

NEW MYLODONTOIDEA (XENARTHRA, PHYLLOPHAGA) FROM THE MIDDLE MIOCENE–PLIOCENE OF VENEZUELA

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SYNOPSIS Two new genera of Mylodontoidea, *Mirandabradys* and *Bolivartherium*, and five new species, *M. socorrensis* (Socorro Formation, Middle Miocene), *M. urumaquensis* and *B. urumaquensis* (Urumaco Formation, Upper Miocene), *M. zabasi* and *B. codorensis* (Codore Formation, Pliocene) are described. There is a high diversity of tardigrades from Middle Miocene to Pleistocene sites of Northern Venezuela. Almost all the recorded species are large and close to the size of the late Pleistocene *Glossotherium robustum* or *Lestodon armatus*. This implies that either the ‘faunas’ were composed only of large-sized tardigrades, or that the smaller taxa are missing because of taphonomic bias and that the faunal diversity was actually higher than currently indicated.

KEY WORDS *Mirandabradys*, *Bolivartherium*, new taxa, Tertiary, ground sloths, South America

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INTRODUCTION

Although the earliest records of tardigrade xenarthrans are from the Eocene of Patagonia and Antarctica, based on a

metacarpal and the apex of a caniniform (Carlini & Scillato-Yané 2004), it is only from the Oligocene to the present that their record becomes more or less continuous. During this period several distinct lineages evolved and

tardigrades extended their range into the Antilles, Central America and North America at different points in geological time. Most of the tardigrades found outside of South America are of uncertain affinities and their relationship to South American forms cannot be confidently determined (Webb 1989; White & MacPhee 2001). Palaeogene vertebrate sites are very scarce at low latitudes and none have yielded tardigrades, although another group of xenarthrans, the Cingulata, are present (Bergqvist *et al.* 2004). Early Neogene vertebrate sites are also scarce in northern South America (Sánchez-Villagra *et al.* 2004). One of the most important is that of La Venta, Colombia, where a diverse fauna of xenarthrans has been recovered, including Cingulata, Tardigrada and Vermilingua (Hirschfeld 1976, 1985; Carlini *et al.* 1997; McDonald 1997; Theodore & Edmund 1997; White 1997). Both the Colombian and Venezuelan faunas include very basal tardigrade taxa, the earliest representatives of new lineages, as well as clades not known from the extensively prospected sites of southern South America (Carlini *et al.* 1997). Other northern sites with Neogene faunas include those of the Acre River and its tributaries in Brazil and Peru (Frailey 1986; Bocquentin & Guilherme 1999; Negri & Ferigolo 2004). The faunas from these sites show closer affinities with the more southern faunas of the 'Conglomerado osífero', Ituzaingó Formation in Entre Ríos, Argentina, which is currently considered Late Miocene (Cione *et al.* 2000).

Previously only two tardigrades have been reported from the late Miocene Urumaco Formation in Venezuela; the rather strange *Urumacotherium garciai* Bocquentin, 1984, of uncertain affinities, and a species referred to the southern genus *Lestodon* Gervais, 1855, *L. urumaquensis* Linares, 2004a. The discovery of a large number of tardigrade remains in the Socorro (Middle Miocene?), Urumaco and Codore formations reported in this paper greatly expands our knowledge of tardigrade diversity in Venezuela. The Urumaco Formation has been assigned to the Late Miocene and its fauna has often been compared with that of the Acre River and Ituzaingó Formations (Aguilera 2004; Cione *et al.* 2000). The Codore Formation, interpreted as Pliocene (Ministerio de Energía y Minas 1997), is much less fossiliferous and only now are the first vertebrate taxa being reported. These faunas differ from previously described faunas and are thus of great interest.

The tardigrade xenarthrans described here include new mylodontoids and the first megatherioids, represented by both megalonychids and megatheriids. Among the mylodontoids and megalonychidae are forms closely related to taxa present in the Antilles, Central America and North America. Curiously, because of taphonomic bias, most taxa recognised here are represented by long bones (most frequently femora) and, consequently, the initial diagnoses for the new taxa are based on this element.

Tardigrade diversity recorded for this region and time period is surprisingly large and comparable to that reached only a few times during their history, including the Late Oligocene of Patagonia (Deseadan Age: see Carlini & Scillato-Yané 2004), Middle Miocene of Patagonia (Santacrucian Age) and Late Miocene of the Argentine Mesopotamian ('Mesopotamian', 'Conglomerado osífero' of the Ituzaingó Formation: see Carlini *et al.* 2001).

Institutional abbreviations

AMU-CURS, Collection of Vertebrate Paleontology of the Alcaldía de Urumaco, Estado Falcón, Venezuela; **MACN**, Museo Argentino de Ciencias Naturales, 'Bernardino Rivadavia', Buenos Aires, Argentina; **MCN**, Museo de Ciencias, Caracas, Venezuela; **MCN-USB PB**, Universidad Simón Bolívar, Laboratorio de Paleobiología; **MLP**, Colección de Paleontología de Vertebrados del Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina; **UNEFM-CIAPP**, Universidad Nacional Experimental Francisco de Miranda, Coro, Falcón, Venezuela.

SYSTEMATIC PALAEOLOGY

XENARTHRA Cope, 1889

PHYLLOPHAGA Owen, 1842

MYLODONTOIDEA Gill, 1872

Genus MIRANDABRADYS nov.

ETYMOLOGY. After Francisco de Miranda, an important figure in the history of American independence after whom the University in Coro is named; and *bradys* = sloth.

TYPE SPECIES. *Mirandabradys socorrensis* gen. et sp. nov.

OTHER SPECIES. *Mirandabradys urumaquensis* gen. et sp. nov. and *M. zabasi* gen. et sp. nov.

OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Socorro Formation (Middle Miocene), Urumaco Formation (Late Miocene) and Codore Formation (Pliocene).

