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A singular Hegetotheriinae (Notoungulata, Typotheria) from the late Oligocene-Early Miocene of the Subandean Region of Bolivia

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Abstract

Geological studies in the northern sector of the Chaco foreland Basin, Bolivia, yielded new fossils coming from late Oligocene-late Miocene of the Petaca Formation. Few fossil mammals were known from the Subandean Region of Bolivia. We report a partially complete mandible of a hegetotheriid Hegetotheriinae (Notoungulata, Typotheria) from Abapó (Río Grande River). The specimen (YPFB-LIT-PAL-005) is very close in size and dental morphology to the late Oligocene (Deseadan South American Land Mammal Age, SALMA) — Santacrucian (early Miocene) *Prohegetotherium schiaffinoi* (Kraglievich 1932) from Fray Bentos (Uruguay and Argentina), Salla (Bolivia), Divisadero Largo-Potrerillos and Quebrada Fiera (Argentina). However, mandibular characteristics, as the shape with a marked change in height along its length, increasing towards the back, a prominent masseteric crest, a deep mandibular groove, and a remarkable thickening of the ventral rim of the mandible, indicate differences between this specimen and *Prohegetotherium schiaffinoi* and the other Hegetotheriinae. The affinity of YPFB-LIT-PAL-005 with *P. schiaffinoi* suggests a late Oligocene to early Miocene for the upper bearing horizon of the Petaca Formation (in Abapó), an older age than previously assigned to the top of this unit (late Miocene), and confirms the taxon distribution between ~ 36 ° to ~ 17 ° south latitude.

KEYWORDS: Notoungulata; Hegetotheriidae; Petaca Formation; late Oligocene-early Miocene; Bolivia.

INTRODUCTION

The South American native ungulates, which include five extinct orders (Astrapotheria, Litopterna, Notoungulata, Pyrotheria and Xenungulata), underwent a remarkable diversification during the major part of the Cenozoic Era. Among them, notoungulates are by far the most diverse (Simpson 1980, Billet 2011, Croft *et al.* 2020).

Typotheria notoungulates include small to medium-sized forms with the following apomorphic traits: a rodent-like anterior dentition with I1 somewhat enlarged and upper molars with obliterated occlusal surface (Cifelli 1993). Within these small Typotheria, Hegetotheriidae and Archaeohyracidae are considered as forming the clade Hegetotheria (Cifelli 1993, Croft *et al.* 2003), an entity previously regarded as a separate suborder (Simpson 1967). Hegetotheriids are small typotherian notoungulates; some of the latest representatives were very similar in overall morphology to modern rabbits or certain caviomorph rodents (Elissamburu 2004, Elissamburu and Vizcaíno 2004, Reguero *et al.* 2007). Many recent studies suggested that hegetotheriids arose from the latest archaeohyracids (Cifelli 1993, Croft *et al.* 2003). Hegetotheriids have been traditionally divided into two subfamilies: Hegetotheriinae and Pachyrukhinae (Simpson 1945). The paraphyletic Hegetotheriinae (Croft and Anaya 2006, Reguero and Prevosti 2010, Cerdeño and Reguero 2015, Seoane *et al.* 2017) includes the following genera: *Prohegetotherium* Ameghino 1897, from the Deseadan (late Oligocene) and Santacrucian (early Miocene, middle Member of the Mariño Formation) South American Land Mammal Ages (SALMAs) of Mendoza, Argentina, and the Deseadan (late Oligocene) of Bolivia and Uruguay; *Sallatherium* Reguero and Cerdeño 2005, from the Deseadan of Bolivia; *Hegetotheriopsis* Kramarz and Paz (2013) from the Deseadan and Colhuehuapian SALMAs (late Oligocene-early Miocene) of Argentina; *Hegetotherium* Ameghino 1887 from the Colhuehuapian, Santacrucian and Colloncuran SALMAs (early Miocene–early middle Miocene) of Argentina, as well as Chile (Croft *et al.* 2004, Flynn *et al.* 2005, Flynn *et al.* 2008, Bostelmann *et al.* 2018), and Bolivia

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(Cerdas and Nazareno localities; Croft *et al.* 2009, Croft *et al.* 2016); and *Hemihegetotherium* Rovereto (1914) (including *Pseudohegetotherium*) from the Collon Curá Formation (middle-late Miocene), the Chasicoan (late Miocene) and Huayquerian (late Miocene) of Argentina (Croft and Anaya 2006, Kramarz and Bond 2017, Vera 2019), and Quebrada Honda (Croft and Anaya 2006) and Muyu Huasi (Villarroel and Marshall 1989), Bolivia.

A few fossil mammals were so far known from the Subandean Region or adjoining areas of Bolivia (López-Murillo 1975; Sanjinés and Jiménez 1976, Marshall and Sempere 1991, Poiré *et al.* 2013). Concerning the notoungulates, Marshall and Sempere (1991) reported that YPFB geologists collected in Quebrada Saguayo, 60 km WNW of Santa Cruz de la Sierra, a right maxilla with P2–M2 assigned to the notohippid ?*Rhynchippus* sp. (considered a typical Deseadan notoungulate). This material was recovered from the lower horizons of the Petaca Formation (i.e., a pink sandstone 2 m above the base of the unit).

