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A new genus and species of Planopinae (Xenarthra: Tardigrada) from the Miocene of Santa Cruz Province, Argentina

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Abstract

Prepoplanops boleadorensis, a new genus and species of Planopinae (Xenarthra, Tardigrada), is described herein. The new taxon is based on a nearly complete specimen recovered from the Cerro Boleadoras Formation (Miocene, Río Zeballos Group), in northwestern Santa Cruz Province, Argentina. The shape and length of the prementary region of the skull and the length of the diastema of *Prepoplanops boleadorensis* differ from those present in the species of *Planops*. The posterolateral opening of the mandibular canal and the position of the posterior margin of the mandibular symphysis differ from those of species of *Prepothierium*. In addition, *Prepoplanops boleadorensis* differs from *Planops martini* in the size of the humeral tuberosities, the development of the deltoid crest, the position of the distal margin of the humeral trochlea, the shape and position of the olecranon, the development of the femoral epicondyles, and the shape of the medial margins of the patellar trochlea and medial condyle. On the other hand, it differs from *Prepothierium potens* in the shape of the medial margin of the medial condyle. The recognition of *Prepoplanops boleadorensis* increases the diversity of Planopinae for the Miocene of Patagonia, Argentina.

Key words: Mammalia, Ground sloths, *Prepoplanops*, Neogene, Patagonia, South America

Introduction

Xenarthrans are characterized by a particular suite of skeletal modifications setting them apart from all other placental mammals, e.g. shape and relationship of the vertebral metapophysis on the last thoracic and lumbar vertebra –xenarthral apophysis–, presence of synsacrum, ischio-sacral union, sacroischial fenestra, reduction or absence of enamel, monophiodonty, hypsodonty (McDonald 2003). Molecular evidence indicates that they represent one of the four major mammalian clades (Delsuc *et al.* 2001, 2002, 2011; Madsen *et al.* 2001; Murphy *et al.* 2001; Moller-Krull *et al.* 2007; Prasad *et al.* 2008; Delsuc & Douzery 2008). Xenarthra, including fossil species, consists of two major clades: Cingulata (armadillos, pampatheres, and glyptodonts), characterized by the development of bony dermal armor, terrestrial lifestyle (with different degree of digging capacities) and omnivorous, with different degrees of carnivorous or herbivorous diet (see Vizcaíno 2009); and Pilosa, without dermal armor (except for some mylodonts that have dermal ossicles) but with a dense hair covering, which in turn comprise Vermilingua and Tardigrada. While both of the former taxa pursue either terrestrial or arboreal lifestyles, or some kind of combination of them (Toledo 2012), Vermilingua (anteaters) show marked adaptations to myrmecophagy, whereas Tardigrada (sloths and ground sloths) are generally herbivorous (see McDonald & De Iuliis 2008; Vizcaíno 2009; Brandoni *et al.* 2010).

Tardigrada (*sensu* Latham & Davies 1795) or Phyllophaga or Folivora (see further discussion on the use of these terms in Delsuc *et al.* 2001; Fariña & Vizcaíno 2003, McKenna *et al.* 2006) constitute one of the characteristic mammalian groups for the Cenozoic of South America. After the Deseadan (Late Oligocene), Tardigrada become abundant in the fossil record, and are represented by several lineages (*e.g.* Megatheriidae,

Nothrotheriidae, Megalonychidae, and Mylodontidae; see Gaudin 2004) that were especially diversified during from the Miocene to the Pleistocene.

Traditionally, Megatheriidae comprises two groups: Megatheriinae, represented by giant ground sloths such as *Megatherium* Cuvier, and *Eremotherium* Spillmann; and Planopinae (De Iuliis 1994; Gaudin 1995, 2004; Scillato-Yané & Carlini 1998; but see Pujos *et al.* 2007). The Planopinae are currently represented by several described genera: *Planops* Ameghino, *Paraplanops* Ameghino (see Ameghino 1891a), *Prepootherium* Ameghino (see Ameghino 1891b), *Proprepootherium* Ameghino, *Prepootheriops* Ameghino, *Pseudoprepootherium* Hoffstetter (see Ameghino 1904, Hoffstetter 1961, Mones 1986); however, only *Planops* and *Prepootherium* are relatively well known. *Planops* is currently represented by the type species *Planops longirostratus* Ameghino, *Planops magnus* Scott, *Planops martini* Hoffstetter, *Planops obesus* Ameghino (see Ameghino 1891a), and *Planops grandis* Scillato-Yané & Carlini, the last two of which are poorly known. *Prepootherium* is represented by *Prepootherium filholi* Ameghino (see Ameghino 1891b), *Prepootherium potens* Ameghino (see Ameghino 1891a), and *Prepootherium moyanoi* Ameghino (see Scott 1903-04, Hoffstetter 1961, Mones 1986).

Planops longirostratus and *Planops magnus* were described on the basis of cranial remains (Ameghino 1887, Scott, 1903-04), whereas *Planops martini* was based on cranial and postcranial remains (Hoffstetter 1961). On the other hand, *Prepootherium filholi* was erected on the basis of cranial remains, *Prepootherium moyanoi* on mandibular remains, and *Prepootherium potens* on molariforms and postcranial remains (Ameghino 1891b, 1894; Scott 1903-04, Hoffstetter 1961).

Most of the above mentioned Planopinae species were found in the Santacrucian SALMA (Early Miocene) deposits of the coast of Santa Cruz Province, in southern Argentina (see Scott 1903-04, Hoffstetter 1961). *Planops grandis* was recovered from the west of Neuquén Province, Argentina, in sediments that were considered Colloncuran in age (Middle Miocene) (see Scillato-Yané & Carlini 1998).

The aim of this contribution is to describe new remains that represent a new genus and species of Planopinae based on a nearly complete specimen (cranium and most of the skeleton) recovered from the Cerro Boleadoras Formation (Miocene, Río Zeballos Group), in northwestern Santa Cruz Province, Argentina (Fig. 1).

Material and methods

Abbreviations. AMNH: American Museum of Natural History, New York, USA; BM (NH) British Museum of Natural History, London, UK; MLP: División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina; YPM-PU, Yale Peabody Museum (Princeton University collection), New Haven, USA; SALMA: South America Land Mammal Age; Fm.: Formation; Cf/cf: upper / lower caniniform; Mf/mf: upper / lower molariform, to avoid homologies with true M/m of the rest of mammals.

Analyzed material. For comparative purposes, the following specimens were examined: *Planops magnus* (AMNH PV 15346); *Planops longirostratus* (AMNH PV 9302); *Planops martini* (BM (NH) M 9204; BM (NH) M 9205 A, B, S, T, U, V, W, X, Y, Z; BM (NH) M 9206; BM (NH) M 9207; BM (NH) M 9208; BM (NH) M 9209; BM M 9210; BM (NH) M 9211; BM (NH) M 9212; BM (NH) M 9213; BM (NH) M 9214; BM (NH) M 9215 A, B, C, D, E; BM (NH) M 9217 A, B, C, D, E, F, G, H); *Prepootherium filholi* (AMNH PV 9597); *Prepootherium potens* (YPM-PU 15345; YPM-PU 15521).