DIAGNOSIS. Large-sized mylodontoid. Skull profile with a marked angle between the rostrum and braincase. Molariforms with some transverse elongation except the last one. Femur with the diaphysis only slightly narrower distally than proximally, widening slightly up to the level of the trochanter minor and anteroposteriorly compressed; trochanter major large and massive; third trochanter developed on the lateral margin, slightly below the midpoint of the diaphysis and continued distally as a laminar area that merges with the ectepicondyle. Tibia and fibula seem proximally and distally immobilised. Tibia without marked torsion in contrast to Quaternary Mylodontinae.

COMPARISONS. *Myrandabradys* is larger than *Pseudopreotherium* but smaller than *Octodontotherium* Ameghino, 1895, *Glossotherium* Owen, 1840 and *Myodon* Owen, 1840 (Table 1). Its distinctive skull profile is somewhat similar to that of *Urumacotherium* Bocquentin, 1984 and derived with respect to *Pseudopreotherium*, *Glossotherium* and *Myodon*. In *Urumacotherium garciai* the rostrum and braincase form an angle of 130° (cf. 160° in *Mirandabradys*). This angled zone is also present in the skull of *Pseudopreotherium confusum* (Collins, 1934) from La Venta (see Hirschfeld 1985: 7), but is much more obtuse and anteriorly placed. *Mirandabradys* is further distinguished from *Pseudopreotherium confusum* by having somewhat laterally expanded molariforms, in contrast to the semicircular molars of that species. Compared to *Urumacotherium*, its molariforms are less transversely elongate.

Table 1 Linear measurements (in mm) of Mylodontoidea as discussed in the text.

Taxon	Specimen	A Skull TL	B Femur TL	C Tibia TL	D Humerus TL	E Ulna TL	B/A	D/A	B/D	B/C
<i>Lestodon trigonidens</i>	MLP 3-3	610	730	370	560	470	1.197	0.918	1.303	1.972
<i>Glossotherium myloides</i>	MLP 3-138	470	490	230	420	345	1.042	0.893	1.166	2.13
<i>Glossotherium myloides</i>	MLP 3-140	460	460	220	380	350	1	0.826	1.21	2.09
<i>Scelidotherium leptcephalum</i>	MLP w-n	490	450	290	370	365	0.918	0.755	1.21	1.551
<i>Pseudopreotherium confusum</i>	Hirschfeld (1985)	430	470	300	343	*370	1.093	0.797	1.37	1.566
<i>Thinobadistes segnis</i>	Webb (1989)	422	443	262	375	262	1.049	0.888	1.181	1.69
<i>Mirandabradys socorrensis</i>	AMU-CURS 29	*430	560	290			1.302			1.931
<i>Bolivartherium urumaquensis</i>	MCN 170-72	*440				260	1.318	0.988		
<i>Bolivartherium urumaquensis</i>	MCN 85-72		580						1.333	
<i>Bolivartherium urumaquensis</i>	MCN 71-72				435					
<i>Bolivartherium codorensis</i>	AMU-CURS 130	323								
<i>Urumacotherium garciai</i>	UNEFM-CIAAP 443		615	310	450	Ca 420			1.366	1.98

TL: total length.

Compared to *Pseudopreotherium* and the Early Miocene tardigades (e.g. *Glossotherium*, *Lestodon* and *Thinobadistes*) *Mirandabradys* has a larger and more massive trochanter major (the derived condition). However, it is not as large and massive as in *Glossotherium*. The neck of the femur is much less marked than in *Pseudopreotherium*. The presence of a laminar area that merges with the ectepicondyle on the femur is a derived condition absent from *Pseudopreotherium*, *Glossotherium* and *Myloodon*. The entepicondyle is prominent and does not project to the degree seen in *Pseudopreotherium confusum*. The diaphysis of the tibia is more strongly curved than in *Pseudopreotherium confusum* and *Urumacotherium garciai*, being completely straight in the latter. Torsion of the tibia is greater than that seen in *Pseudopreotherium* but less than in the Quaternary species of *Glossotherium* and *Lestodon*.

The ratio of the length of the femur to tibia is 1.93, closer to *Lestodon* (1.97) than to *Glossotherium* (2.13) or *Thinobadistes* (1.69). The impressions for the tendons of the flexors of the foot are shallower than those in *Lestodon* and *Glossotherium*. The tibia of *Mirandabradys socorrensis* is quite different from that of *Urumacotherium garciai*, being proportionally shorter (Table 1), straight, with well-marked articular facets for the fibula and less rotated. The medial and lateral astragalar facets are similar in both taxa.

Mirandabradys socorrensis sp. nov. (Fig. 1)

ETYMOLOGY. In reference to its stratigraphical provenance, the Socorro Formation.

HOLOTYPE. AMU-CURS 29: partial skull strongly compressed laterally in the cranium and nasal region; with palatine not very deformed; lacking dentition; alveoli with labial margins in different stages of preservation; one thoracic vertebra and three caudals; proximal fragment of left ulna; right femur, tibia and fibula (partial); two ungual phalanges; left pelvic girdle with ilium and ischium almost complete, partial pubis and complete acetabulum; all belonging to the same specimen.

REFERRED SPECIMEN. We tentatively include the specimen figured by Linares (2004b: 12, fig. 4A) as *Glossotheriopsis*,

based on its angled skull roof, low rostrum and the posterior position of the maxillary zygomatic root.

OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Socorro Formation (Middle Miocene?) (Ministerio de Energía y Minas 1997; Aguilera 2004).

DIAGNOSIS. A *Mirandabradys* whose femur has a shorter neck and which has the trochanter major positioned lower than in *M. urumaquensis*. Trochanter minor differentiated but not prominent. The patellar facet is shorter proximodistally than in *M. urumaquensis*.