This study describes a material of hegetotheriid Hegetotheriinae represented by a mandible (YPFB-LIT-PAL-005) from the upper section of the Petaca Formation, Río Grande Tatarenda section (near the town of Abapó), southwest of the department of Santa Cruz, Bolivia (Fig. 1). This specimen was previously reported by Reguero *et al.* (2018) as a hegetotheriine closely related to the Deseadan species, *Prohegetotherium schiaffinoi* (Kraglievich 1932), from Argentina, Bolivia, and Uruguay. Stratigraphically, this Bolivian hegetotheriid provides insight into the Hegetotheriinae diversity and allows valuable comparisons between late Paleogene — early Neogene South American ungulate faunas of low and high latitudes.

GEOLOGICAL SETTING

The syn-orogenic sequences accumulated in the Chaco foreland basin during the Oligocene — Pleistocene are called the Chaco Group (Stebinger 1920, Harrington 1922, White 1925). In the study area (northern sector of the basin), the Chaco Group consists of the Petaca, Yecua, Tariquía, Guandacay and Emborozú Formations (Ayaviri 1967) (Fig. 2A). Particularly, in the studied area, the Petaca Formation overlies discordantly (erosive surface) the Cajones sequences, and the contact with the overlapping Yecua Formation is sharp and unconformable (transgressive surface) (Fig. 2B). This is evidenced by the change from semi-arid fluvial (Petaca) to inland wetland/lacustrine (Yecua) depositional environments (Fig. 3A).

The Petaca Formation (Birkett 1922) consists of greenish-gray to reddish massive sandstones, cross-bedded sandstones and massive conglomerates, with notable presence of calcareous nodules and calcrete levels (Requena 1981, Uba *et al.* 2006, Vergani *et al.* 2012, Poiré *et al.* 2013). The fossil remains were found within the sandy beds (Fig. 3B). The deposits of this unit consist of tabular to lenticular bodies with erosive bases, 0.5–7 m thick, and lateral extensions between 50–150 m (Fig. 3C). Their width/thickness ratio ranges between 50 and 100, classified as narrow to broad sheets (Gibling 2006). The bodies generally show a vertical and lateral stacking forming multiepisodic channel belts, up to 20 m thick, which are delimited by basal concave erosive surfaces (Fig. 3C). Paleocurrent data show a predominant direction to the west (Uba *et al.* 2005, 2006). Channel bodies are sporadically interbedded with massive to laminated mudstone beds with mudcracks. Both fine-grained deposits and sandy bodies present pedogenic features such as soil aggregates, rhizoconcretions and bioturbation.

The Petaca Formation is interpreted as interconnected fluvial system deposits with floodplain development (Marshall *et al.* 1993, Uba *et al.* 2005, 2006, Vergani *et al.* 2012). The channels are dominated by the sandy bed-load, accumulated from the construction of bars originated by the migration of 3D

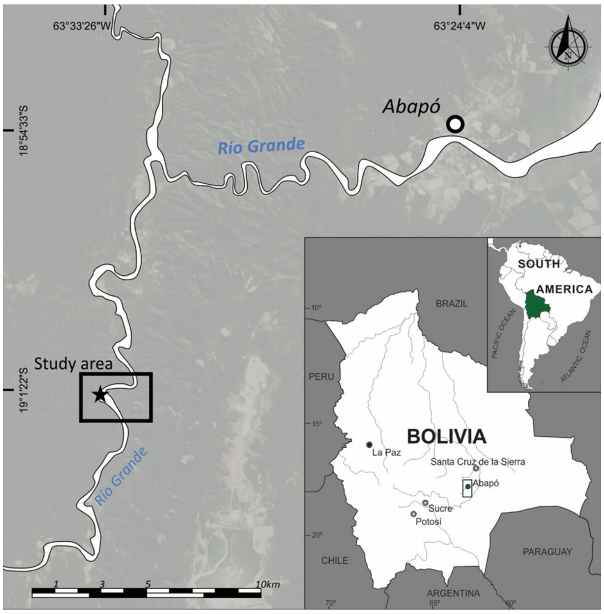
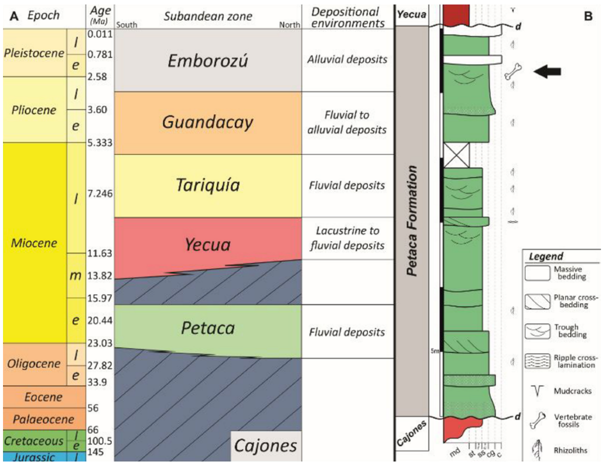


Figure 1. Location map of the study area in the Río Grande Tatarenda section of the Petaca Formation. Black star indicates locality where *Prohegetotherium* cf. *P. schiaffinoi* was collected.



C: calcrete; cg: conglomerate; md: mudstone; ss: sandstone (f: fine; c: coarse); st: siltstone; *d*: unconformity.

