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NOTA PALEONTOLÓGICA

THE SCELIDOTHERIINE *PROSCELIDODON* (XENARTHRA: MYLODONTIDAE) FROM THE LATE MIOCENE OF MAIMARÁ (NORTHWESTERN ARGENTINA, JUJUY PROVINCE)

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Xenarthra constitutes one of the most peculiar clades of the South American mammalian fauna and includes sloths (Tardigrada), anteaters (Vermilingua), and armored xenarthrans (Cingulata). Its phylogenetic affinities among placental mammals and their origins remain doubtful (Asher and Helgen, 2010). Xenarthrans first appear in the Itaboraian age (late Paleocene–early Eocene; Oliveira and Goin, 2011) represented by the Dasypodidae in the locality of Itaboraí, Brazil. Sloths are first recorded from the early Oligocene (Tinguiririan age) of Chile and became abundant during the late Oligocene (Deseadan age), mainly in Argentina and Bolivia with representation of Mylodontidae and Megalonychidae (Pujos *et al.*, 2012).

The mylodontid clade is divided into two subfamilies: Mylodontinae and Scelidotheriinae following Gaudin (2004) and St-André *et al.* (2010). The Scelidotheriinae includes some of the most spectacular of the giant tardigrades, with several medium- to large-sized Quaternary forms. For example, *Scelidotherium leptocephalum* Owen, 1839, attained the size of a cow; it was a selective browser (Bargo *et al.*, 2006a), capable of digging and excavated extensive burrows (Vizcaíno *et al.*, 2001). These ground sloths were mainly characterized by an extremely specialized, elongated, and tubular skull, increasing number of lobes on the distal lower molariforms, pentadactyl manus and pes, flattened femur, and a concave cuboidal facet in the astragalus.

Proscelidodon Bordas, 1935 appeared during the Huayquerian in Argentina and survived until the Chapadmalalan. The Quaternary witnessed the taxonomic diversification of the Scelidotheriinae, with four species belonging to the genera *Scelidodon* Ameghino, 1881, *Catonyx* Ameghino, 1891, and *Scelidotherium* Owen, 1840, which ranged across more than half of southern South America.

Pre-Quaternary Scelidotheriinae are uncommon. The discovery of a nearly complete maxilla of *Proscelidodon* from the Maimará Formation (late Miocene), Jujuy Province (Fig. 1), provides new data on the plesiomorphic condition of the clade, the biogeographic history of the group during the Mio–Pliocene, and on the Maimará faunal assemblage.

MATERIALS AND METHODS

Based on the phylogenetic hypotheses of McDonald and Perea (2002), Gaudin (2004), and Miño-Boilini *et al.* (2011) the principal taxa for comparison are *Proscelidodon patrius* Ameghino, 1888, *P. rothi* Ameghino, 1908, and *P. gracillimus* Rovereto, 1914, *Scelidodon chilensis* (Lydekker, 1886), *Catonyx cuvieri* Lund, 1839 and *C. tarijensis* (Ameg-

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hino, 1891), and *Scelidotherium parodii* Kraglievich, 1923 and *S. leptocephalum* Owen, 1840. Within the description, the orientation of the maxilla is anterior/posterior and lateral/medial and the orientation of the teeth is mesial/distal and labial/lingual.

Institutional abbreviations. **JUY-P**, Museo de Geología, Mineralogía y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy, San Salvador de Jujuy, Argentina; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN-Bol**, Museo Nacional de Historia Natural de Bolivia, La Paz, Bolivia; **MMP**, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina.

Anatomical abbreviations. **C**, upper caniniform; **M/m**, upper and lower molariform.

GEOLOGICAL CONTEXT

The Maimará Formation was defined and described by Salfity *et al.* (1984) on the left margin of the Arroyo Huasamayo, Jujuy Province. A Huayquerian age (late Miocene) for the vertebrate-bearing horizons was suggested by Berman (1989) based on the presence of *Cyonasua* that comes from the same area of the scelidotheriine described here. The specimen JUY-P-47 was found in the Maimará Formation which crops out in the Maimará locality of the Quebrada de Humahuaca. This locality is situated in the Eastern Cordillera, about 35km south of Humahuaca and about 2800m.a.s.l. (Fig. 1). The Maimará Formation varies between 35 to 330m in thickness of sandstones and conglomerates with tuff levels (Fig. 2). The deposits are ordered in an upwardly coarsening sequence developed in an ephemeral fluvial system under arid and semi-arid conditions. The level from which the *Proscelidodon* maxilla was retrieved is 134m from the base (Fig. 2). Pliocene–Pleistocene deposits overlie the Maimará Formation (Salfity *et al.*, 1984).