Geographic and stratigraphic provenance. Ugarte (1956) proposed the term “Río Zeballos Group” for an assemblage of sedimentary rocks that outcrop between 46°30′S and 47°00′S, between the Andes mountain range and the plateau of Buenos Aires lake (Fig. 1). They form a succession of sandstones and limolites with interspersed argillites and conglomerates, generally with light yellowish gray color, with important presence of pyroclasts. Ugarte (1956) defined three successive formational units, Río Jeinemeni Fm., Cerro Boleadoras Fm., and Río Correntoso Fm. The fossil bearing unit, Cerro Boleadoras Fm., consists of well-consolidated magnetiferous medium-grained sandstone, grayish yellow with greenish hues in color (Fig. 2). It occurs as highly homogeneous sequences, sometimes intercalated with banks of cineritic tuffs, petrified trunks of trees and characteristic spheroidal concretions, with a sedimentary profile that is about 130 stratigraphic meters thick (Dal Molín & Colombo 2003). Regarding the age previously inferred for this unit, Ugarte (1956), based on the identification of the mammalian fauna by Rosendo Pascual, considered the age of the fauna found in the Cerro Boleadoras Fm. to correlate with the Friasian *s.l.* SALMA as defined by Kraglievich (1930). Subsequently, Carlini *et al.* (1993) reported the presence of mammal remains of Santacrucian *s.l.* (Early Miocene) age, and Scillato-Yané *et al.* (1993)

considered it to be somewhat more modern than the typical Santacrucian of the coast of Santa Cruz province, and that its age would be similar to that of Río Frías Fm. (early Middle Miocene of Chile, see Marshall & Salinas 1990). Vucetich (1994), based on the study of the rodents from Cerro Boleadoras Fm., assigned it to an Early Miocene age and, although she established correlations with the Santacrucian age, and did not consider them as typically Santacrucian, but as a northwestern Patagonian variation, probably controlled by biogeographical factors.

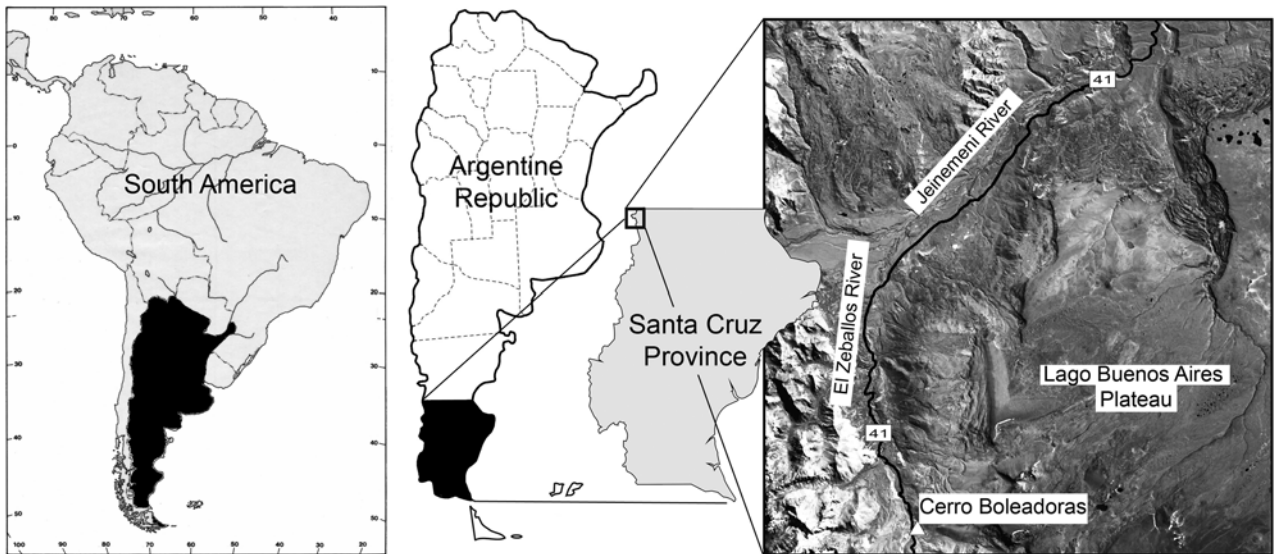


FIGURE 1. Map showing the location of Cerro Boleadoras site.

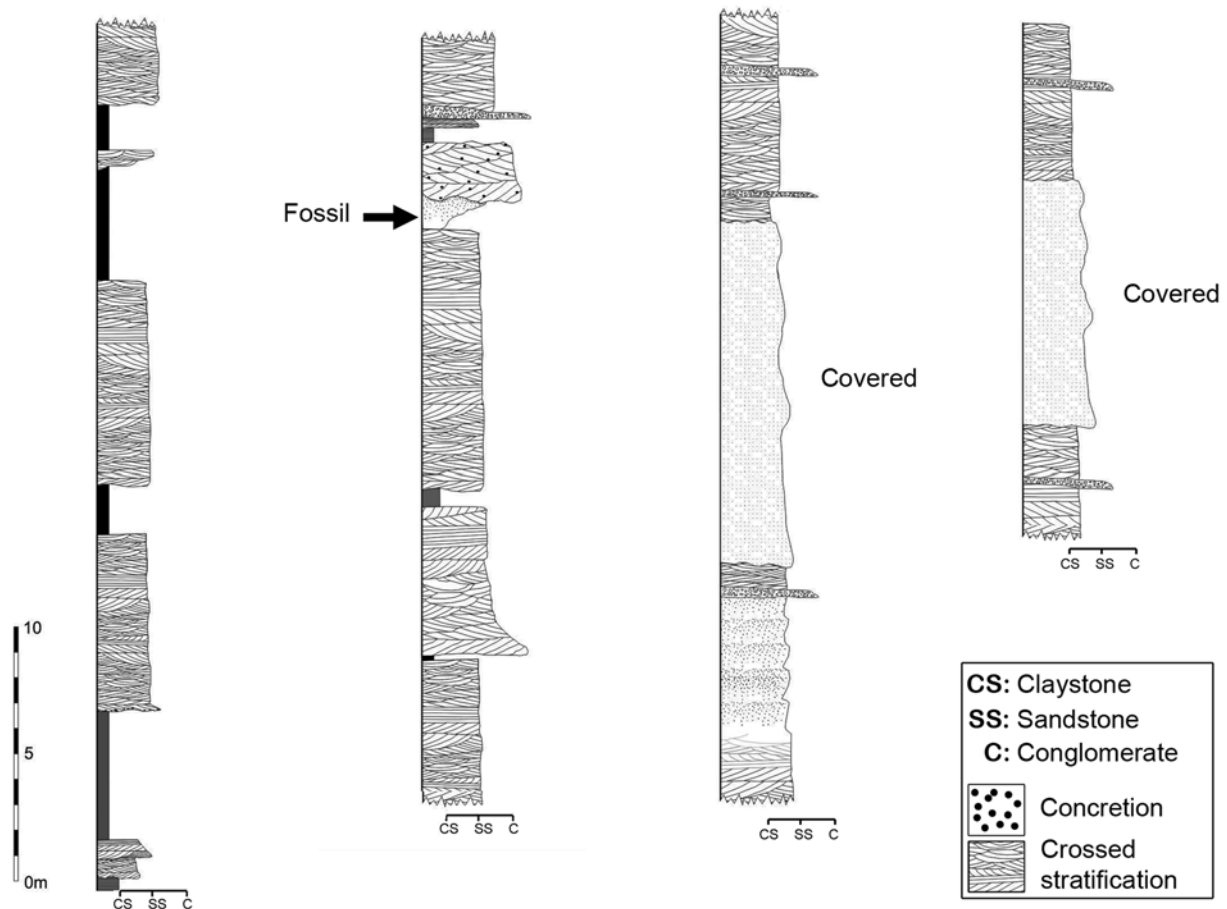


FIGURE 2. Stratigraphic profile of Cerro Boleadoras Formation at Cerro Boleadoras. Black arrow indicates the precise level where the *Prepoplanops boleadorensis* remains were collected.