DESCRIPTION. The skull is of an adult specimen since none of the sutures are evident. It is deformed having been laterally compressed, especially at the level of the parietals, frontals and nasal cavity, but is not strongly compressed at the basal region of the skull and palatal area between the dental series. The jugal and the free zygomatic part of the squamosal and maxilla are not preserved, nor are the pterygoid wings. The skull profile in lateral view is strongly angled, with the rostrum and braincase forming an angle of 130°. Unfortunately the state of preservation does not allow details of the basicranial structure to be observed. The occipital condyles seem to be positioned closer to the occiput and are less developed than in *Pseudopreotherium confusum*. In palatal view the alveoli of five teeth can be observed, but the original separation between the first tooth and the rest cannot be seen clearly because of its poor preservation.

Based on the structure of the preserved alveoli, the last tooth is the smallest and seems to have a constriction that indicates the presence of a small posterior lobe. The fourth molariform is elongate mesiolaterally. The third molariform is also elongated but less so than the fourth. Only the posterior part of the second alveoli is preserved.

The diaphysis of the femur is elongate and slightly narrower distally, anteroposteriorly depressed and it widens slightly towards the trochanter minor. The trochanter major is large and massive with the greater trochanter being similar to that of *Mirandabradys urumaquensis*, but positioned closer to the head of the femur. The trochanter minor is less developed than in *M. urumaquensis*. A third trochanter is present on the lateral margin positioned slightly below the midpoint of the diaphysis. It continues distally with a laminar

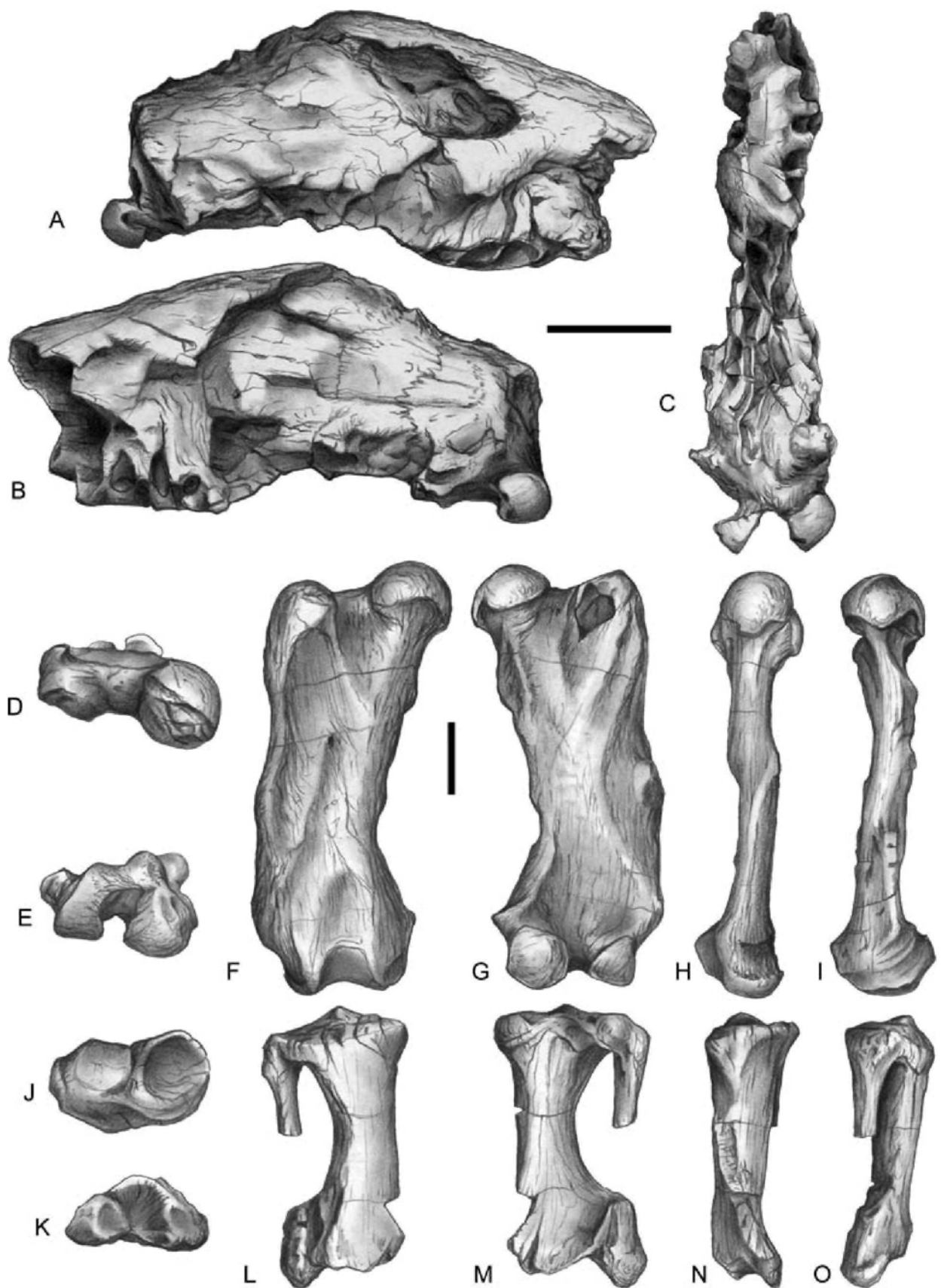


Figure 1 *Mirandabradys socorrensis* gen. et sp. nov., AMU-CURS 29 (holotype). **A–C**, skull, in **(A)** right lateral view, **(B)** left lateral view and **(C)** palatal view; **D–I**, right femur, **J–O**, right tibio-fibula. **(D)**, **(J)** proximal view; **(E)**, **(K)** distal view; **(F)**, **(L)** anterior view; **(G)**, **(M)** posterior view; **(H)**, **(N)** mesial view; **(I)**, **(O)** lateral view. Scale bar = 10 cm.