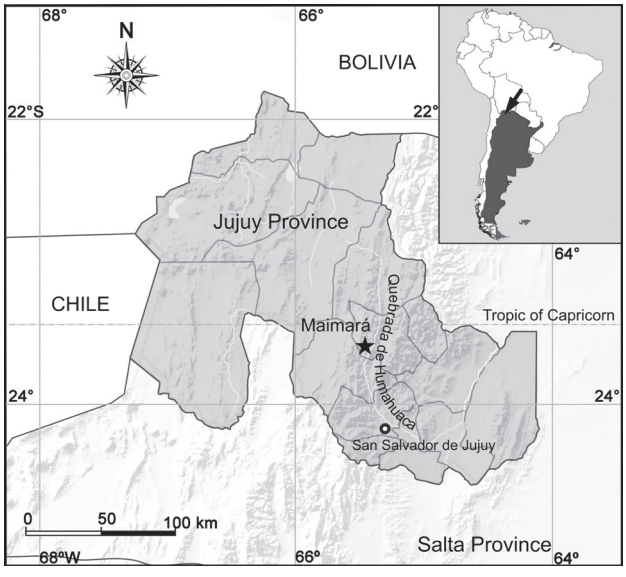

Figure 1. Map of the Jujuy of Province indicating the Maimará locality from which the specimen JUY-P-47 of ***Proscelidodon patrius*** was discovered/ *Mapa de la provincia de Jujuy indicando la localidad de Maimará donde fue descubierto el espécimen JUY-P-47 referido a* **Proscelidodon patrius**.