Figure 2. (A) Simplified stratigraphy of the Cenozoic Chaco foreland Basin. Summary of the Depositional systems (*l*, *m*, and *e* refer to late, middle, and early, respectively). (B) Lithologic log of the Petaca Formation in the study area, showing facies associations and their vertical relationships. Note the bone indicating the stratigraphic provenance of *Prohegetotherium* cf. *P. schiaffinoi* in the upper section (black arrow).

megaripples and current ripples. The bars are represented by lateral and frontal accretion components generating both simple and compound forms. The presence of amalgamated sandy bodies separated by erosive surfaces is interpreted as a design of active channels of moderate to low sinuosity that represent braided channel belts. The thin mudstone beds in the top-sets represent floodplain deposits accumulated during the migration of the channels (Page *et al.* 2003). Calcretes and paleosols indicate low sedimentation rates in a semi-arid climate (Cecil 1990, Uba *et al.* 2005, 2006, Vergani *et al.* 2012). Marshall *et al.* (1993) dated biostratigraphically the upper part of the Petaca Formation based on the Chasicoan-Montehermosan (late Miocene — early and middle Pliocene) cf. *Vassallia minuta* (Xenarthra, Pampatheriidae). However, there are some inconsistencies about the provenance and the systematic treatment of this material (see below).

MATERIALS AND METHODS

The YPFB-LIT-PAL-005 specimen is housed in the vertebrate paleontology collection of the Yacimientos Petrolíferos Fiscales de Bolivia (YPFB, Santa Cruz de la Sierra).

The anatomical study has been carried out through direct and bibliographic comparisons, using type specimens and reference material from collections in the institutions listed below (see "Institutional abbreviations"), as well as using several scientific contributions on Hegetotheriidae (e.g., Rovereto 1914, Reguero 1999, Reguero and Cerdeño 2005, Croft and Anaya 2006, Kramarz and Paz 2013, Cerdeño and Reguero 2015; Kramarz and Bond 2017, Seoane *et al.* 2017, Vera and Ercoli 2018, Ercoli *et al.* 2019, Seoane and Cerdeño 2019).

Hypsodonty index follows Reguero *et al.* (2010) and was calculated by dividing the m1 height by the m1 anterior/posterior length.

Teeth measurements were taken with a Mitutoyo digital caliper (0.01 mm accuracy). Two variables were measured for each tooth: length, corresponding to maximum mesiodistal diameter; and width, measured perpendicular to length.

Photographs were taken with a Nikon D3000 digital camera.

Institutional abbreviations

AMC, Amherst College Museum, Amherst, Massachusetts, USA; AMNH, American Museum of Natural History, New York, USA; MAMC, Museo de Arqueología de Canelones, Uruguay; MCNAM-PV, Museo de Ciencias Naturales y Antropológicas "J.C. Moyano", colección Paleontología de Vertebrados, Mendoza, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MNHN-DP, Museo Nacional de Historia Natural de Montevideo, Montevideo Uruguay; PZ-Ctes, PRINGEPA (Programa de Investigación Geológica y Paleontológica), Corrientes, Argentina; UATF-V, Vertebrate Paleontology Collections, Universidad Autónoma Tomás Frías, Potosí, Bolivia; UF, University of Florida, Gainsville, USA; YPFB-LIT-PAL, Yacimientos Petrolíferos Fiscales, colección paleontológica, Santa Cruz de la Sierra, Bolivia.

Abbreviations of teeth nomenclature

c, lower canine; i, lower incisor; m, lower molar; p, lower premolar.