Table 2 Linear measurements (in mm) of the femur from the three new species of *Mirandabradys* and other Mylodontoidea compared in the text.

	<i>P. confusum</i> UCMP 41137	<i>M. socorrensis</i> (type)	<i>M. urumaquensis</i> (type)	<i>M. zebasi</i> (type)	<i>M. zebasi</i> (Linares, 2004)	<i>G. myloides</i> MLP 3-138	<i>G. myloides</i> MLP 3-140	<i>L. armatus</i> MLP 3-3
TL total length	50.4	56	59.4	57.1	53.5	49	46	73
DW distal width	19.7	21.2	21.1	18.5	17.8	19.3	18.5	23.5
PW proximal width	21.4	23.2	23.7	23.4	22.4	23.5	22.7	31.4
PW/DW	1.09	1.09	1.12	1.26	1.26	1.22	1.23	1.34
TL/DW	2.55	2.64	2.81	3.08	3.01	2.53	2.48	3.1
TL/DW/2	1.28	1.32	1.41	1.54	1.51	1.26	1.24	1.55
HD/TMw	1.24	1.28	1.19	1.11	1.1	0.84	0.82	0.91

P., *Pseudopreotherium*; *M.*, *Mirandabradys*; *G.*, *Glossotherium*; *L.*, *Lestodon*.

Dw, transverse distal width at the epicondilar level; **HD**, anteroposterior head diameter; **PW**, transverse proximal width at the head-major trochanter level; **TL**, total length; **TMw**, anteroposterior major trochanter width.

area that makes it continuous with the ectepicondyle, as in *M. urumaquensis*. The head of the femur is hemispheric and its diameter is a quarter larger than the width of the trochanter major. It is separated by a neck, similar to that in *M. urumaquensis*. The distal half of the femur is less rotated relative to the sagittal plane than it is in *M. urumaquensis*. The trochanteric fossa is deep and short. The medial condyle is larger than the external condyle, the difference in size between these being similar to that in *M. urumaquensis*. The intercondylar fossa is half the width of the external condyle. The entepicondyle is prominent and does not project to the degree seen in *Pseudopreotherium confusum*. The condylar surfaces are rounded and more convex than that of the internal condyle. They are continuous with the trochlear surface of the patellar facet, which is elevated and surrounded by

acute margins. The patellar facet is shorter proximodistally than in *M. urumaquensis*. The medial margin of the trochlea is positioned more anteriorly than the lateral. The femur is smaller than that of *Urumacotherium garciai* (Tables 1, 2; Fig. 2).

The tibia and fibula are distinctive. The diaphysis of the tibia is curved, narrowing at the middle and widening both proximally and distally. The axis of the proximal and distal faces are offset as a result of torsion of the tibia. The ratio of the length of the femur to tibia is 1.93.

The astragalar surface has the two typical major facets. The medial facet is elliptical and concave with its major axis oblique with respect to the sagittal plane. It is separated from the lateral facet by a gently rounded margin. The lateral facet is slightly concave mediolaterally and almost flat

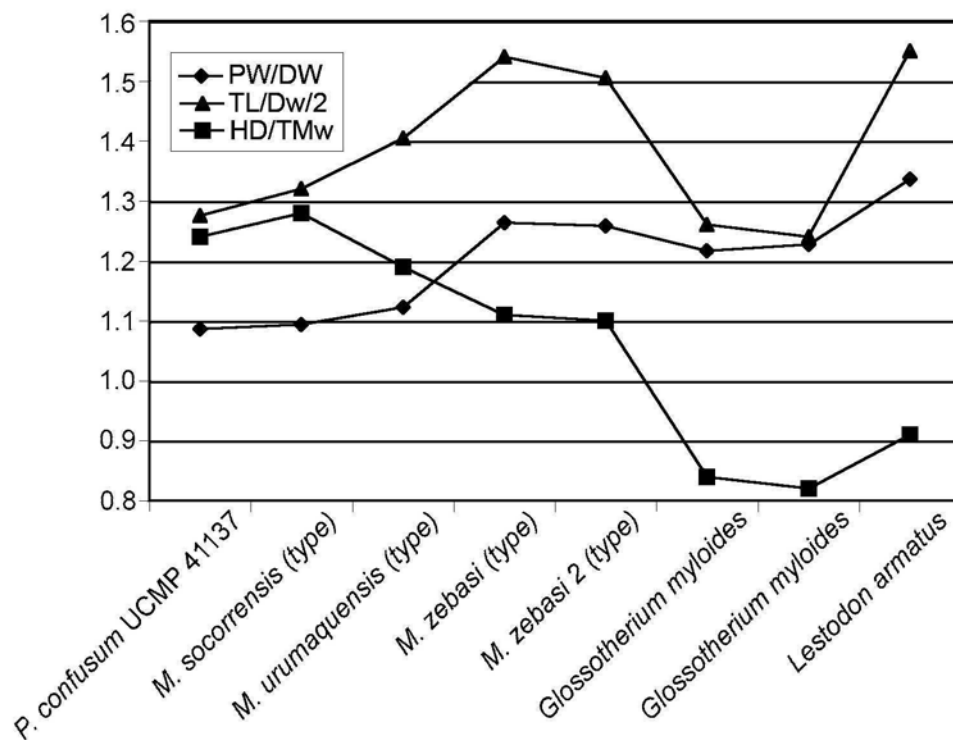


Figure 2 Graph showing three different interactions between pairs of measurements from the new species of *Mirandabradys* and other mylodontoids. DW, transverse distal width at the epicondilar level; HD, anteroposterior head diameter; PW, transverse proximal width at the head-major trochanter level; TL, total length; TMw, anteroposterior major trochanter width. See Table 2 for measurements.

anteroposteriorly. It is partially bilobate because of a concavity of the margin that separates it from the medial facet that is coincident with the concavity of the contact area with the astragalar facet of the fibula. The astragalar facet is subcircular and almost flat. The impressions for the tendons of the flexors of the foot are located on the posterior internal surface of the distal part of the tibia and are relatively shallow. The proximal and distal epiphyses of the fibia widen at their contacts with the tibia.