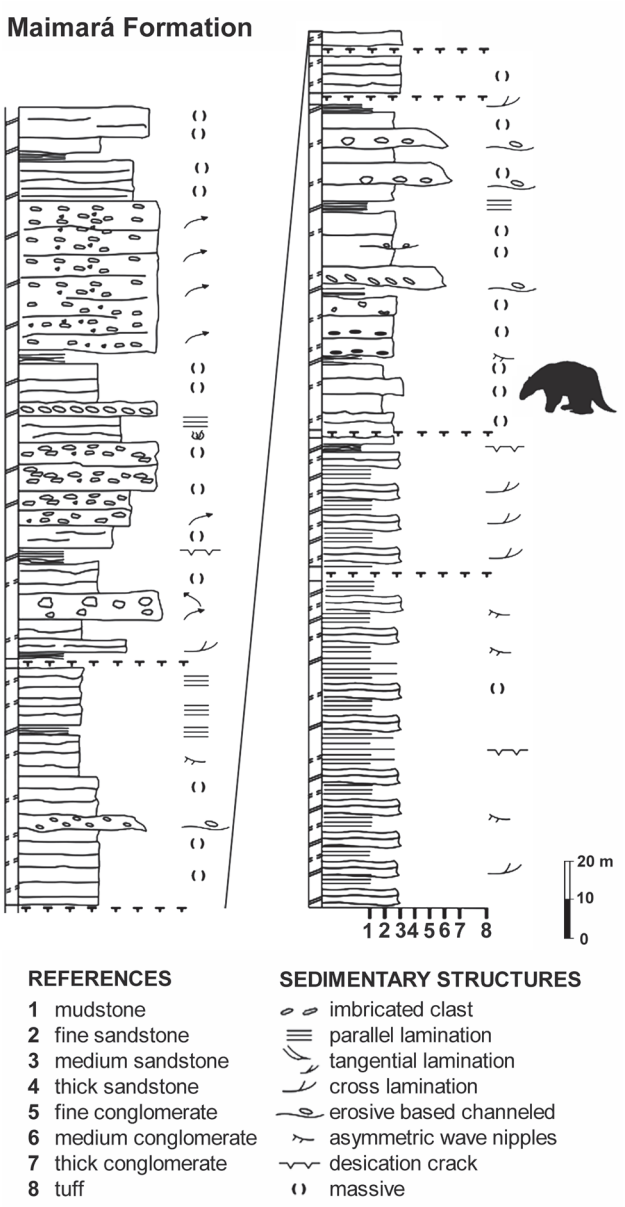

Figure 2. Stratigraphic section of Maimará Formation; the silhouette of the sloth indicates the level from which the specimen JUY-P-47 was discovered/ *Sección estratigráfica de la Formación Maimará; la silueta del perezoso indica el nivel donde el espécimen JUY-P-47 fue encontrado.*

SYSTEMATIC PALEONTOLOGY

Superorder Xenarthra Cope, 1889

Order Tardigrada Latham and Davies in Forster, 1795

Family Mylodontidae Gill, 1872

Subfamily Scelidotheriinae Ameghino, 1904

Genus *Proscelidodon* Bordas, 1935

Type species. *Proscelidodon patrius* (Ameghino, 1888).

Temporal and geographic occurrence. Huayquerian to Chapadmalalan in Argentina (McDonald, 1987) and Montehermosan to Chapadmalalan in Bolivia (Anaya and MacFadden, 1995).

Proscelidodon patrius Ameghino, 1888

Figure 3, Table 1

Referred material. JUY-P-47, right portion of a skull with maxilla, bearing M1–M5, and lacrimal (Fig. 3.1–3, 3.6).

Locality and age. Maimará Formation (late Miocene), Maimará locality, Jujuy Province, Argentina.

Description. The specimen is a small-sized adult. The M1–M5 are clearly molariform, lacking well-developed cusps. As all Scelidotheriinae, M1 is oval, diastema is missing, M2–M4 are roughly triangular, with the major axis mesiolabial/distolingual, and M5 is "keyhole shaped" (Fig. 3.3–5). Tooth row length of JUY-P-47 (Tab. 1) is similar to that of the smallest specimens of *Proscelidodon patrius*, especially the holotype of "*Scelidodon pendolai*" (MACN 8075) and *P. gracillimus*, but shorter than in *P. rothi* and Pleistocene taxa such as *Scelidotherium leptocephalum* and *Catonyx tarijensis* (Fig. 4). In occlusal view, the anteroposterior axis of the tooth row is labially convex, slightly more than in *P. patrius* MACN A-223; in MNHN-Bol-V 3353 the tooth row is slightly convex but not as much as in the Maimará specimen. All upper molariforms have a vertical groove (= sulcus) on their labial and lingual surfaces (Fig. 3.4).

***Table 1 - Measurements in mm of upper molariforms of* Proscelidodon patrius *(JUY-P-47) from the late Miocene of Maimará/* Dimensiones en mm de los molariformes superiores de *Proscelidodon patrius* (JUY-P-47) del Mioceno tardío de Maimará.**

Diameter of M1 (MDxT)	*12.6x7*
Diameter of M2 (MDxT)	*13.8x12.1*
Diameter of M3 (MDxT)	*14x11.6*
Diameter of M4 (MDxT)	*12.8x10.1*
Diameter of M5 (MDxT)	*10x7.4*
Length of the tooth row	*68.6*

Abbreviations/Abreviaturas: MD*, mesiodistal/* mesiodistal; ***T****, transverse/* transverso.

The M1 is oval, mesiodistally long, with its width decreasing slightly posteriorly (Fig. 3.3–5), and similar to *P. patrius* (MACN A-223 and MNHN-Bol-V 3353); the M1 of *P. rothi* is more sinuous (Fig. 4.2). In occlusal view, the labial side is rectilinear and the lingual side concave. Lophs are not apparent. Following the cusps terminology of Bargo *et al.* (2009) and Pujos *et al.* (2011), cusp C is damaged but relatively prominent and located at the center of the mesial side of M1. Cusps B and A are extremely reduced, located at the center of the labial and lingual sides, respectively, and only visible laterally. The sulci are barely visible on M1 in contrast to the posterior multilobed molariforms (Fig. 3.3–5).