Results

Systematic Paleontology

Tardigrada Latham & Davies 1756

Megatheriidae Gray 1821

Planopinae Ameghino 1887

Genus *Prepoplanops* new gen.

(Figs. 3, 4, 5, 6, 7E)

Type species: *Prepoplanops boleadorensis* new sp.

Derivation of name: from the combination of characters that resemble a mixture characteristic of *Planops* and *Prepotherium*.

Diagnosis: Similar in size to *Planops magnus*. Occipital condyles prominent, with their ventral margins below the level of the occlusal plane. Palatal prementary portion very long, lateral margins of the maxillae converge anteriorly up to the premaxillae notch, but diverge forward; palate flat at its anteriormost portion and nearly convex at the Mf3-5 level; posterior margin of the palate behind the Mf5; maxillo-palatal suture between the Mf2-3. Alveoli of the Cf oval in cross-section and separated from the Mf tooth-row by a very short diastema (similar in length to the anteroposterior length of the caniniform); Mf1-Mf4 subquadragular in outline with rounded edges and a labiolingual major axis, Mf5 oval and with a posterior notch. Mandibular prementary length greater than the tooth-row cf1-mf3 length; very short lower diastema (shorter than the anteroposterior length of cf1) between the caniniform and the molariform tooth-row. Slender ulna.

Prepoplanops boleadorensis new sp.

(Figs. 3, 4, 5, 6, 7E)

Referred species: only the type species.

Derivation of name: from Cerro Boleadoras, its geographical provenance.

Holotype: MLP 97-XI-3-1, nearly complete specimen with, skull and mandible with almost all teeth, dorsal vertebra (cervicals, thoracics, lumbar) and ribs, almost complete left scapula, partial right scapula, partial left and right humeri, partial left and right ulna, partial radius, carpals, damaged pelvic girdle, partial left (without the head) and partial right femora (distal third), left and right tibia, partial right fibula, left and right astragali, left and right calcanei, left navicular, left cuboid, left metatarsal IV and V, phalanges.

Geographic and stratigraphic occurrence: 60 km S from Los Antiguos town on Provincial Route 41, NW of Santa Cruz Province, south from Lago Buenos Aires, Argentina (46° 50' 04" S 71° 49' 29" W). Río Zeballos Group, Cerro Boleadoras Formation (Miocene).

Diagnosis: As the genus by monotypy.

Description: Similar in size to *Planops magnus*. Although with several cranial sutures (naso-frontal, fronto-parietal) persisting, the specimen corresponds to an adult, because the intermaxillary, interpalatal, maxillopalatal sutures, and those of the postcranial long bones are closed.

The skull of *Prepoplanops boleadorensis* (Fig. 3), although somewhat modified by postmortem compression, is nearly complete, but lacks the premaxillae, the descending lamina of both pterygoids, the right condylus, right jugal, right Mf2 and left Cf1. The skull is elongated, slender, tubular in shape, and presents its greater width at the level of the preorbital processes and mastoid area.

In dorsal view (Fig. 3A), as in *Planops magnus* the sagittal crest is almost absent. The frontals are elongated, nearly twice the length of the parietals or nasals. The rostrum (pre-orbital area forward the maxillary zygomatic root) is long and its lateral walls are slightly distally divergent, whereas in *Planops longirostratus* the lateral walls of the rostrum tend to converge distally. The infraorbital passage for the trigeminal-fascial nerves is divided into two foramina as in *Planops magnus* and *Planops longirostratus*, and is not a single foramen as in *Planops martini*.