REMARKS. *Glossotheriopsis* Scillato-Yané, 1978, was reported from the Socorro Formation based on a partial skull (Linares 2004b: fig. 4A). However, this skull differs in several respects from the holotype of *Glossotheriopsis pascuali* Scillato-Yané, 1978 (McDonald 1997: fig. 15.3). Whereas in *Glossotheriopsis* the rostrum is short and high (as in *Glossotherium*) in the Venezuelan specimen it is longer and more depressed. Equally important is the skull profile, which rises in the middle to an angle in the Venezuelan specimen as it does in *Pseudopreotherium*, *Urumacotherium* and, especially, *Mirandabradys socorrensis*. For these reasons, the Venezuelan specimen described by Linares is included in *Mirandabradys socorrensis*.

Mirandabradys socorrensis is similar in size to *Mirandabradys zabasi*. The head of the femur of *M. socorrensis* is separated by a neck that is shorter than that of *M. urumaquensis* and the trochanter major is positioned lower in *M. socorrensis* than in *M. urumaquensis*.

***Mirandabradys urumaquensis* sp. nov. (Fig. 3A–F)**

ETYMOLOGY. In reference to its stratigraphical provenance, the Urumaco Formation.

HOLOTYPE. AMU-CURS 157; left femur and 10 thoracic vertebrae.

OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Urumaco Formation, Late Miocene (Ministerio de Energía y Minas 1997; Aguilera 2004).

DIAGNOSIS. *Mirandabradys* species larger than *M. socorrensis* and *M. zabasi*. Proximal half of the femur more expanded mediolaterally than in *M. socorrensis* and with the distal half of the femur more rotated toward the sagittal plane. Trochanteric fossa well developed. Trochanter minor more developed than in *M. socorrensis* and *M. zabasi*; third trochanter more distinguishable. Entepicondyle prominent and projecting medially as in *M. socorrensis*. Patellar facet more developed and straighter than in the other two species of *Mirandabradys*.

DESCRIPTION. The femur is slightly compressed at its diaphysis by diagenesis, but the epiphyses do not seem to be deformed. It is smaller than the femur of *M. socorrensis*. In morphology it is similar to *M. socorrensis*, but with the ectepicondyle apparently a little more developed and with the distal half of the femur rotated more toward the sagittal plane. The trochanteric fossa is well developed although not very extended proximodistally.

The main differences separating the femur of *M. urumaquensis* from *M. socorrensis* are: the larger expansion of the proximal half, the greater height of the trochanter major, the greater curvature of the distal half (which is also nar-

rower), and the greater development of the trochanter minor (Table 2; Fig. 2).

***Mirandabradys zabasi* sp. nov. (Fig. 3G–N)**

ETYMOLOGY. In honour of Mr Zabas García Colina, one of the founders of the town of Urumaco and one of the last members of the indigenous people from the area.

HOLOTYPE. AMU-CURS 127, left femur almost complete, lacking the area between the trochanter major and the head, and the patellar facet.

OTHER MATERIAL. AMU-CURS 128, the distal half of a left femur; MCN-USB 16–04 PB, a right femur without the external margin of the distal two-thirds. This material was originally assigned by Linares (2004a) to *Lestodon codorensis* Linares, 2004.

OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Codore Formation, Pliocene (Ministerio de Energía y Minas 1997; Aguilera 2004).

DIAGNOSIS. Femur with diaphysis more curved longitudinally and the distal section narrower than in *Mirandabradys socorrensis* and *M. urumaquensis*. Trochanter major massive, more so than in the other species of *Mirandabradys*. Trochanter minor less developed than in *M. socorrensis* and *M. urumaquensis*.

DESCRIPTION. Femur morphology as in *Mirandabradys socorrensis* but with the distal half of the femur more rotated towards the sagittal plane than in *M. socorrensis*. Other differences include the larger expansion of the proximal half of the femur, the greater height of the trochanter major, the larger curve of the distal half (which is narrower) and the greater development of the trochanter minor (Table 2; Fig. 2). The femur is smaller than that of *Urumacotherium garciai* and slightly larger than that of *M. socorrensis*.

MYLODONTIDAE Gill, 1872

LESTODONTINAE Ameghino, 1889

Genus *BOLIVARTHERIUM* nov.

ETYMOLOGY. In honour of the Libertador General Simón Bolívar, American revolutionary; and *therium* = mammal.

TYPE SPECIES. *Lestodon urumaquensis* Linares, 2004.

REFERRED SPECIES. *Lestodon urumaquensis* Linares, 2004 and *L. codorensis* Linares, 2004.

OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Urumaco Formation (Late Miocene?), Codore Formation (Pliocene) (Ministerio de Energía y Minas 1997; Aguilera 2004).