The M2–M4 are triangular in occlusal view as in *P. patrius* (MACN 8075 and MACN A-223); in MNHN-Bol-V 3353, M2–M4 are less inclined labially (Figs 4.1, 4.4). M2 and M3 exhibit the typical scelidotheriine morphology, with the distal portion of the triangular-shaped teeth moved lingually. The mesial surface of M2 is rectilinear and perpendicular to the anteroposterior axis of the maxilla; it has a transverse mesial loph that connects cusps C (mesiolabial) and A (mesiolingual). The distal lobe of M2 is displaced lingually (Fig. 3.4–5). A similar M2 morphology is present in *Proscelidodon patrius* and *P. rothi*. A small secondary cusp is located at the distal extremity of the peripheral wall of M2. Two wear facets are present on M2; the mesial facet is produced by a cuspid of m1 and the distal by a cuspid of m2 (Fig. 3.5).

The M3 is more complex and less triangular than the preceding molariforms, as occurs in *P. patrius*. In *P. rothi* (MLP 3-72: Fig. 4.2), the M3 is more quadrangular than M2 and the labial sulcus is more distal. In JUY-P-47 the mesiolabial loph is well marked, mesiolingually to distolabially extended, and delimits posteriorly the wear facet produced by m2. This loph connects cusps C and B; cusps B and A are more prominent than cusp C. A deep depression, the wear facet produced by the posterior cuspid of m2, lies at the center of the dentine (Fig. 3.5). A small secondary cusp is located at the center of the labial side. The distal portion of the tooth descends and its width decreases distally.

The M4 is more sinuous and exhibits a prominent mesial wear facet for m3. This facet is bordered distally by a mesiolabial loph that is delimited by cusps C and B; a mesiolingual cusp A is also visible. The mesiolingual surface of M4 is convex as in MNHN-Bol-V 3353. As in M3, the wear facet produced by a mesial cuspid of m4 is prominent and located at the center of the dentine. As in M3, the distal lobe of M4 is deeper than the mesial (Fig. 3.3–5).