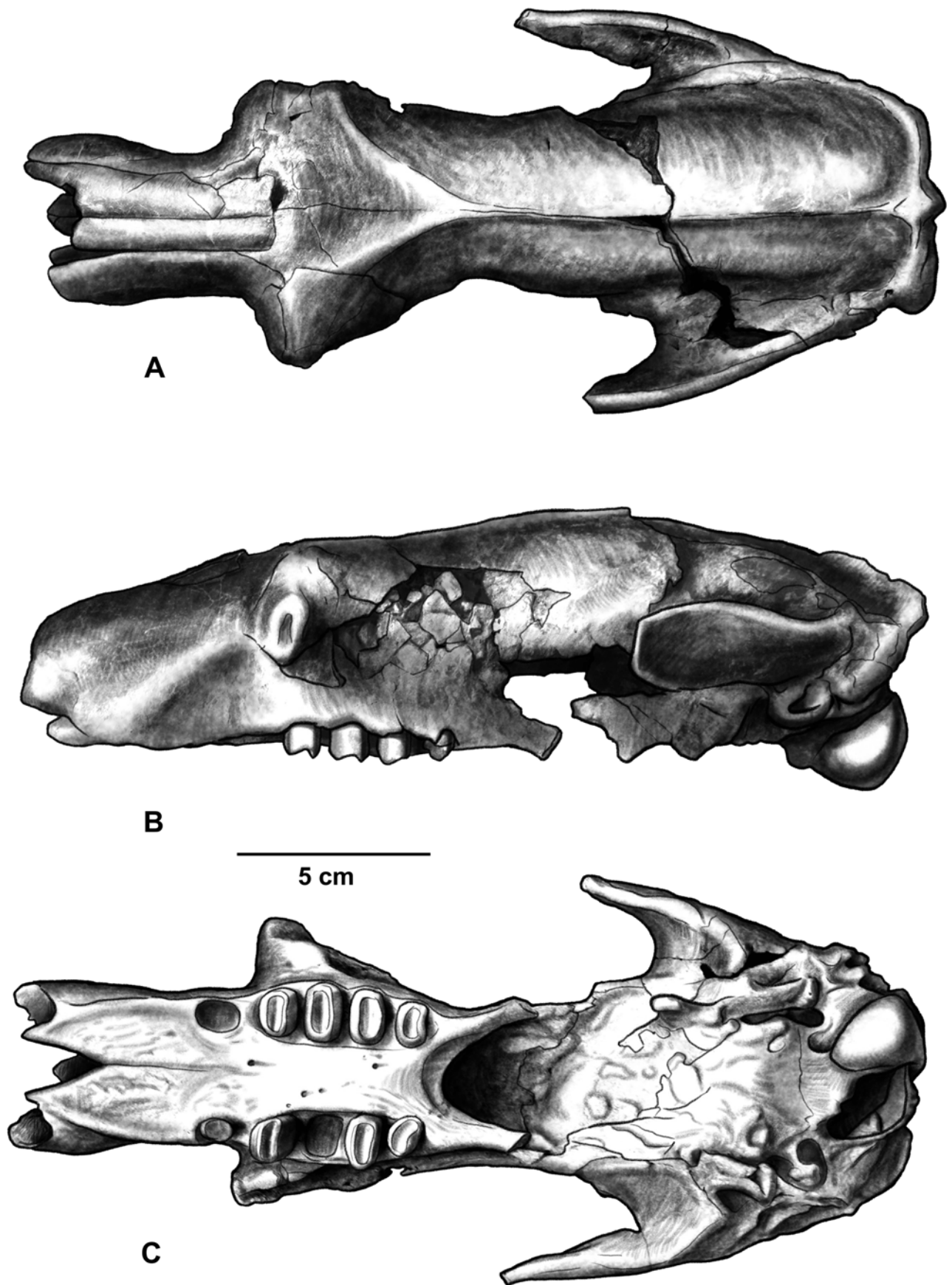


FIGURE 3. Skull of *Prepoplanops boleadorensis* (MLP 97-XI-3-1). (A) dorsal view, (B) left lateral view, and (C) palatal view.

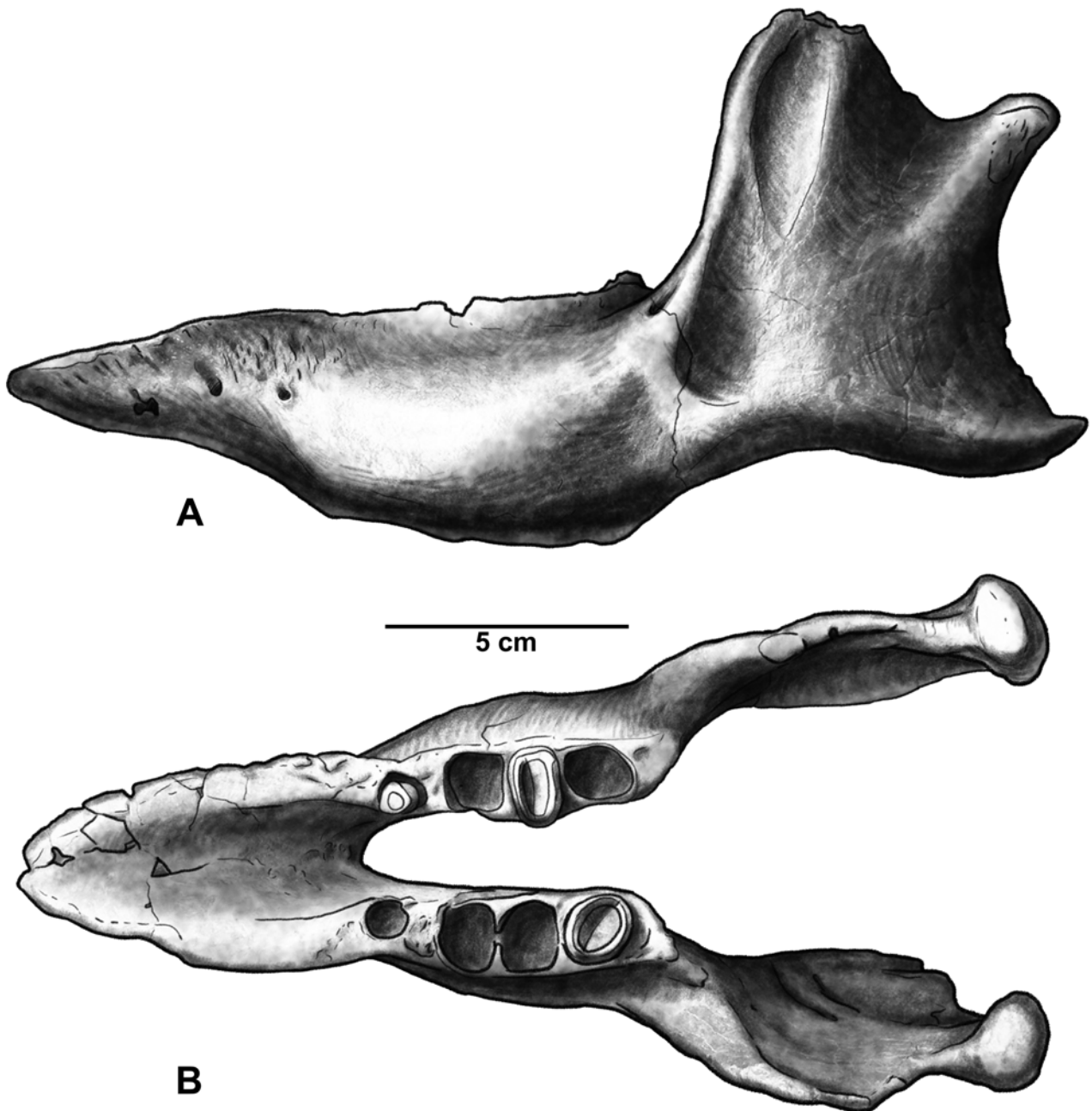


FIGURE 4. Mandible of *Preoplanops boleadorensis* (MLP 97-XI-3-1) (A) left lateral view and (B) occlusal view.

In lateral view (Fig. 3B), the skull roof is slightly convex along its anteroposterior axis; with its highest point located behind the contact between frontals and parietals, whereas in *Planops magnus* the highest point lies at the level of the midpoint of the frontals. The maxillo-jugal junction lies on the plane of the middle part of Mf1 and clearly over the level of the alveolar plane (similar to *Planops longirostratus* and *Planops magnus*). The squamosal presents a long subtriangular zygomatic process pointed anteriorly and with dorsal and ventral convex edges. As in *Planops magnus*, the ventral margin of the pterygoid seems to be below the ventral plane of the occipital condyles. The occipital condyles are more prominent than in *Planops magnus*, and their ventral margins lie below the level of the occlusal plane. Despite Hoffstetter's (1961) statement, the lacrimals appear to be located similarly to those of *Planops martini*, *Planops magnus*, and *Planops longirostratus*.