DIAGNOSIS. Middle-sized lestodontine, smaller than Quaternary species of *Lestodon* (Table 1). Rostrum lower (plesiomorphic) and upper caniniform more curved than in *Lestodon*, like the '*Lestodon*' sp. from the Montehermosan of Argentina. The edentulous zone (= diastema) in front of the molariforms is elevated with respect to the occlusal plane (an apomorphic character with respect to the rest of the Lestodontines), consequently, the alveolar margin of the caniniforms is dorsal to the molariforms, like '*Lestodon*' sp. from

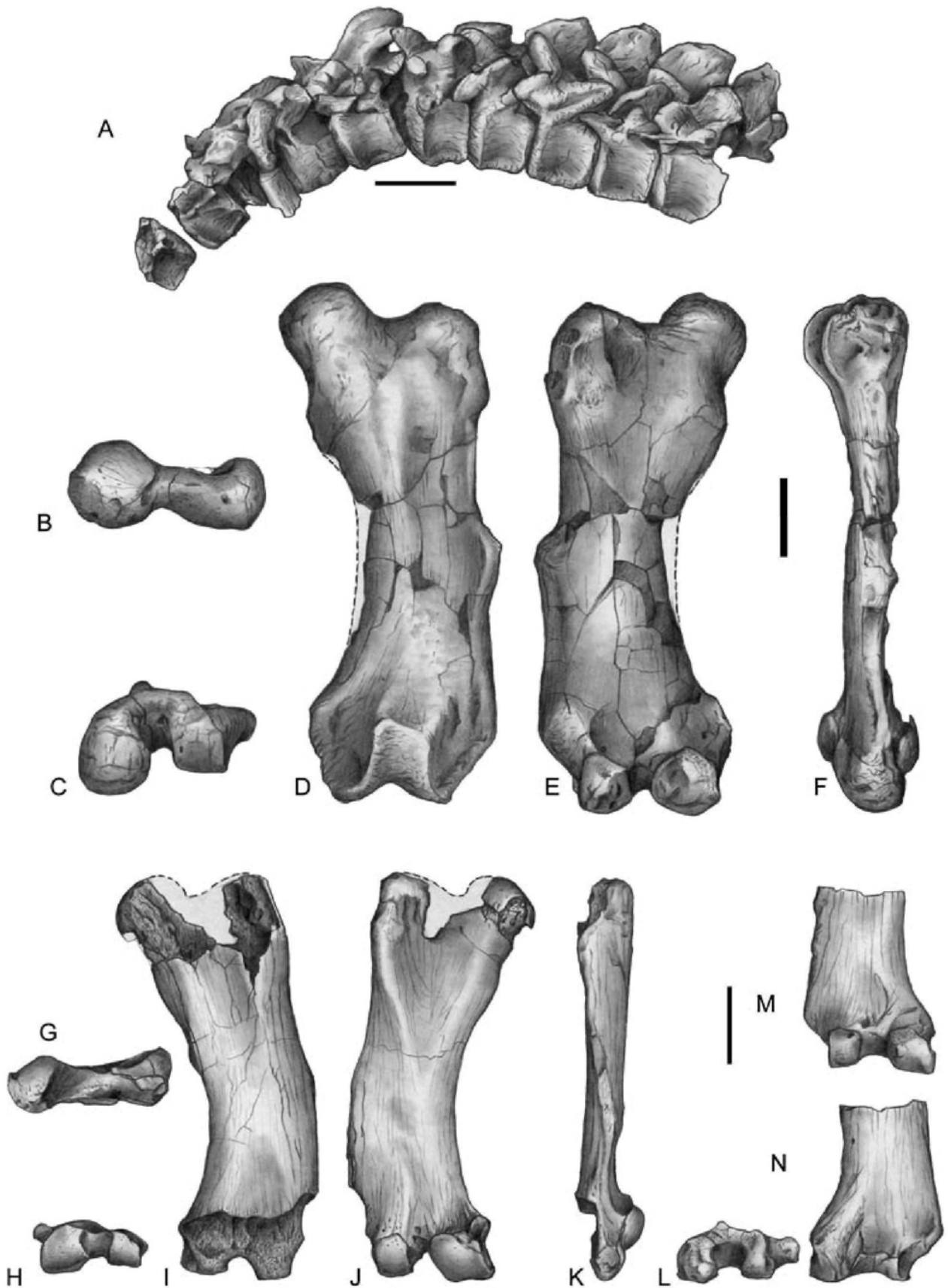


Figure 3 A–F, *Mirandabradys urumaquensis* gen. et sp. nov., AMU-CURS 157 (holotype): (A) vertebral column in left lateral view. (B–F) left femur in: (B) proximal, (C) distal; (D) anterior, (E) posterior and (F) lateral views. G–N, *Mirandabradys zabasi* gen. et sp. nov. G–K, AMU-CURS 127 (holotype): left femur in: (G) proximal, (H) distal, (I) anterior, (J) posterior and (K) lateral views. L–N, AMU-CURS 128: left distal femur in: (L) distal, (M) posterior and (N) anterior views. Scale bars = 10 cm.

the Montehermosan of Monte Hermoso, Argentina in contrast to all the known species of *Lestodon*. Upper and lower caniniforms are positioned laterally with respect to the molariform series, as in *Lestodon*, but more closely placed to the molariform series, plesiomorphic with respect to this last genus. Upper molariform series more strongly divergent anteriorly than in *Lestodon*, an apomorphic character of this new genus.

REMARKS. *Bolivartherium* is distinguished from *Promylodon* by its much more developed caniniform and by its much longer diastema (both derived characters). In addition, the caniniform is more labially displaced from the molariform series. However, both genera share the primitive symphysis structure of being 'beak'-like. *Bolivartherium* differs from *Prolestodon* by the subquadrangular cross-section of its first molariform (subelliptic in *Prolestodon*). In both genera the lateralisation of the caniniform is equivalent, but in *Prolestodon* the symphysis is much wider (apomorphic with respect to *Bolivartherium*). In *Ranculcus* the caniniform, although very lateralised, is proportionally smaller and the diastema is much longer than that of *Bolivartherium*. Furthermore, the symphysis is wider in *Ranculcus* (apomorphic) and the first molariform is subtriangular, not subquadrangular. In *Megabradys*, the mandibular body is higher (an apomorphy shared with *Promylodon*, *Ranculcus* and *Prolestodon*), the caniniform is proportionally more lateralised and triangular with its axis orientated differently. The alveoli suggest that molariforms 1 and 2 had a well-defined lingual furrow and molariform 2 had very well-defined edges, derived features that are absent in *Bolivartherium*. The most similar mylodontids to *Bolivartherium* are those recorded in the 'Mesopotamian' of Argentina and the Late Miocene of Uruguay and Brazil (Acre).