The M5 is "keyhole-shaped," similar to that of *P. patrius*

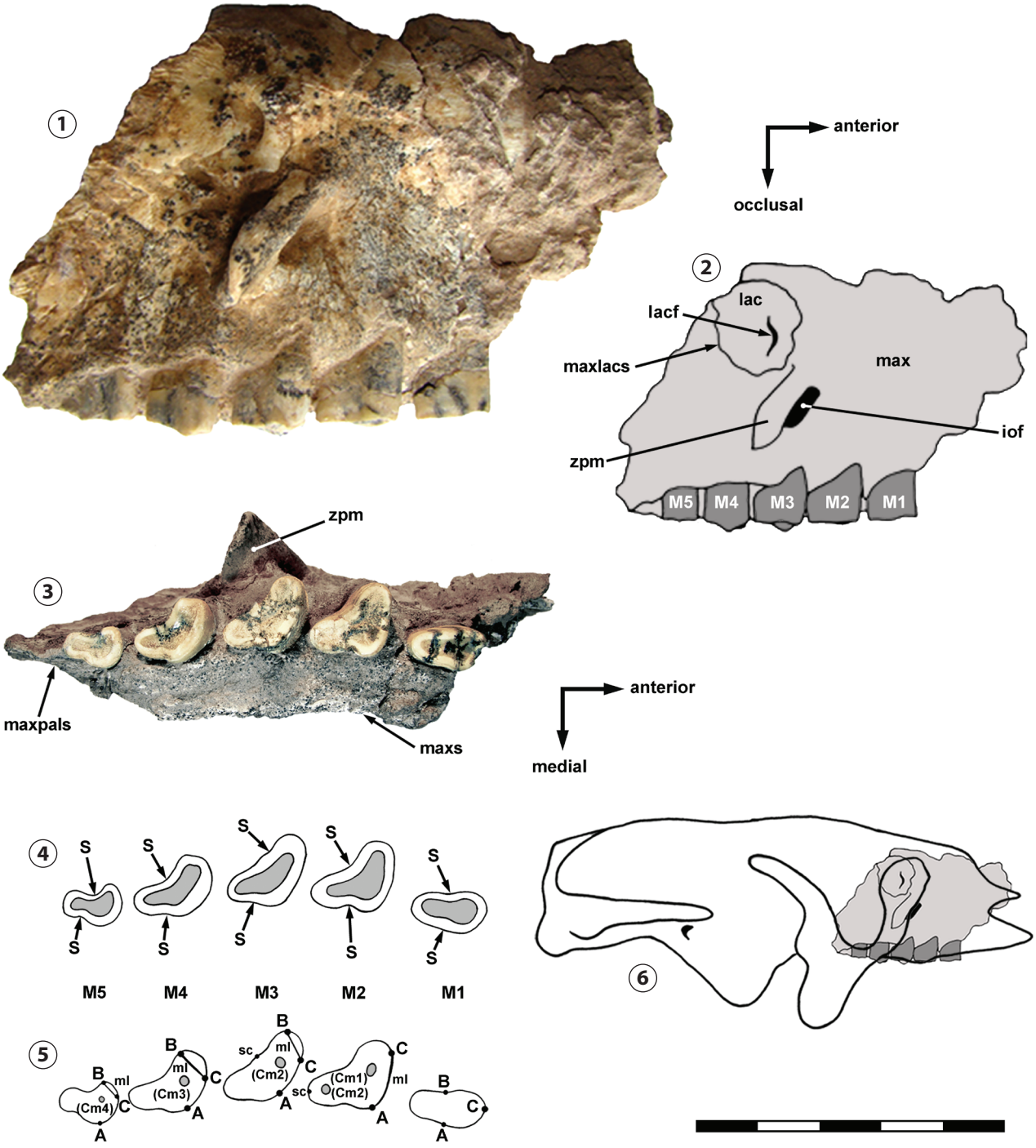

Figure 3. Right skull fragment of ***Proscelidodon patrius*** (JUY-P-47) from the late Miocene of Maimará/ *Fragmento derecho del cráneo de* **Proscelidodon patrius** *(JUY-P-47) del Mioceno tardío de Maimará*. **1**, Photograph in lateral view/ *fotografía en vista lateral*; **2**, interpretive illustration of 1*/ ilustración interpretativa de 1*; **3**, photograph in occlusal view/ *fotografía en vista occlusal*; **4–5**, illustrations of M1–M5 with representation of the dentine (gray, **4**), cusps, lophs, and wear facets produced by cuspids (gray, **5**)/ *ilustraciones de M1–M5 con representación de la dentina (gris, **4**), cúspides, lofos y facetas de desgaste producidas por los cúspides (gris, **5**)*; **6**, line drawing of JUY-P-47 (gray) superimposed on the illustration of a skull of *Proscelidodon/ esquema de JUY-P-47 (gris) superpuesto a la ilustración del cráneo de* Proscelidodon. **Abbreviations**: **A**, **B**, **C**, cusps/ *cúspides*; **(Cm-)**, wear facets produced by cuspids of lower molariform/ *facetas de desgaste producidas por los cúspides de los molariformes inferiores*; **iof**, infra-orbital foramen/ *foramen infraorbitario*; **lac**, lacrimal/ *lacrimal*; **lacf**, lacrimal foramen/ *foramen lacrimal*; **M–**, upper molariform/ *molariforme superior*; **max,** maxilla/ *maxilar*; **maxlacs**, maxillolacrimal suture/ *sutura maxilolacrimal*; **maxpals**, maxillopalatine suture/ *sutura maxilopalatina*; **maxs**, suture between the maxillae/ *sutura entre los maxilares*; **ml**, mesial loph/ *lofo mesial*; **S**, sulcus (lingual or labial vertical groove)/ *sulcus (surcos verticales lingual o labial)*; **sc**, secondary cusp/ *cúspide secundaria*; **zpm**, zygomatic process of the maxilla/ *proceso cigomático del maxilar.* Scale bar/ *escala*= 50 mm (2 and 6 not to scale/ *2 y 6 no en escala*).