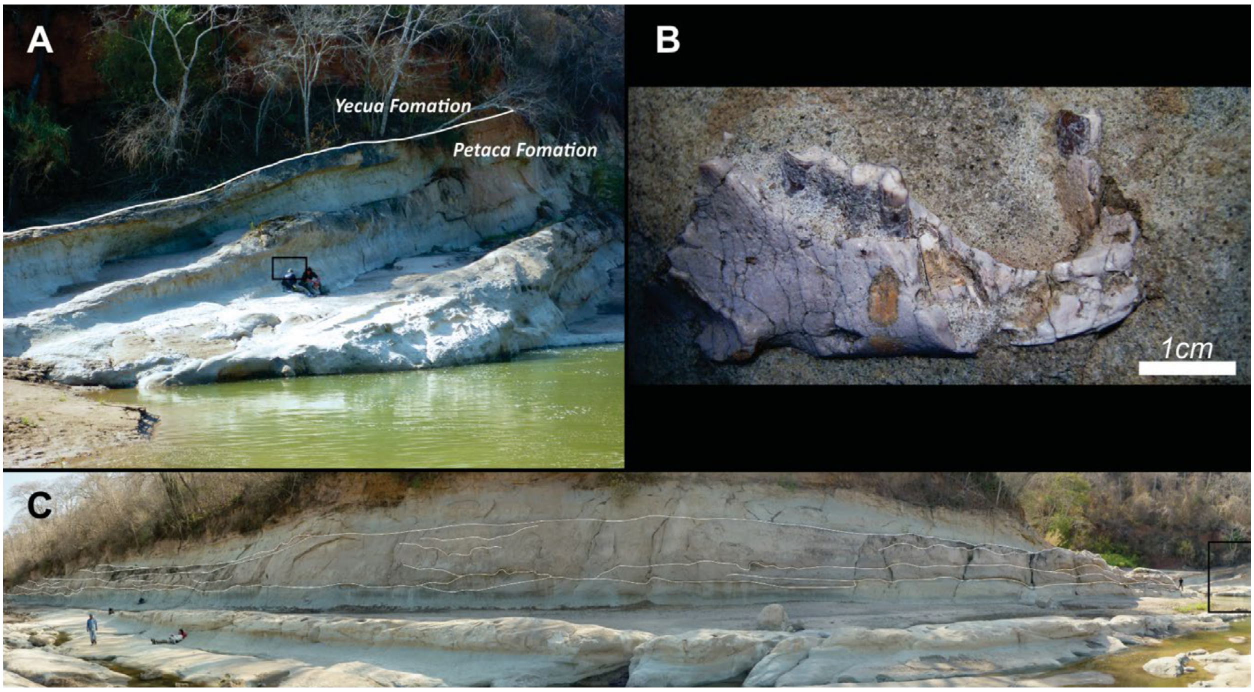


Figure 3. (A) Photograph of the outcrop showing the contact between the Petaca and Yecua formations (white line). Note the layer where the material was preserved (black rectangle, see detail in Figure 3B); (B) detail of the bed where *Prohegetotherium* cf. *P. schiaffinoi* was found; (C) upper Petaca Formation at overview of channel belts. Interpreted photomosaic showing architectural style of braided fluvial channels. Note how each sandstone-filled channel belt affects both old channel belts and floodplain deposits. Black rectangle on the right, corresponds to Figure 3A.

RESULTS

Systematic paleontology

Order NOTOUNGULATA Roth (1903)

Suborder TYPOTHERIA Zittel (1893) (*sensu* Reguero and Castro 2004)

Family HEGETOTHERIIDAE Ameghino (1894)

Subfamily HEGETOTHERIINAE Ameghino (1894)

Genus *Prohegetotherium* Ameghino (1897)

Type species

Prohegetotherium sculptum Ameghino (1897).

Included species

The type species *Prohegetotherium shumwayi* Loomis (1914), *P. schiaffinoi* (Kraglievich 1932), and *P. malalhuense* Cerdeño and Reguero (2015).

Geographic and stratigraphic distribution

Prohegetotherium occurs in several Deseadan (late Oligocene) localities of Argentina (Patagonia, Mendoza and Corrientes) (Ameghino 1897, Bond *et al.* 1998, Cerdeño and Reguero 2015). It was also recorded in the Santacrucian (early Miocene) of the Mariño Formation (Cerdeño *et al.* 2008). Outside Argentina *Prohegetotherium* has been recorded in Cachapoal, Chile (early Oligocene, Croft *et al.* 2008a, Croft *et al.* 2008b), Salla, Bolivia (late Oligocene, Reguero and Cerdeño 2005), and Fray Bentos, Uruguay (late Oligocene, Fray Bentos Formation, Reguero and Cerdeño 2005).

Remarks on the systematic status of Prohegetotherium

Florentino Ameghino (1897) erected this genus based on the two syntypes, probably from the Deseadan locality Cabeza Blanca in central Patagonia. Ameghino did not provide a detailed description of this taxon, but remarked that the upper premolars have an anterolabial sulcus (parastylar sulcus, in the current dental terminology) and a well-developed canine. Recently, Kramarz and Bond (2017) re-examinated the type specimens of *Prohegetotherium sculptum* (MACN A 52-443, left maxillary fragment with the alveolus for the canine and P1–P3; paralectotype: MACN A 52-444, left portion of maxillary with incomplete P3–M3, and part of nasals and frontals). They found that this material exhibits several dental and cranial characters not recognized in previous studies (Reguero 1999, Reguero and Cerdeño 2005), and concluded that no specimen other than the types can be assigned to *P. sculptum*. Seoane and Cerdeño (2019) suggested the need for a deep revision of all the materials assigned to *Prohegetotherium*, particularly those excluded from *P. sculptum* by Kramarz and Bond (2017).

Comparison with the other species of Prohegetotherium

YPFB-LIT-PAL-005 cannot be properly compared with *Prohegetotherium sculptum*, because the species is only known by the upper dentition (Kramarz and Bond 2017). Chaffee (1952, pl. 16, Figs. 2 and 3) described a mandible, AMNH 29605, from the Deseadan of Patagonia and referred to *P. sculptum* although there is no anatomical correspondence between the type material of *P. sculptum* and AMNH 29605. The similar size and matching occlusion allowed it to hypothesize that AMNH 29605 could represent the lower dentition of *Prohegetotherium sculptum*. The lower teeth of AMNH 29605 have the p4 in line with the tooth row and are also larger than those of the YPFB-LIT-PAL-005.

Prohegetotherium shumwayi Loomis (1914) is based on only one specimen, a right maxillary fragment with upper premolars and molars (Loomis 1914, p. 64, Fig. 29). According to the figure and the dental measurements given by Loomis (1914), the premolars are slightly shorter and narrower than in the lectotype of *P. sculptum*.

The cheek teeth morphology of YPFB-LIT-PAL-005 is very similar to that of the specimens assigned to *Prohegetotherium schiaffinoi* rather than to those of *P. malalhuense*, as Reguero and Cerdeño (2005) suggest from comparison with the Bolivian material from Salla. Later, Cerdeño and Reguero (2015) assigned to *Prohegetotherium schiaffinoi* several specimens from the Deseadan locality of Quebrada Fiera and Divisadero Largo (Mendoza Province, Argentina). Comparing directly with the latter sample, YPFB-LIT-PAL-005 shows a similar imbrication of the p4, with elongated trigonid and a posterolingual inflexion of m3, but a different elongation of p3 and a distinctive inflexion/groove in m3. These features can be present in some Miocene hegetotheriids (Cerdeño and Reguero 2015, Seoane and Cerdeño 2019, Vera 2019). However, several morphological features seen on the mandibular ramus of YPFB-LIT-PAL-005, i.e., dentary exhibiting a marked change in height along its length, a prominent masseteric crest and a remarkably thick ventral margin of the dentary, make differences between this specimen and *Prohegetotheium schiaffinoi*.