In occlusal view (Fig. 3C), the prementary portion is very long. In *Preoplanops boleadorensis*, the lateral margins of the maxillae converge anteriorly up to the premaxillae notch, but diverge forward. In *Planops magnus* and *Planops martini*, these margins are subparallel, and in *Planops longirostratus* they are nearly convex but not diverging anteriorly. At the diastema level, between the caniniform and the molariform tooth-row, the edges of the

maxillae are straight; whereas in *Planops magnus*, *Planops longirostratus*, and *Planops martini*, these margins are relatively concave (Fig. 7 A to D). As in *Planops magnus*, *Planops longirostratus*, and *Planops martini*, at the level of the molariform tooth-row, the margin of the maxillae is convex on its anteroposterior axis (Fig. 7). In *Prepoplanops boleadorensis* the palate is flat at its anteriormost portion (from the Mf1 level up to its end) although it presents two keels, and is nearly convex at the Mf3-5 level, whereas in *Planops* species the entire surface of the palate is slightly convex. The posterior margin of the palate is behind the Mf5; whereas in *Planops longirostratus* this margin is at the midpoint plane of the Mf5 (Fig. 7 C, D). In the new species the maxillo-palatal suture lies between the Mf2-3, whereas in *Planops magnus* is at the level of the midpoint of Mf3. As in *Planops magnus*, the glenoid fossa extends over the squamosal zygomatic process, and is slightly concave and wide. The margins of the occipital condyles are nearly straight, showing subtriangular shape; whereas in *Planops magnus* the margins bear two opposite notches (one medio-distal and one latero-proximal) that result in an eight-shaped outline in lateral view.

The alveoli of the caniniforms are oval in cross-section and are separated from the molariform tooth-row by a very short diastema (similar in length to the anteroposterior length of the caniniform). In *Planops longirostratus* the diastema is longer, and is even longer in *Planops magnus* and *Planops martini* (almost twice the length of the anteroposterior Cf1) (Fig. 7). The caniniform is elliptic in cross-section and its occlusal surface is separated into two parts (not as in *Planops* or even in *Prepootherium*), one larger surface facing backward and a shorter one facing rearward. Except for the right Mf2, all the upper molariforms are preserved in *Prepoplanops boleadorensis*. As in *Planops magnus*, *Planops longirostratus*, and *Planops martini*, the Mf1-Mf4 are subquadrangular in outline with rounded edges and a labiolingual major axis (Fig. 7 A to D). As in *Planops magnus* and *Planops longirostratus* the Mf5 are oval and present a posterior notch, which is absent in *Planops martini* (see Hoffstetter 1961). The occlusal surface of the molariforms resembles that of Megalonychidae (see Bargo *et al.* 2009) having two transverse crests separated by a valley.

The mandible (Fig. 4) is nearly complete, but only the right cf1, right mf2, and left mf3 are preserved.

In lateral view (Fig. 4 A), as in *Prepootherium*, the anterior margin of the coronoid process lies posterior to the posterior edge of the mf3, and this molariform is entirely visible in lateral view. The abovementioned margin forms a 100° angle with the occlusal plane. The posterolateral opening of the mandibular canal lies on the base of the coronoid process slightly below the occlusal plane, entirely posterior to the mf3, and is visible in lateral view. In *Prepootherium filholi* the posterolateral opening of the mandibular canal lies on the lateral side of the coronoid process. In *Prepoplanops boleadorensis* the mandibular condylar process lies over the plane of the molariform tooth-row. The ventral margin of the angular process is convex along its major axis. The symphyseal part of the mandible is subtriangular in shape and extended as a spout, with an anterior apex. Its dorsal edge lies at the molariform tooth-row plane and its walls are slightly concave and converge at the symphyseal plane. The anterior opening of the mandibular canal lies at the midpoint of the prementary length. The ventral margin of the dentary, at the tooth row level, is nearly flat being convex in *Prepootherium filholi* (see Scott 1903-04).

In occlusal view (Fig. 4 B), the lateral margins of the prementary area are nearly convex and converge to the tip of the mandible. The prementary length is greater than the tooth-row cf1-mf3 length, whereas it is shorter in *Prepootherium filholi*. The posteroventral edge of the mandibular symphysis lies anterior to the caniniform plane, but is slightly posterior in *Prepootherium*. The mandibular condylar process is oval in outline, with its major axis oriented transversally. The molariform tooth-rows are parallel, as in *Planops*. Scott (1903-04) and Hoffstetter (1961) indicated that in *Prepootherium* the molariform tooth-rows converge posteriorly (but see Discussion). A very short diastema (shorter than the anteroposterior length of cf1) occurs between the caniniform and the molariform tooth-row, whereas *Prepootherium filholi* has a longer diastema (greater than the anteroposterior length of cf1). The cf1 is subcircular in cross-section, and bears a forward-facing wear surface. The mf2 is oval in cross-section and the mf3 is subcircular (as in *Prepootherium filholi*).

In ventral view, the distal half of the symphysis bears a keel-like structure, whereas the proximal half is almost flat.

The humerus (Fig. 5 A, B) is slender and distally broad and flat; the humeral head is hemispheric to pyriform; the tuberosities are well developed and separated by a distinct groove from the articular surface of the head. Its general morphology is similar to that of *Prepootherium potens* and *Planops martini*. However, as in *Planops martini*, both tuberosities lie at the same level and their proximal margins do not reach the proximal level of the humeral head. As in *Prepootherium potens* (see Scott 1903-04: 338), the greater tuberosity is slightly more robust

