters were rescored based exclusively on the type specimens. Consequently, the characters of the upper incisors (characters 1 and 5), lower dentition (characters 12–14, 22 and 23), postcranium and some cranial characters (characters 15–21) were re-scored as missing data.

In *Medistylus dorsatus*, character 21 was re-scored as missing data following Reguero & Prevosti (2010, character 68).

In '*Prohegetotherium*' *schiaffinoi*, character 20 was re-scored with state 1 following Billet *et al*. (2009, character 38).

Character 0 (width of the cement layer): Kramarz & Paz (2013) described the cheek teeth of *Hegetotheriopsis sulcatus* as having a thin layer of cement. Nevertheless, Cerdeño & Reguero (2015), who did not examine the specimens, scored *Hegetotheriopsis* as having thick cement (state 1), as in the species of *Hemihegetotherium*. A re-examination of the cheek teeth of *H. sulcatus* revealed that the width of the cement is nearly 4% of the maximum width of M1. This width is less than in other taxa scored by Cerdeño & Reguero (2015) as having thin cement (e.g. approximately 6% in *P. sculptum*, 5% in *Hegetotherium mirabile*), and much thinner than in other taxa scored as with broad cement (e.g. 10–11% in *Paedotherium*, 12% in *Hemihegetotherium*). Therefore, we re-scored *Hegetotheriopsis sulcatus* with state 0.

Character 4: This character was originally intended to capture the condition in species of *Hemihegetotherium* in which the C1 and p1 are placed labial to P1 and p2, respectively. Croft & Anaya (2006), followed by Reguero & Prevosti (2010) and Cerdeño & Reguero (2015), incorrectly gave state 1 of this character as 'root of C lingual to P1 and p1 lingual to p2'. Here we corrected the definition of state 1, replacing 'lingual' with 'labial'. *Prohegetotherium sculptum* is here re-scored with state 1, as in the species of *Hemihegetotherium*.

Character 6: Cerdeño & Reguero (2015) scored *Prohegetotherium sculptum* as having P2 less than 75% of the length of P3. According to our measurements taken on the lectotype of *P. sculptum*, the length of the P2 is nearly 94% the length of the P3 (see Supplemental Appendix 1), and the taxon is re-scored with state 0.

Character 7: Cerdeño & Reguero (2015) defined a new state of this character to capture the condition of *Hegetotheriopsis* (lingual groove shallow on upper molars). A similar condition is present in moderately worn molars of *Archaeohyrax* (after the central fossette isolation), and thus it is re-scored with the same state as *Hegetotheriopsis*.

The parsimony analysis was performed using the computer program TNT 1.1 (Goloboff *et al.* 2008). The character analysis was conducted assuming equal weights, by heuristic searches with tree bisection reconnection (TBR) using 1000 random-addition sequences and saving 10 trees per round. The analysis resulted in seven most-parsimonious trees (MPT) of 66 steps with a consistency index (CI) of 0.65, and a retention index (RI) of 0.76. The strict consensus tree is shown in Figure 5. The results do not resolve satisfactorily the relationships among the hegetotheriids, except for the position of *Hegetotheriopsis*

sulcatus, which represents the most basal member of Hegetotheriidae in all the MPTs, in agreement with the results of Kramarz & Paz (2013). *Hegetotheriopsis sulcatus* is excluded from the clade including all the remaining hegetotheriids by having upper molars with shallow lingual groove (character 7), a plesiomorphy shared with *Archaeohyrax*. The results also indicate that none of the species previously attributed to *Prohegetotherium* (e.g. '*P*'. *schiaffinoi* and '*P*'. *malalhuense*) group with the type species *P. sculptum*. On the contrary, in all the MPTs produced by our analysis, the Quebrada Fiera species '*P*'. *malalhuense* clusters with *Hegetotherium mirabile*, as in the analysis of Cerdeño & Reguero (2015). Consequently, the genus *Prohegetotherium* as currently conceived is not monophyletic, corroborating the conclusions of Billet *et al*. (2009), Kramarz & Paz (2013) and Cerdeño & Reguero (2015). Interestingly, the only species that groups with *P. sculptum* in all the obtained MPTs is '*Hegetotherium*' *novum*. In the strict consensus tree, this grouping is supported by the shared presence of C1 labial to P1 (character 4) and ectoloph of M1 forming an angle grater than 90° with the distal wall (Character 8). The clade *H. achataleptum* + *H. trilobus* and the monophyletic Pachyrukhinae are also recovered in all the MPTs, which essentially agrees with the results of previous analyses (Croft & Anaya 2006; Reguero & Prevosti 2010; Cerdeño & Reguero 2015). All the nodes have low support, except those grouping the Pachyrukhinae taxa.