Prohegetotherium schiaffinoi (Kraglievich 1932)

Holotype

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

Geographic and stratigraphic distribution

Uruguay: Fray Bentos Formation; Bolivia: Salla, "Upper Salla Beds"; and Argentina: Corrientes and Entre Ríos (Deseadan SALMA, Fray Bentos Formation).

Remarks

Kraglievich (1932) erected the species *Propachyrucos*? *schiaffinoi* (holotype MNHN-DP-186) on a maxillary fragment with P2–M2 from the Fray Bentos Formation, Uruguay. Reguero (1999) and Reguero and Cerdeño (2005) considered it as part of the genus *Prohegetotherium*, and these latter authors provided a more complete description of *Prohegetotherium schiaffinoi* based on the Bolivian material.

Remarks on the taxonomic status of "Ethegotherium carettei" from the Mariño Formation (Miocene) of Mendoza and its affinity with Prohegetotherium schiaffinoi

"*Ethegotherium carettei*" was first described as a new species of *Prohegetotherium* (Minoprio 1947) and later assigned to a new genus *Ethegotherium* by Simpson *et al.* (1962). Later, López (2002, 2010) revalidated the species *Ethegotherium carettei*. López and Manassero (2008) indicate that the sediment containing the holotype of *E. carettei* was found to share more similarities with the sediments of the Mariño Formation than the Divisadero Largo Formation. The stratigraphic provenance of this species therefore does not likely correspond to the Divisadero Largo Formation and should not pertain to the Divisaderan Fauna. Reguero and Cerdeño (2005) and Cerdeño and Reguero (2015) subsumed it within *Prohegetotherium schiaffinoi* and extended the chronological distribution of this species to the early Miocene (Cerdeño *et al.* 2008).

Prohegetotherium cf. *P. schiaffinoi*

(Figs. 4A–4D)

Material

YPFB-LIT-PAL-005, mandible with left p4-m3 and right m2-m3 (Fig. 4A).

Geographic occurrence

Vicinity of the town Abapó (19°1'17"S - 63°33'25"W), 160 km SW of Santa Cruz de la Sierra, Bolivia (Fig. 1).

Age and distribution

Petaca Formation, late Oligocene-early Miocene (Marshall and Sempere 1991).

Description

In lateral view, the horizontal ramus of YPFB-LIT-PAL-005 is sturdy and low, being proportionally shorter and lower than in other hegetotheriids, i.e. *Hegetotherium* and *Hemihegetotherium* species. The horizontal mandibular ramus is very low at the level of p4 (9.6 mm), increasing in height backwards (15.3 mm at m1/m2 level); its ventral border is slightly convex and very thick, especially in the posterior sector; the posterior end of the symphysis extends up to the level of the alveolus of p3. In the masseteric area, there is a well-defined masseteric crest (best exhibited on the right ramus) and its anterior process has its maximal development at the level of the posterior end of m3 (Fig. 4B). A deep masseteric groove is present immediately anterior to the masseteric crest (Figs. 4C and 4D). The angular process has a rounded contour, and the ventral masseteric fossa, which is associated with the insertion of mm. masseter lateralis, is well defined as in Hegetotheriidae Pachyrukhinae (Ercoli *et al.* 2019) (Fig. 4C). There is a large mental foramen between m2 and m3, close to the inferior border of the ramus.

The p4 (Fig. 4B) is not molariform and is the smallest tooth of the series. It has two labial lobes being the anterior (trigonid) slightly smaller than the posterior (talonid) and anterolingually rounded and posterolabially elongated. The anterior face of this tooth shows a thin dentine band, and the lingual face is rather straight. The labial groove is deeply marked. It is imbricated with the m1; the distolingual extremity of each tooth (p4 and m1) is just lingual to the mesial end of the next most distal tooth. The size and morphology of the posterior lobes of the p4 and molars are similar to those observed in *Prohegetotherium schiaffinoi* (Reguero and Cerdeño 2005, Cerdeño and Reguero 2015). On the contrary, in other hegetotheriid species, i.e., *Hegetotherium mirabile*, the p4 has a square trigonid, very narrow labial sulcus, and a linguodistal projection on the talonid.

The m1–m2 (Fig. 4B) are similar to each other. These two cheek teeth are characterized by a straight lingual face with a lingual projection near the distal end; a trigonid with a rounded to slightly pointed labial face; a talonid with a triangular lingual face; and absence of mesial and distal enamel where the tooth contacts the adjacent teeth, and without posterolingual projection unlike *Hegetotherium*. Their posterolingual corner projects lingually, unlike other species of *Prohegetotherium*, e.g. *P. shumwayi*.

The m3 displays a rounded trigonid similar to m1–m2, but smaller, a subtriangular talonid and a posterolingual groove (plg) like some specimens of the Santacrucian *Hegetotherium mirabile* Ameghino 1887. It is bilobate, but with the posterior lobe much longer than the anterior and its labial face convex, without talonid groove unlike *Hegetotherium* and *Hemihegetotherium*. The m3 of YPFB-LIT-PAL-005 differs from m1–m2 by several characteristics, including a narrower talonid; absence of enamel along the distal end of the lingual face; presence of a notch near the distal end of the lingual face (Figs. 4B and 4D); and similar in size to m2, a character not seen in other species of *Prohegetotherium* in which the m3 is always longer than m2 (Fig. 4B, Tab. 1). The first three features are also present in other hegetotheriid species, e.g., *Hegetotherium mirabile* and *H. cerdasensis*, although the lingual talonid notch tends to be smaller than in YPFB-LIT-PAL-005. In this regard, YPFB-LIT-PAL-005 resembles *Prohegetotherium schiaffinoi* (see Cerdeño and Reguero 2015: Fig. 5F). As in *Prohegetotherium schiaffinoi,* there is a posterolingual groove on m3 (best seen on right m3).