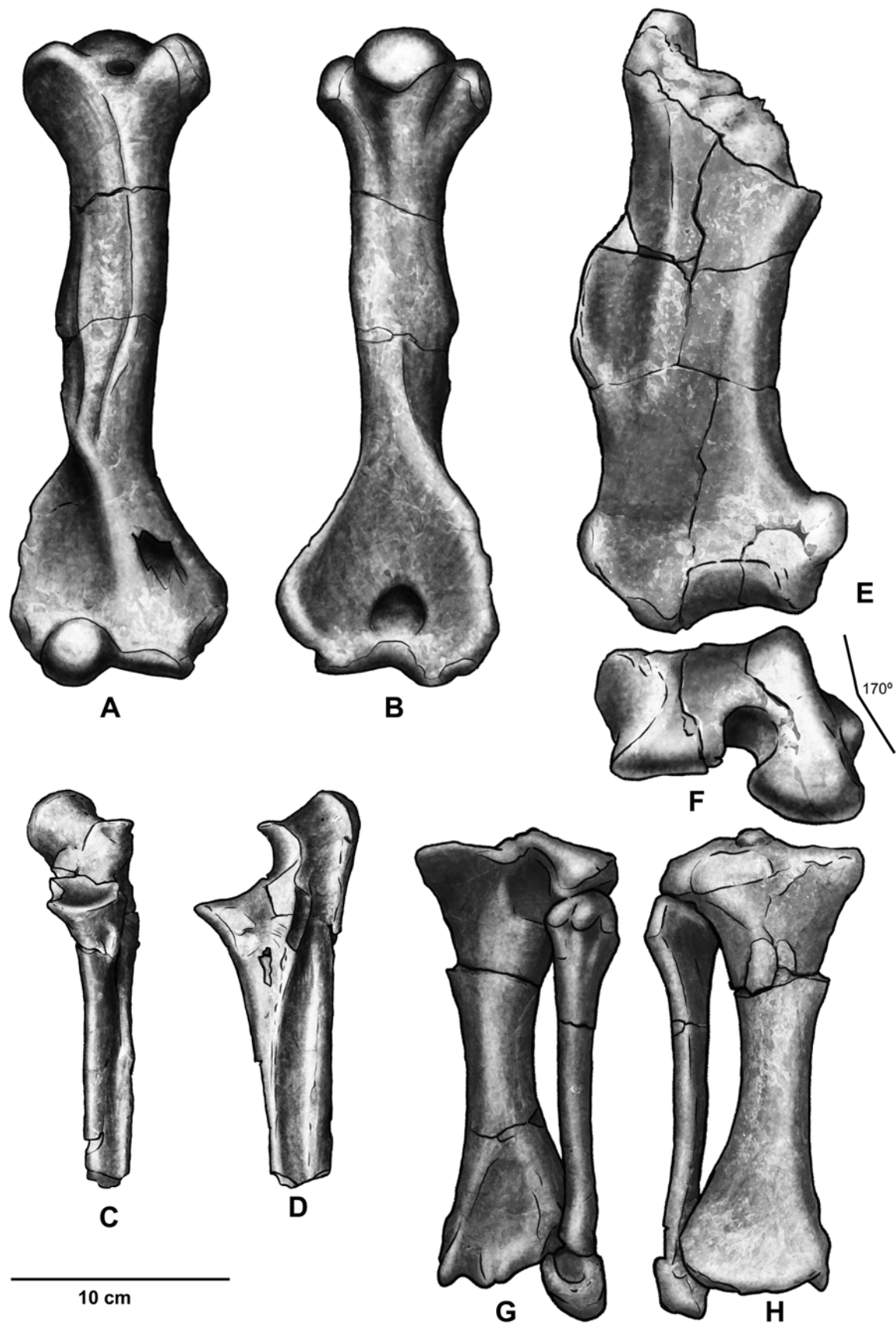


FIGURE 5. Pos-cranial elements of *Prepoplanops boleadorensis* (MLP 97-XI-3-1). Right humerus in (A) anterior view and (B) posterior view; right ulna (proximal half) in (C) anterior view and (D) medial view; right femur (without its head) in (E) anterior view and (F) distal view; right tibia and fibula (articulated) in (G) posterior view and (H) anterior view.

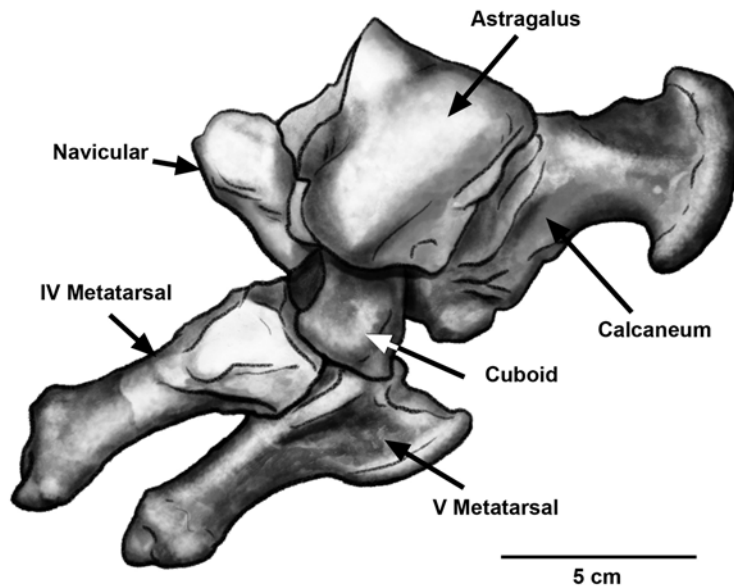


FIGURE 6. Left articulated partial pes of *Prepoplanops boleadorensis* (MLP 97-XI-3-1).

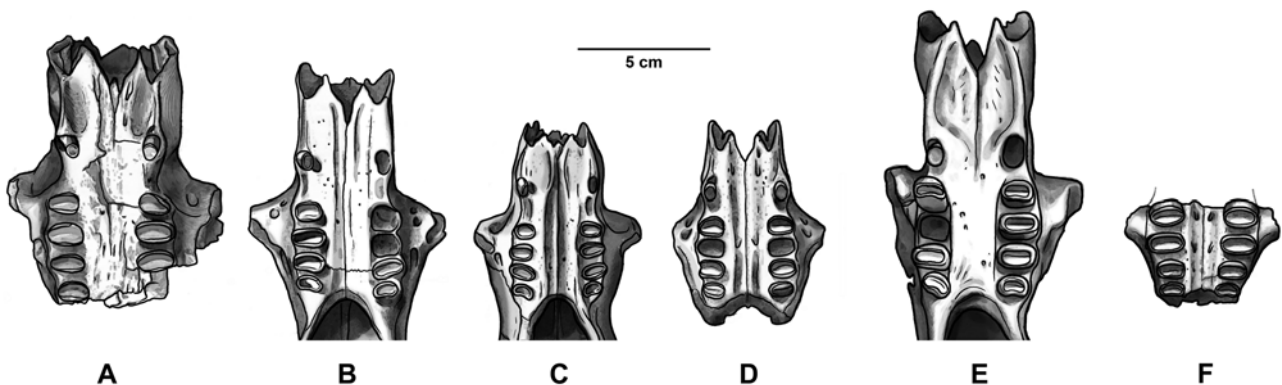


FIGURE 7. Comparative palatal views of the best known Planopinae. (A) Holotype of *Planops martini* (BM (NH) M 9204); (B) holotype of *Planops magnus* (AMNH PV 15346); (C) holotype of *Planops longirostratus* (no collection number); (D) *Planops longirostratus* (AMNH 9302); (E) Holotype of *Prepoplanops boleadorensis* (MLP 97-XI-3-1); (F) Holotype of *Prepothierium filholi* (no collection number).

than the lesser tuberosity; whereas in *Planops martini* both tuberosities are similar in size (Hoffstetter 1961: 75). The deltopectoral crest (formed by the merge of the deltoid and pectoral crests) (Fig. 5 A) is well developed and extends from the greater tuberosity along the anterior surface of the diaphysis to its distal third. The deltoid crest is not well preserved, but seems to be a thin lamina that extends medially and reaches the pectoral crest; whereas in *Planops martini* the deltoid crest is well developed and laterally projected. At the distal end of the deltopectoral crest, the diaphysis has its greatest anteroposterior depth.

The entepicondylar foramen (Fig. 5 A) is 22 mm long at its major axis, and its anterior edge is formed by a thin bone bridge, 13 mm wide. The epitrochlea is relatively more projected than the epicondyle.

As in *Planops martini*, the capitulum is hemispheric, and its articular surface is pyriform in outline and pointing backward. In anterior view, the distal outline of the trochlea is angled with respect to the distal plane (*i.e.* the plane perpendicular to the vertical diaphyseal axis); but in *Planops martini* this trochlear margin is more angled with respect to the abovementioned plane and ventromedially projected. In addition, in *Prepoplanops* the distal margin of the capitulum is distally extended relative to the distal margin of the trochlea; whereas *Planops martini* presents the opposite condition.

Posteriorly (Fig. 5 B), the olecraneal fossa is 25 mm in diameter (along its major axis).

The ulna of *Prepoplanops boleadorensis* (Fig. 5 C, D) is more slender than that of *Planops martini*.