MACN A-223 but distinct from MNHN-Bol-V 3353 and in contrast to the crescentic M5 of *P. rothi* (MLP 3-72, Fig. 4.2) and *P. gracillimus* (MACN 8470, Fig. 4.4). In JUY-P-47 cusps C and B are connected by mesiolabial loph as in M3–M4 that delimits posteriorly a wear facet for m4. As in M3-M4 a deep depression, the wear facet produced by a distal cuspid of m4 is located at the center of the dentine (Fig. 3.5).

The maxilla of JUY-P-47 preserves medially the sutures for the left maxilla and posteriorly for the palatine (Fig. 3.3). The latter reaches the middle of M5. The zygomatic process of the maxilla is located at the level of M3 as in *P. patrius* (MACN A-223; Fig. 4.1). The infraorbital foramen is relatively small and opens anteroventrally (Fig. 3.1). The maxilla is dorsally bordered by the lacrimal which bears the lacrimal foramen, opening posteriorly (Fig. 3.2). The nearly complete lacrimal of JUY-P-47 is oval, resembling *P. patrius* (MACN A-223).

DISCUSSION AND CONCLUSIONS

The morphology of JUY-P-47 and in particular the presence of five upper multilobed molariforms is characteristic of Scelidotheriinae, represented during the Huayquerian by *Proscelidodon.* The size and morphology of the teeth (oval M1, triangular M2–M4, and "keyhole shaped" M5) correspond to *Proscelidodon patrius*. The Maimará specimen represents the oldest record of this species, which is contemporaneous with *P. gracillimus*. The teeth of the latter are unknown, hindering comparisons with the specimen of Maimará. The Huayquerian record of *P. patrius* in Jujuy and *P. gracillimus* in Mendoza suggests that the genus appeared in the northwest part of Argentina, then populating Bolivia and the rest of Argentina during the Montehermosan and Chapadmalalan. *P. patrius* is now formally recognized in the Argentinean provinces of Buenos Aires and Jujuy and in the Bolivian locality of Inchasi.

This species exhibits a high degree of morphological variation, in contrast with low variability observed among Quaternary taxa such as *Scelidodon chiliensis* (Pujos and Salas, 2004). If the Bolivian specimen MNHN-Bol-V 3353 belongs to *Pro-*