DISCUSSION

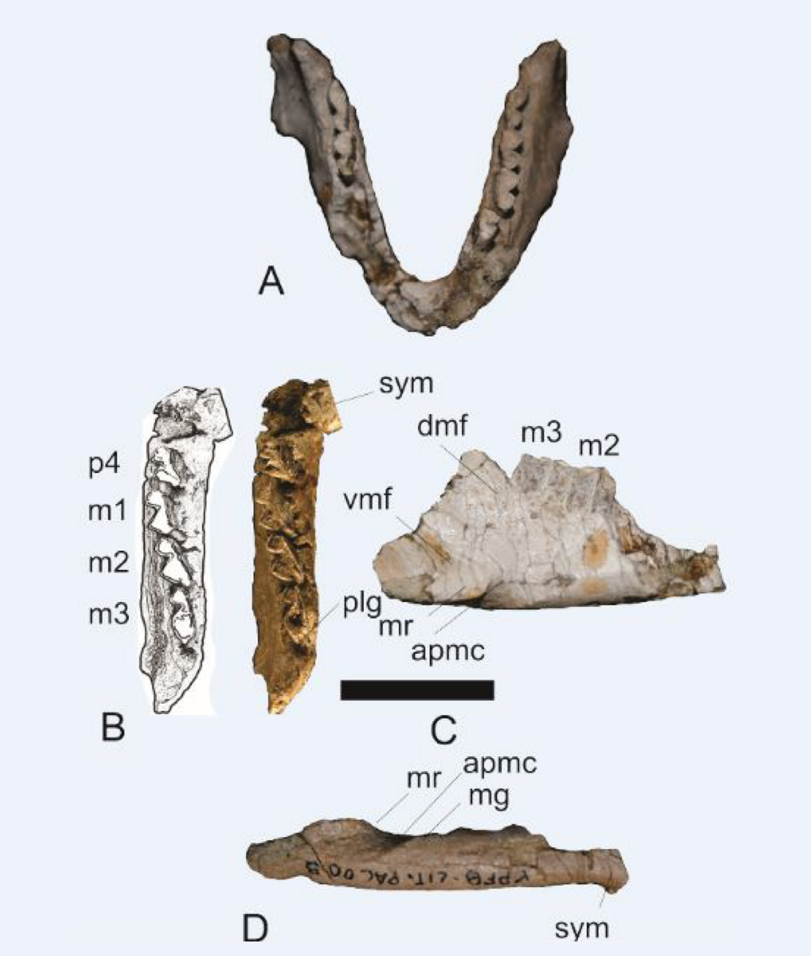
Mandibular morphology of YPFB-LIT-PAL-005

The dental morphology and dimensions of YPFB-LIT-PAL-005 (Tab. 1) show several similarities with the Deseadan species *Prohegetotherium schiaffinoi* from Salla (Bolivia), Fray Bentos (Uruguay), Corrientes and Mendoza (Argentina). However, several morphological distinctions of the mandibular ramus between this specimen and the holotype and referred material of *P. schiaffinoi* should be mentioned: i.e., dentary of YPFB-LIT-PAL-005 with a marked change in height along its length, and the ventral rim of the dentary remarkably thick. The particular mandibular anatomy of YPFB-LIT-PAL-005 is not frequent in *Prohegetotherium*. It is probably associated with a shortening of the mandible and narrowing of the symphysis (broken and badly preserved in YPFB-LIT-PAL-005). A similar mandibular characteristic is present in the holotype of *Sallatherium altiplanensis* (UF 91621) from the Deseadan (late Oligocene) of Salla (Bolivia), but in this species the mandible is higher and robust and has a marked symphyseal narrowing at the level of i1-c.

The mandible YPFB-LIT-PAL-005 exhibits a mosaic of features similar to the pachyrukhine species. Ercoli *et al.* (2019), based on the study and reconstruction of the masticatory muscles of some hegetotheriidae pachyrukhines, i.e., *Paedotherium* and *Tremacyllus*, recognize the presence of a true sciuromorph condition, defined by an anterior portion of the deep masseter muscle originating from a wide zygomatic plate that reaches the rostrum, a trait traceable since the Oligocene in Hegetotheriidae. In lateral view of YPFB-LIT-PAL-005, the horizontal rami are low, shorter than in other hegetotheriine species, and have a deep groove posteriorly immediately in front of the masseteric crest, and a prominent anterior process (Figs. 4C and 4D). This groove is linked to the passage of the masseter muscle superficialis pars reflexa (Ercoli *et al.* 2020). The ventral and dorsal masseteric fossae are well defined and associated with the insertions of muscle masseter lateralis and medialis respectively (Fig. 4C). The singularity of the mosaic of masticatory features of the mandible YPFB-LIT-PAL-005 is interpreted as related to a large mediolateral component in chewing movements, more similar to *Paedotherium* (Ercoli *et al.* 2019).