Proximally, as in other Tardigrada, the ulna has an articular facet for the humerus divided into two successive areas (one for the capitulum and another one for the trochlea), and a third proximal facet for the radius. In the new species the olecranon projects posteromedially, and the angle of the trochlear facet (with respect to the antero-posterior vertical plane) is approximately 80°, whereas in *Planops martini* the olecranon is not projected, and the angle is greater.

In the femur (Fig. 5 E, F) the femoral diaphysis is anteroposteriorly compressed, with the greater anteroposterior thickness on the medial margin. The third trochanter (Fig. 5 E) is thin, subtriangular in section, and forming a lamina as in *Planops martini*. The patellar facet is broad and slightly concave latero-medially; it is connected with both articular condyles by an isthmus as in Santacrucian sloths, mylodontids, several Megalonychidae, and some Megatheriinae. In *Planops martini* the isthmuses have nearly the same width, whereas in *Prepoplanops boleadorensis* and *Prepotherium potens* the external isthmus is wider than the internal one. As in *Prepotherium potens*, the angle between the medial margin of the patellar trochlea and the medial margin of the medial condyle is almost 170° (Fig. 5 F), but in *Planops martini* both medial margins form a 130° angle between them.

The articular condyles are prominent and the intercondylar fossa is deep and narrow. As in other Planopinae, in *Prepoplanops boleadorensis* the articular surface of the medial condyle is pyriform in outline (Fig. 5 F); however, the medial margin of the medial condyle is not as rounded as in *Prepotherium potens* or *Planops martini*. The articular surface of the lateral condyle is subpentagonal in outline and latero-medially concave. Both epicondyles are well developed, but not as projected as in *Prepotherium potens* or *Planops martini*.

The general morphology of the tibia (Fig. 5 G, H) resembles that of *Planops martini* and *Prepotherium potens* but seems to be more slender than those. Proximally, the facets for the femoral condyles are similar in size; the medial facet is concave and trapezoidal in outline, and the lateral one is slightly convex and quadrangular. The proximal facet for the fibula is flat and located slightly posterior to the diaphyseal shaft. Distally, there are three contiguous facets; two for the astragalus, and one for the distal end of the fibula. The canals (two) for the tarsal extensor tendons are very laterally placed, and the laminae that delimit them are extended and strongly project postero-ventro-medially.

In the fibula (Fig. 5 G, H), the proximal epiphysis bears a main bilobated facet for articulation with the tibia and, posteriorly, a smaller facet (for a sesamoid?). The diaphysis is slender and subtriangular in section, with the medial surface slightly concave on its anteroposterior axis. Distally the external malleolus is very massive as in *Planops martini* and *Prepotherium potens*. Distally, the facet for the tibia is not well preserved but seems to be oval in outline.

The pes (Fig. 6) is almost complete proximally. The fibular facet of the astragalus is subtriangular in outline with posteriorly directed apex, and almost flat; dorsomedially it is limited by and contacts with the discoid facet, at a 90° angle. Its antero-ventrolateral portion contacts the ectal facet forming a 92° angle. Lateromedially and distoproximally the discoid facet is nearly convex, and contacts the odontoid facet forming a 130° angle. The navicular facet is sessile and located on the anteriormost part of the astragalus, it is subtriangular to oval in section, with its major axis oriented dorsolateral-ventromedially. This facet presents two portions: one (dorsolateral) is concave and the other (ventromedial) convex. Medially with respect to the navicular facet, the cuboidal facet is almost flat, with a subtriangular to pyriform outline. The ectal facet is oval to subtriangular and antero-posteriorly concave; the sustentacular facet is smaller, trapezoidal, and nearly flat. Both facets are separated by a deep *sulcus calcanei*.

The calcaneum is large, its diaphysis is dorso-ventrally compressed and its proximal and distal ends are expanded. The central part of the diaphysis is subtriangular in section with dorsolateral apex; ventrolaterally the diaphysis is concave along its anteroposterior axis. The *tuber calcaneus* is well developed, being particularly prominent on its medial portion. The ectal facet is broad, subtriangular in section, and slightly convex on its lateromedial axis. Proximo-medially, the ectal facet is very close to the sustentacular facet; but latero-distally, both facets are separated by a broad *sulcus calcanei*. The sustentacular facet is subtriangular in section, and it lies next to the cuboidal facet, forming a continuous sigmoid articular area. There is no evidence of ligament fosses in *Prepoplanops*, whereas they were described by Hoffstetter (1961) for the calcaneum and astragalus of *Planops martini*.

The navicular is anteroposteriorly compressed and oval to subtriangular in shape, with its major axis dorsolaterally to ventromedially oriented. The astragalar facet, located on its proximal surface, is divided into a

dorsolateral half that is nearly circular and forms a condylar prominence, and a ventromedial half that is concave along its major axes. A small subtriangular facet that articulates with the cuboid is present ventrolateral to the concave ventromedial part.

Distally, three facets are developed and clearly recognizable; they articulate with the mesocuneiform, entocuneiform, and ectocuneiform respectively. The facet for the mesocuneiform (dorsally and laterally placed) is oval and nearly flat; the facet for the entocuneiform (medially placed) is subtriangular and convex; the facet for the ectocuneiform (ventrally and laterally placed) is rhomboidal and convex.

The cuboid is irregular in shape, more or less cubic, massive, and has two important and complex articular surfaces separated by non-articulating bone. The posteromedial surface bears facets for the calcaneum, astragalus, navicular and ectocuneiform. The laterodistal surface bears facets for metatarsals III, IV, and V. The dorsal and ventral surfaces of the cuboid are rugose, relatively flat, and without articular facets. The calcaneal facet is posterolateral in position, trapezoidal in section, and nearly flat. The astragalar facet is posteromedial, approximately subtriangular in section, and contacts the calcaneal facet at straight angle. The navicular facet, which forms a straight angle with the astragalar facet, is flat and suboval in section. The facet for the ectocuneiform is dorsolaterally placed, just over the navicular facet and continuous with it.

The facets for the Mt IV and Mt V form a single surface that is subtrapezoidal in shape. The portion that corresponds to the Mt IV is relatively flat and subrectangular in outline. The portion that corresponds to the Mt V is square and slightly convex. Medially with respect to the facet for Mt IV, and forming a 90° angle with it, there is a very small facet that probably articulates with Mt III.

The proximal end of the Mt IV bears three facets that contacts with the Mt III, cuboid, and Mt V, respectively. The anteromedial facet for the Mt III is almost trapezoidal in shape, with its anterior half anteroposteriorly convex and its posterior half concave. The facet for the cuboid is dorsoventrally rectangular. The facet for Mt V is located laterally; it is flat and pyriform with the apex pointed ventro-medially. The distal epiphysis is subtriangular in cross-section with laterodorsal apex. The facet for the proximal phalanx of digit IV, located at the distal end of the Mt IV, is keel shaped. A very small subtriangular and convex facet lies ventromedially to this latter facet; it probably contacts with a sesamoid.