Discussion

The hegetotheriid *Hegetotheriopsis sulcatus* was described based on specimens from the Trelew Member of the Sarmiento Formation exposed at Bryn Gwyn in Chubut Province (Kramarz & Paz 2013), from the lower section of the Chichinales Formation at Paso Córdoba in Río Negro Province, and from the lower levels of the Cerro Bandera Formation on the north-east slope of the Barda Negra in Neuquen Province, Argentina (see Fig. 1). There are as yet no absolute ages for these horizons. According to the mammal association, the Trelew Member and the Chichinales Formation are equivalent to the Lower Fossil Zone of the Colhue Huapi Member of the Sarmiento Formation at the Gran Barranca of Colhue Huapi Lake, type section of the Colhuehuapian Land Mammal Age, dated at 21.1–20.1 Ma (Dunn *et al*. 2013). The Cerro Bandera Formation was originally assigned to the Colhuehuapian Age too (Kramarz *et al*. 2005), but the most recent discovery of some Deseadan taxa combined with the occurrence of typical Colhuehuapian taxa suggests a somewhat older, as yet undetermined age (Kramarz *et al*. 2011).

The re-examination of hegetotheriid specimens from Quebrada Fiera revealed that at least two isolated cheek
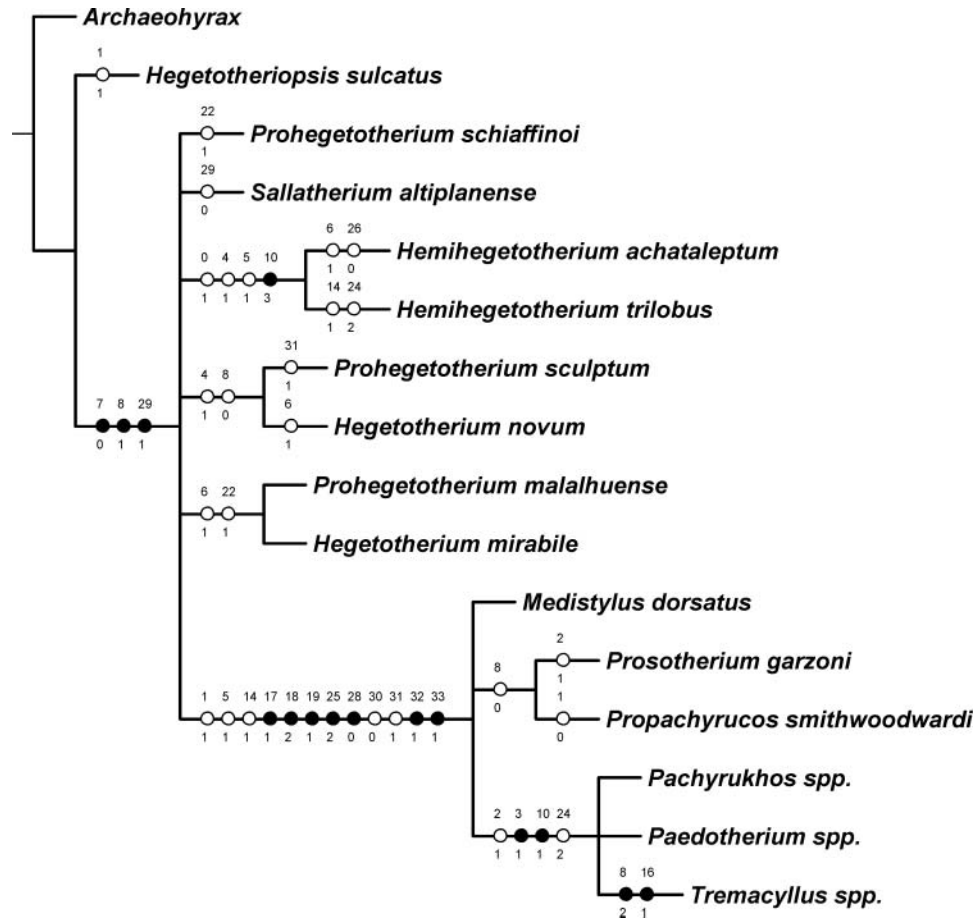
Figure 5. Strict consensus tree from seven most-parsimonious trees of 66 steps (CI = 0.65, RI = 0.77) obtained from the parsimony analysis employing 34 characters coded for 14 hegetotheriid taxa (using *Archaeohyrax* as the outgroup). Numbers above/below the nodes are characters/character states listed in Supplemental Appendix 2. The data matrix is given in Supplemental Appendix 3. Characters indicated with black circles are synapomorphies; characters indicated with white circles are homoplasies.