Bolivartherium is a lestodontine mylodontid that is 40% smaller than the Quaternary species of the genus *Lestodon*, 20% larger than *Lestodon* sp. from the Montehermosan of Argentina (see Deschamps *et al.* 2001) and 35% larger than the species of the Codore Formation.

***Bolivartherium urumaquensis* (Linares, 2004a)** (Fig. 4)

HOLOTYPE. MCN 170-72v, fragment of right maxilla with alveoli of the caniniform to the fourth molariform; posterior part of the cranium with the occipital, right occipital condyle, part of the parietals; part of the mandible with both rami joined at the symphysis, without ascending ramus, with the alveoli of the caniniform to molariform 3; left ulna.

OTHER MATERIAL. MCN 85-72, both femora of a single specimen and 12 associated dorsal vertebrae; MCN 71-72, right humerus. All belong to adult specimens.

OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Urumaco Formation, Late Miocene.

DIAGNOSIS. Species of *Bolivartherium* much larger than *B. codorensis* and with skull less elongate and the outline of the occiput markedly subtriangular; no occipital protuberance in the uppermost mid-line of the occipital plane.

DESCRIPTION. The material described here is from an adult specimen to judge by the cranial sutures and the fused epiphysis of the humerus and femur.

The posterior skull fragment does not show the sagittal crest described by Linares (2004a), while the section level with the parietals describes an inverted parabola. The occipital develops a rounded lambdoidal crest at the intersection of the parietals, giving it a subtriangular outline with rounded angles and a sigmoid crest in dorsal view. No occipital protuberance is observed. The occipital condyle is well defined and from its dorsal portion projects from the inclined occipital plane. The preserved part of the anterior portion of the skull is formed essentially by the maxilla, although small fragments of the nasal, lachrymal and frontal are preserved. All of the the alveoli for the molariforms and an intra-alveolar portion of the last molariform are preserved. The alveolus for the caniniform is strongly lateral in position and is very curved; the outline of the alveolus suggests that the caniniform would have been subtriangular. The following four alveoli are separated by a diastema one and a half (anteroposterior diameter) times the length of the caniniform and they form a continuous series. They are poorly preserved, but the first three are subtrapezoidal and quite simple. The last alveoli has a posterior lobe approximately half the diameter of the anterior lobe. The dental series seems to diverge strongly towards the anterior. The lachrymal tubercle is level with the first and second molariforms. The rostrum is low and the diastema in front of the molariforms elevated with respect to the occlusal plane, making the alveolar margin of the caniniforms dorsal in position.

The preserved mandibular fragment has both mandibular rami joined at the symphysis, but lacks the ascending rami; consequently the angular, coronoid and condylar areas are unknown. The mandibular rami are low, with approximately uniform height and join at a symphysis that is as low as the rami. This results in a primitive 'beak' structure similar to that seen in many tardigrade groups, both Mylodontoidea and Megatherioidea. The most anterior part of the symphysis is very narrow and inclined upward at 45°. The posterior alveolar foramen is positioned on the external side of the coronoid process, level with the third molariform. In front of the caniniform, there are two successive anterior alveolar foramina. Only the dental alveoli are preserved and their outlines permit an interpretation of the form and size of the original dentition. The caniniforms are positioned laterally, but less so than the upper ones, and are separated from the molariforms by a diastema equal in length to their anteroposterior diameter. The molariforms form a continuous series. The two anterior molariforms are subtrapezoidal and the third is typically bilobate. The molariform series are subparallel and diverge only slightly to the anterior. The estimated total length of the skull, by comparison with homologous parts in complete skulls of the species of *Lestodon*, was approximately 45–48 cm from the premaxillae to the occipital condyles.

The humerus is approximately two thirds of the femur length and has, as in other mylodontids, broad pronator and supinator processes. The head does not exceed the height of the major and minor tuberosities and is not markedly projected posteriorly. The major tuberosity is slightly larger than the minor tuberosity. The pectoral and deltoid crests are prominent, but they are a little more separated from each other and less massive than in the latter genus. The entepicondyle foramen is absent and the pronator and supinator processes not strongly developed, the projected line that joins the medial-most and lateral-most projections being oblique with respect