Paleobiology of the Hegetotheriidae from Abapó

Hegetotheriids are generally reconstructed as grassers and open habitat specialists that might have lived in burrows resembling rabbits (leporids) or various South American rodents (caviids, chinchillids) in lifestyle (Sinclair 1909, Genise 1989, Elissamburu 2004, Croft 2016, Ercoli *et al.* 2020). The Petaca hegetotheriid has a moderate hypsodonty (HI ~ 2.4). Janis (1988) pointed out that hypsodonty occurs in herbivores feeding on any type of low vegetation that would be subjected to abrasive dust and grit coverage. In the context of hypsodont



apmc: anterior process of the masseteric crest; dmf: dorsal masseteric fossa; mg: mandibular groove; mr: mandibular ridge; pbs: posterior border of the mandibular symphysis; plg: posterior lingual groove; sym: mandibular symphysis; vmf: ventral masseteric fossae.

Figure 4. *Prohegetotherium* cf. *P. schiaffinoi*, YPFB-LIT-PAL-005. (A) Pair of mandibles bearing left p4-m3 and right m2-3 in occlusal view; (B) original and schematic drawing of the occlusal view of the left horizontal ramus; (C) labial view of the right horizontal ramus; (D) ventral view of the right horizontal ramus. Scale bar equals 10 mm.

species, this ungulate was probably a wide-ranging species that lived in gallery forests, being able to eat close to water bodies and lagoons that occurred in the floodplains developed under humid and subtropical climate (Croft 2016).

Based on sedimentologic and paleontologic analyses, Poiré *et al.* (2013) suggested a paleoenvironment for the Chaco Foreland (Petaca Formation) characterized by open habitats with grasslands under a semiarid climate during the late Oligocene. The hegetotheriid from Petaca probably was a mixed feeder, consuming a variable diet obtained close to the ground subjected to abrasive dust and grit coverage (Reguero *et al.* 2010). In other hegetotheriids, e.g., *Hemihegetotherium trilobus*, with similar morphology of the teeth to *Prohegetotherium schiaffinoi*, the type of mesowear is more similar to that of a browsing mammal (Croft 2016).

The mandibular features of YPFB-LIT-PAL-005 are more compatible with dietary habits that include hard and brittle or turgid fruits, emphasizing crushing, and secondarily grinding, instead of the extensive grinding of grazers (Ercoli *et al.* 2020).

Diversity of Hegetotheriinae in the Paleogene-Neogene of Bolivia

Prohegetotherium cf. *P. schiaffinoi* from the Petaca Formation increases the diversity of hegetotheriids during the Paleogene/Neogene in low and mid-latitudes of South America. The presence of *Prohegetotherium* cf. *P. schiaffinoi* in the top of the Petaca

Table 1. Measurements (in mm) of the lower teeth and mandible bone of *Prohegetotherium* cf. *P. schiaffinoi* and compared specimens.

Specimens	**p1**		**p2**		**p3**		**p4**		**m1**		**m2**		**m3**	
	L	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
Prohegetotherium cf. *P. schiaffinoi*														
YPFB-LIT-PAL-005							5.1	2.4	6.1	2.4	7.1	2.3	6.5	3.2
Hemihegetotherium trilobus														
MNHN-BOL-V- 3671	2.3	2.5	5.5	4.0	7.3	5.0	8.7	5.7	8.9	5.5	9.0	5.5	12.2	4.9
Hemihegetotherium lazai														
MLP 57-X-10-95							8.6	5.2	8.4	4.8	8.5	5.0		
Hemihegetotherium achataleptum														
MACN Pv 8491									12.0	6.2	12.6	6.7	15.4	6.0
Sallatherium altiplanense														
UF 91621					5.6	4.5	6.5	4.9	7.1	4.9	7.3	4.5	9.7	4.2
Hegetotheriopsis sulcatus														
MACN PV CH2014					6.0	3.8	6.9	4.5	7.2	4.6	7.1	4.5	8.9	3.7
Hegetotherium cerdasensis														
UATF-V-000067							4.6	2.9	5.2	2.7	5.2	2.8	5.6	2.2
UATF-V-1069							4.2	2.8	5.7	3.1	5.9	3.3	6.4	2.5
Prohegetotherium schiaffinoi														
MCNAM PV 4054							4.9	3.1	5.5	3.3				
MCNAM PV 4061			3.4	1.7	3.7	2.6	4.7	2.9	5.2	2.9	5.6	2.9	6.4	2.3
MCNAM PV 4071					3.8	2.0	4.4	2.7	4.6	2.9				
MCNAM PV 4604					5.2	3.0	5.4	3.4	6.0	3.6	6.3	3.6		
MCNAM PV 4637							4.7	3.0	5.2	3.1	5.6	3.0	6.6	2.6
PZ-Ctes 3744													6.0	2.6
PZ-Ctes 3748-49					4.0	2.4	5.0	2.9	7.0	3.1	> 4.7	2.7	7.2	3.1
PZ-Ctes 3751									4.7	2.8	5.2 >	2.3	--- >	1.8
PZ-Ctes 3755					3.8	2.7	(4.3)	(2.8)						
PZ-Ctes 3756							3.0	1.5	4.0	3.1				
PZ-Ctes 7872					3.1	1.8	3.6	2.1	4.6	2.7	4.0	2.5	(5.4)	(2.2)
UF 91661							4.4	2.7	4.7	2.8	5.9	3.5	7.2	3.1
UF 91662					3.8	2.3	4.3	2.7	5.4	3.1	5.8	3.2	6.9	3.1
UF 172129			2.9	2.0	3.9	2.5	4.7	2.9	5.6	3.4	6.0	3.4	6.6	2.9
Prohegetotherium malalhuense														
MCNAM PV 3847									6.5	3.2			7.7	2.9
MCNAM PV 4679									6.0	3.4				

*data from Reguero (1999), Reguero and Cerdeño (2005), Croft and Anaya (2006), Cerdeño and Reguero (2015), Croft *et al.* (2016), Kramarz and Bond (2017), Vera (2019). Approximate values in parenthesis. L: Length; W: Wide.