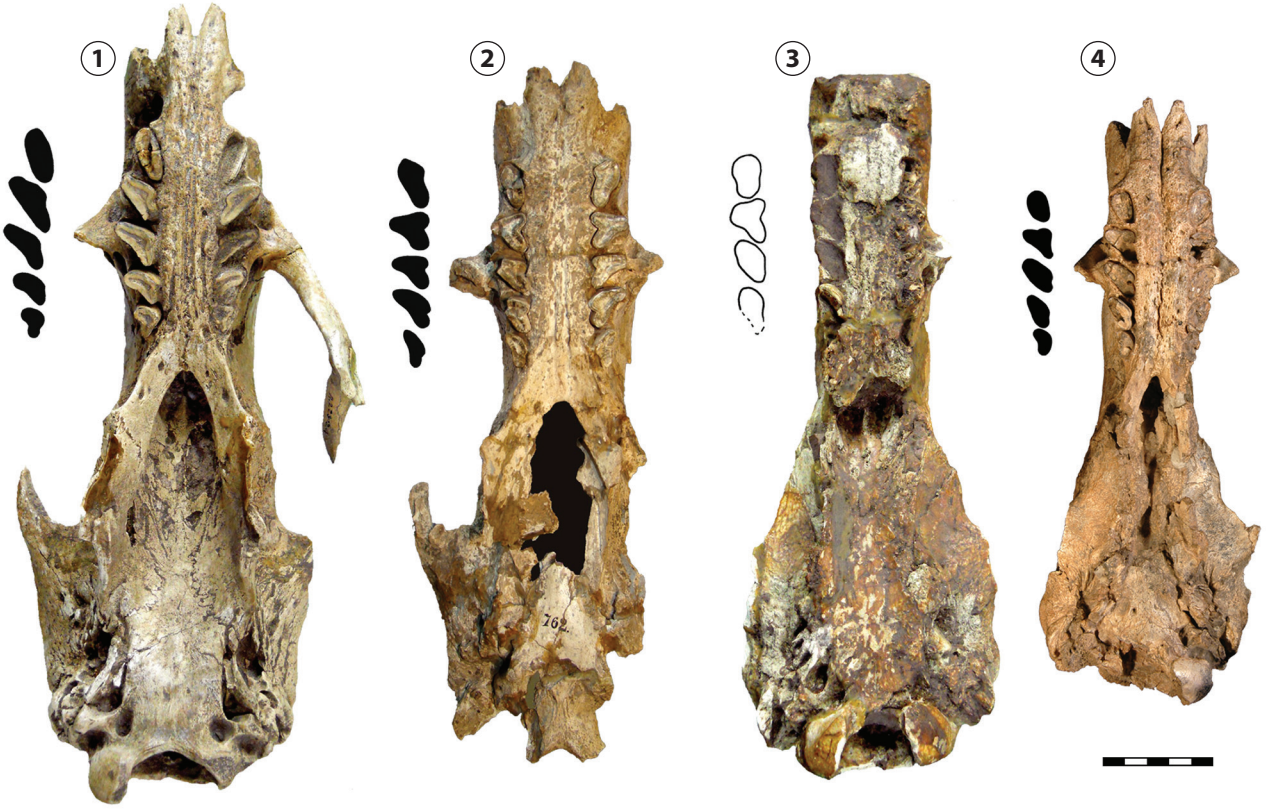

Figure 4. Photographs of the skulls and outline drawings of upper molariforms (alveoli for *P. gracillimus*) of ***Proscelidodon*** species in occlusal view/ *Fotografías de los craneos y esquemas de los molariformes superiores (alveoli para* P. gracillimus*) de las especies de* **Proscelidodon** *en vista occlusal*. **1**, ***P. patrius*** MACN A-223 holotype/ *holotipo*; **2**, ***P. rothi*** MLP 3-72 holotype (outline drawings based on left side and reversed from the original)/ *holotipo (esquemas basados en el lado izquierdo e invertido a partir del original)*; **3**, ***P. gracillimus*** MLP 65-VII-29-1; **4**, ***P. patrius*** MNHN-Bol-V 3353. Scale bar/ *escala*= 50 mm.

scelidodon, its allocation to *P. patrius* (see Anaya and MacFadden, 1995) may be questionable. Indeed, its convex tooth row, regularly oval M1 (without vertical grooves), M3–M4 without labial sulcus, M2–M4 with principal axis nearly aligned to the anteroposterior axis of the skull, and "bracket shaped" M5 may indicate affinity to another or a new *Proscelidodon* species.

The morphology of the upper dentition of *Proscelidodon* is intermediate between Santacrucian taxa and more derived forms such as the Pampean *Scelidotherium*. The M1 is regularly oval in basal scelidotheriines. *Proscelidodon* has a large mesial cusp C and an incipient lateral sulcus. As the plesiomorphic dental condition of basal Oligocene sloths is 1/1C-4/3M, we may suppose that in the "pre-scelidothere" condition, the caniniform became molariform. As occurs among the more derived species, such as *Scelidotherium leptocephalum*, *Proscelidodon* is highly hypsodont and probably a mixed or selective feeder (Bargo *et al.*, 2006b). This condition in Mylodontidae is very frequent and even more so in Scelidotheriinae in relation to the multiplication of the lobes on posterior molariforms. Lophs are less well marked and their interpretation is more difficult.

JUY-P-47 corresponds to the first sloth recorded from the late Miocene of Maimará locality (Reguero and Candela, 2008). The Maimará fauna, traditionally included within the Huayquerian age, is constituted by *Cyonasua* (Procyonidae), which represents the oldest North American immigrant in northwestern Argentina, the marsupial *Sparassocynus* (Didelphoidea, Sparrasocynidae; Abello *et al.*, in press), an indeterminate Sclerocalyptinae Glyptodontidae (Glyptodontidae), and the material assigned here to *Proscelidodon patrius*. The Maimará fauna is interesting for a better understanding of mammalian paleobiogeography and evolution between central (*i.e.*, Bolivia and the Peruvian Amazon) and southern South America (*i.e.*, Pampa) during the Mio–Pliocene.

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