teeth (MCNAM-PV 3984 and 4620) described by Cerdeño & Reguero (2015) as belonging to *Prohegetotherium* are more properly attributable to *Hegetotheriopsis*. Similarly, the teeth of the mandibular fragment MACN PV CH2137 from the Deseadan levels of the Sarmiento Formation at Cabeza Blanca perfectly matches the lower dentition of *H. sulcatus*. Both the Quebrada Fiera and Cabeza Blanca fossil-bearing levels belong to the Deseadan Land Mammal Age, spanning from 29.4 to 24.2 Ma (Dunn *et al*. 2013). Therefore, these new taxonomic identifications extend the known distribution of *Hegetotheriopsis* back to the late Oligocene.

A re-study of the type specimens of *Prohegetotherium sculptum* leads to the identification of differential characters, especially the labial position of the C1 with respect to P1 and the distinct development of the parastylar lobe and of the parastylar sulcus on the anterior premolars. Based on these features, it is concluded that all of the specimens referred to *P. sculptum* in previous studies (e.g. Reguero & Cerdeño 2005; Cerdeño & Reguero 2015) are either not conspecific with the type specimens or cannot

be confidently assigned to this species. Consequently, *P. sculptum* is currently known only from the syntypes, and its proposed synonymy with *P. shumwayi* and *P. crassus* is rejected.

A cladistic analysis of the Hegetotheriidae, using a new data matrix combining those of Croft & Anaya (2006) and Billet *et al*. (2009), supports the position of *H. sulcatus* as the most basal member of this clade, as previously proposed by Kramarz & Paz (2013). This result does not resolve the relationships among most of the analysed hegetotheriids but suggests that some taxonomic rearrangements are required. As in previous analyses, our results do not support the referral of the Deseadan species '*P*'. *schiaffinoi* and '*P*'. *malalhuense* to *Prohegetotherium*. The most proper generic placement of '*P*'. *malalhuense* would be within *Hegetotherium*; a suitable systematic location of '*P*'. *schiaffinoi* requires additional evidence but it definitively does not belong to *Prohegetotherium*. The only hegetotheriid unambiguously allied to *P. sculptum* is the Colhuehuapian '*H*'. *novum*, thus suggesting that this species should be formally transferred to *Prohegetotherium*.

Croft & Anaya ([2006]) highlighted the existence of important temporal gaps within the record of Hegetotheriidae. Kramarz & Paz ([2013]), who described *Hegetotheriopsis sulcatus* exclusively from Colhuehuapian beds, noted that the basal position of this taxon with respect to all the Deseadan hegetotheriids introduced an additional hiatus of at least 4 myr. The new remains studied here document the Deseadan occurrence of *H. sulcatus*, and therefore they fill one of the main hiatuses in the fossil record of Hegetotheriidae.

Acknowledgements

Supplemental material

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