Formation in Abapó suggests an age consistent with other contemporaneous Deseadan faunas from northern and southern latitudes of South America. In close geographic proximity to the Abapó locality, the Deseadan Salla Beds have yielded extremely abundant remains of *Prohegetotherium schiaffinoi* (Reguero and Cerdeño 2005). Kay *et al.* (1999) assigned an age between 27 and 25.8 Ma for the richest fossiliferous levels.

Abapó is the sixth locality in Bolivia in which hegetotheriine have been found, and the eighth in South America located north of approximately 23° south latitude. Other records of Bolivian hegetotheriids are: two species, *Prohegetotherium schiaffinoi* and *Sallatherium altiplanense* from the Deseadan of Salla, western Bolivia (Reguero and Cerdeño 2005); *Hemihegetotherium trilobus* from Quebrada Honda, unnamed formation (Honda Group), southern Bolivia, middle Miocene, Laventan SALMA (Croft and Anaya 2006, McGrath *et al.* 2018); *Hegetotherium cerdasensis* from the ?late Miocene fauna of Nazareno and Cerdas, Potosí, Bolivia (Croft *et al.* 2016); and *Hemihegetotherium* from the ?late Miocene of Muyu Huasi, southern Bolivia (Villarroel and Marshall 1989). Hegetotheriids have also been reported from the late early Miocene (Santacrucian) Chucal fauna from northern Chile (*Hegetotherium* cf. *H. mirabile*; Croft *et al.* 2004), and dubiously from the middle to late Miocene Urumaco Formation, Venezuela (Linares 2004).

Temporal implications of the hegetotheriid of Abapó section

Traditionally, the Petaca Formation was assigned to the late Oligocene-late Miocene (Sempere *et al.* 1990, Marshall and Sempere 1991, Marshall *et al.* 1993). No absolute dating (magnetostratigraphy or isotope analysis) has been performed for this unit; the age of the Petaca Formation is constrained by biostratigraphic data coming from different localities of the Subandean belt.

The base of this unit was assigned to the Deseadan (late Oligocene-earliest Miocene) based on the notohippid cf. *Rhynchippus* found in Quebrada Saguayo, about 60 km WNW of Santa Cruz (Sempere *et al.* 1990, Marshall and Sempere 1991, Marshall *et al.* 1993). Few data are available for this specimen. Marshall *et al.* (1993) did not illustrate this material or not provide it a catalogue number. The only reference provided by these authors is that YPFB's geologists collected a right maxilla with P2-M2 of ?*Rhynchippus* which come from a pink sandstone 2 m above the base of the unit (p. 294).

Marshall *et al.* (1993) mentioned the presence of the pampathere cf. *Vassallia minuta* (Chasicoan-Montehermosan SALMA) in the top of the Petaca Formation. The identification of this material is doubtful. It is based on five right dentary teeth coming from the Río Yapacani (90 km WNW of Santa Cruz de la Sierra), not properly described or illustrated (Pascual *et al.* 1973, Villarroel 1974, Sanjinés and Jiménez 1976, Marshall *et al.* 1993, p. 294). Even more, the stratigraphic position and collection number of this specimen are not available. About its geographical position, Marshall *et al.* (1993, p. 294) pointed out:

> An attempt was made by LGM to relocate this site on November 14,1990, and it was discovered that the Petaca Formation occurs in fact about 20 km more to the southwest than originally illustrated. Despite the biostratigraphic importance for the late Miocene-early Pliocene of the pampathere *Vassallia*, there is no certainty about the provenance of this material.

We consider all this evidence unreliable to justify the age assigned to the unit. Instead, the only other hypothetical possibility is that the bearing horizon of cf. *Vassallia minuta* could be stratigraphically higher than that of cf. *P. schiaffinoi*. Our working hypothesis is that *Vassallia minuta* and cf. *Prohegetotherium schiaffinoi* come from different stratigraphic levels, and probably from different units. Moreover, *Vassallia minuta* could come from the Yecua Formation.

Here we describe in detail and accurately documents the presence of a hegetotheriid with close affinity to the Deseadan-Santacrucian *Prohegetotherium schiaffinoi* in the top of the Petaca Formation (Abapo section) based on more precise stratigraphic and biostratigraphic evidence. Thus, an older age, late Oligocene to early Miocene, is suggested for the top of this unit at Abapó section.

CONCLUSIONS

The study of the Hegetotheriinae from Abapó resulted in the record of the genus *Prohegetotherium* for the first time in the Petaca Formation.

The Abapó specimen is very close to the Deseadan-Santacrucian *Prohegetotherium schiaffinoi*. However, some features of the mandible, as the shape with a marked change in height along its length, increasing towards the back, a prominent masseteric crest and a deep mandibular groove, are different from that of this species.

The YPFB-LIT-PAL-005 broadens the knowledge of Hegetotheriinae for the late Oligocene – early Miocene of Bolivia and expands the geographic distribution of the genus *Prohegetotherium* to low latitudes of Chaco foreland in Bolivia.

The close affinity of the YPFB-LIT-PAL-005 to the Deseadan-Santacrucian species *Prohegetotherium schiaffinoi* suggests an older age, from late Oligocene to early Miocene, for the upper levels of Petaca Formation cropping out in Abapó.

Overall, new geochronological studies, regional stratigraphic correlations of the Petaca Formation, and more fossil evidence are needed to resolve the age of this unit in the Chaco foreland basin.

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