The Mt V is slightly longer than Mt IV. Its proximal half is depressed dorso-plantarly, and laterally expanded. It bears two contiguous facets on its proximo-medial surface, which are articulated with the cuboid and Mt IV. The cuboid facet is concave and suboval in shape. The facet for Mt IV, located distally with respect to the cuboid facet, is flat and pentagonal in outline. MtV is expanded distally, and does not show well-defined articular surfaces.

Measurements (in mm): Skull, preserved total length, 247; prementary length 46; c1-m4 length, 61; m1-m4 length, 44; diastema length, 4.8; maximum prementary width, 38.7; maximum palatal width on M2, 48. Mandible, total length, 222; prementary length, 79.5; c1-m3 length, 52.4; m1-m3 length, 37.9; diastema length, 4.9; mandibular depth at m2, 49.1. Humerus, total length, 298; max proximal width, 80; max distal width, 101; distal facet width, 63.5. Femur, preserved total length, 268; max distal width, 113; internal condyle width, 47; external condyle width, 43; trochlear width, 46.5. Tibia, total length, 235; proximal width, 101; distal width, 81.2. Fibula, total length, 219.

Comparisons. The morphology described for MLP 97-XI-3-1 justifies the recognition of a new genus of Planopinae. *Prepoplanops* differs from *Planops* and *Prepothierium* in: the shape of the lateral walls of the rostrum (slightly distally divergent in *Prepoplanops*, tending to converge distally in *Planops*); highest point of the skull roof located behind the contact between frontals and parietals in *Prepoplanops*, at the level of the midpoint of the frontals in *Planops*; the occipital condyles of *Prepoplanops* are more prominent than in *Planops magnus*; the margins of the occipital condyles are nearly straight, showing a subtriangular shape in *Prepoplanops*, bearing two opposite notches (one medio-distal and one latero-proximal) that result in an eight-shaped outline in *Planops magnus*; the lateral margins of the maxillae converge anteriorly up to the premaxillae notch in all taxa, but diverge forward in *Prepoplanops*, are subparallel in *Planops magnus* and *Planops martini*, and are nearly convex not diverging anteriorly in *Planops longirostratus*; at the diastema level, between the caniniform and the molariform tooth-row, the edges of the maxillae are straight in *Prepoplanops* and relatively concave in *Planops*; the palate is flat at its anteriormost portion (from the Mf1 level up to its end) although it presents two keels, and is nearly convex at the Mf3-5 level in *Prepoplanops*, the entire surface of the palate is slightly convex in *Planops*, the posterior margin of the palate is behind the Mf5 in *Prepoplanops*, and is at the midpoint plane of the Mf5 in *Planops longirostratus*; the maxillo-palatal suture lies between the Mf2-3 in *Prepoplanops*, is at the level of the

midpoint of Mf3 in *Planops magnus*; a very short diastema (similar in length to the anteroposterior length of the caniniform) is in *Prepoplanops*, is longer in *Planops longirostratus* and even longer in *Planops magnus* and *Planops martini*; the posterolateral opening of the mandibular canal lies on the base of the coronoid process slightly below the occlusal plane, entirely posterior to the mf3 in *Prepoplanops*, and lies on the lateral side of the coronoid process in *Prepotherium filholi*; the ventral margin of the dentary, at the tooth row level, is nearly flat in *Prepoplanops* and is convex in *Prepotherium filholi*; the predentary length is greater than the tooth-row cf1-mf3 length in *Prepoplanops*, and is shorter in *Prepotherium*; the posteroventral edge of the mandibular symphysis lies anterior to the caniniform plane in *Prepoplanops*, and is slightly posterior in *Prepotherium*; a very short diastema (shorter than the anteroposterior length of cf1) occurs in *Prepoplanops*, whereas a longer diastema (greater than the anteroposterior length of cf1) occurs in *Prepotherium filholi*; the deltoid crest of the humerus seems to be a thin lamina that extends medially and reaches the pectoral crest in *Prepoplanops*, and is well developed and laterally projected in *Planops martini*; in the humerus, the distal outline of the trochlea is angled with respect to the distal plane in *Prepoplanops*, is more angled with respect to the abovementioned plane and ventromedially projected in *Planops*; the distal margin of the capitulum is distally extended relative to the distal margin of the trochlea in *Prepoplanops*, whereas *Planops martini* presents the opposite condition; the ulna of *Prepoplanops boleadorensis* is more slender than that of *Planops martini*; in the femur, both epicondyles are well developed, but not as projected as in *Prepotherium potens* or *Planops martini*; in *Prepoplanops* the medial margin of the medial condyle of the femur is not as rounded as in *Prepotherium potens* or *Planops martini*; the general morphology of the tibia resembles that of *Planops martini* and *Prepotherium potens* but seems to be more slender than those; there is no evidence of ligament fosses in *Prepoplanops*, but they were described by Hoffstetter (1961) for the calcaneum and astragalus of *Planops martini*.

Discussion

The recognition of *Prepoplanops boleadorensis* increases the diversity of Planopinae for the Miocene of Patagonia. Nevertheless, not all of the genera and species that have been referred to Planopinae are well described or possess diagnostic features. As mentioned by Hoffstetter (1961) and until the description of *Prepoplanops*, only *Planops* and *Prepotherium* were well described. Given that the type specimens of the species of *Paraplanops*, *Prepotheriops*, and *Proprepotherium* are fragmentary or not well preserved, the validity of *Paraplanops oblongus* Ameghino, *Prepotheriops megatherioides* Ameghino, and *Proprepotherium deseadense* Ameghino is unclear; thus, it could be preferable to consider these genera and species as *nomina dubia*.

Despite advances in the knowledge of the relationships among the Tardigrada (see De Iuliis 1994; Gaudin 1995, 2004; Carlini & Scillato-Yané 2004; Pujos *et al.* 2007), the affinities of Planopinae with the other groups of Tardigrada are not totally resolved. De Iuliis (1994: 589) indicated that the weight of the evidence, though weak, favors a sister-group relationship between Planopinae and Megatheriinae. Recent cladistic analyses that include *Planops* (see Gaudin 1995, 2004; Pujos *et al.* 2007) have obtained different results for the relationships between this genus and the other sloths considered. In agreement with De Iuliis (1994), Gaudin (1995, 2004) indicated that *Planops* is the sister group of the clade Megatheriinae (only the megatherines *Megatherium* and *Eremotherium* were considered in Gaudin's analysis). On the other hand, Pujos *et al.* (2007) indicated that the relationships of *Planops martini* to other Tardigrada is uncertain, and that Megatheriidae (represented by *Megatherium americanum* Cuvier and *Eremotherium laurillardii* Lund) are related to Nothrotheriidae. In turn, Carlini & Scillato-Yané (2004) indicated that *Prepotherium* is the sister group of the Megatheriidae + Nothrotheriidae clade.

Prepoplanops boleadorensis shows some characters of its dentition (*e.g.* the shortest diastema between Cf/cf and the Mf/mf among the Planopines) that could place it (and the Planopines) close to the Megatherines (where no diastema is present and the Cf/cf are totally molarized). Moreover, this scenario could fit with a supposed younger age for the Cerro Boleadoras deposits (according with the speculations of Scillato-Yané *et al.* 1993).

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