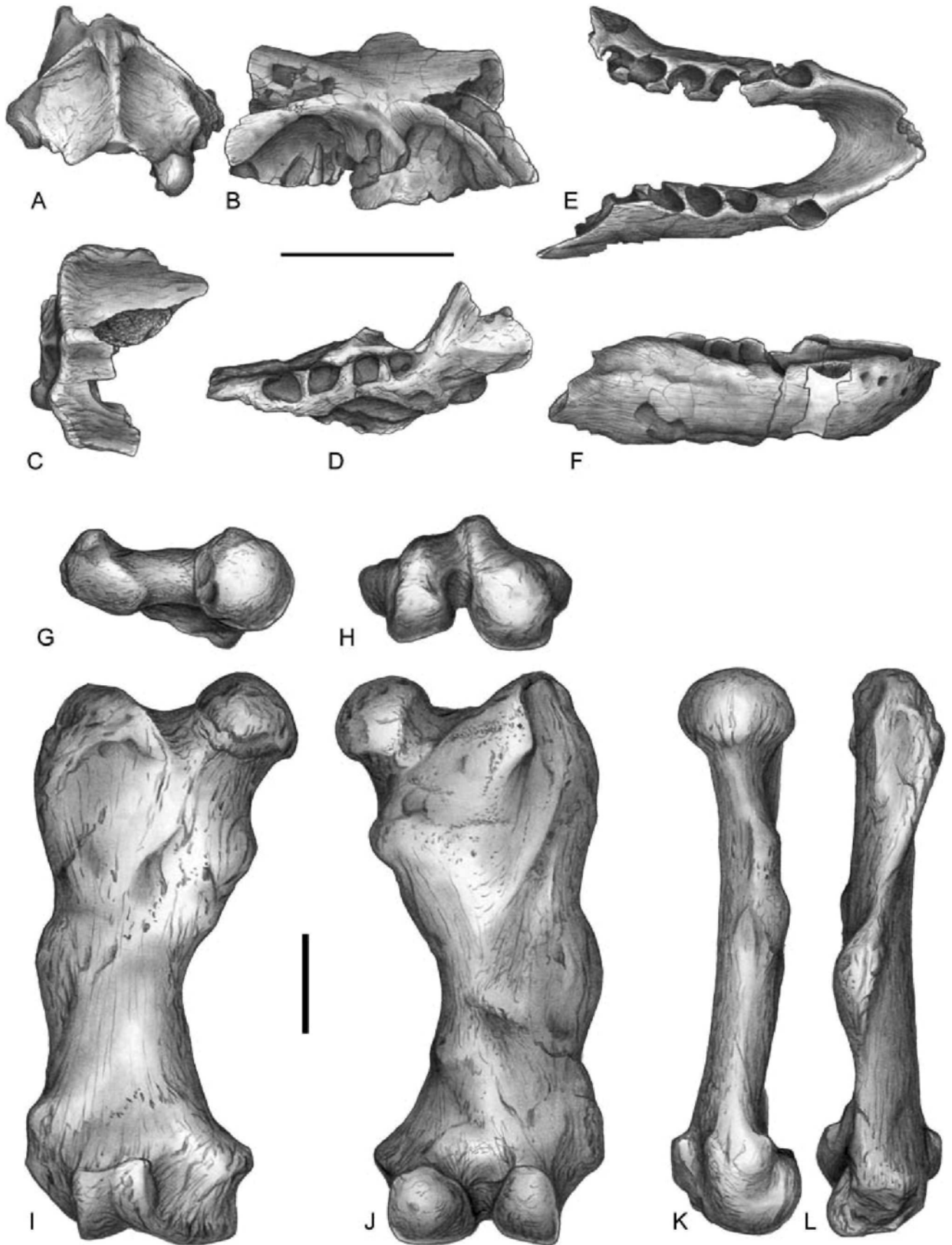


Figure 4 *Bolivartherium urumaquensis* (Linares, 2004). **A–F**, MCN 170-72 (holotype): **A–D**, skull in: **(A)** occipital, **(B)** right lateral view of the rostrum, **(C)** dorsal and **(D)** palatal view. **E–F**, mandible in: **(E)** occlusal and **(F)** right lateral view. **G–L**, MCN 85-72 right femur in: **(G)** proximal, **(H)** distal, **(I)** anterior, **(J)** posterior, **(K)** mesial and **(L)** lateral view. Scale bars = 10 cm.

to the line of tuberosities. The olecranon fossa is not deep and the distal line of the trochlea is slightly concave. The distal articular surface is too badly preserved to allow comparison with other taxa.

The diaphysis of the femur is long and strongly curved medially, its proximal half is widened to give the bone an almost triangular appearance. The trochanter major is large and massive, but less developed anteroposteriorly and its maximum width is less than the width of the head. It is positioned slightly below the level of the head, which is set off by a neck. The trochanter minor is clearly outlined and placed directly below the head, at a distance similar to the diameter of the articular area. A third trochanter is clearly observed at the middle of the diaphysis and set off by two concavities, a dorsal one that separates it from the trochanter major and, ventrally, by one that separates it from the ectepicondyle. This latter concavity is not seen in *Mirandabradys*, where a prominent bony lamina forms a continuous surface with the ectepicondyle. A long and shallow trochanteric fossa is present. In lateral view the anterior and posterior surfaces are plane. Distally the internal condyle is larger than the external one, the intercondylar fossa is narrow and deep, the adductor tubercle of the entepicondyle is well developed, enlarging the medial portion of the diaphysis. The posterior profile of the internal condyle is convex, while the external condyle is almost flat. Both condyles are continuous with the patellar facet, which is wide and limited medially by a strong and rounded margin.

The vertebrae belong to the posterior thoracic and anterior lumbar region and are partially broken.

REMARKS. The posterior contour of the skull is quite different from that of *B. codorensis* from the Codore Formation, as in the latter the outline is not subtriangular and, in dorsal view, the curves of the sigmoid crest are much more abrupt.

***Bolivatherium codorensis* (Linares 2004a) (Fig. 5)**

HOLOTYPE. AMU-CURS 130 (MPU 015 of Linares, 2004a); almost complete skull, without teeth, jugals and mandible. The femur assigned by Linares (2004a) to this species is here transferred to *Mirandabradys zabasi* gen. et sp. nov.

GEOGRAPHICAL AND STRATIGRAPHIC OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Codore Formation (middle part of the El Jebe Member: Linares 2004a), Pliocene (Ministerio de Energía y Minas 1997; Aguilera 2004).

DIAGNOSIS. Species of *Bolivatherium* much smaller than *B. urumaquensis*. Skull more elongate than in *B. urumaquensis* with occiput proportionally much more depressed and with the lambdoid crest forming a regular curve. Diastema between the upper first molariform and caniniform shorter, curved and directed more laterally than in *B. urumaquensis*. Upper molariforms subelliptic in cross-section.

DESCRIPTION. The skull belongs to an adult, based on the fact that its occipital sutures are fused, and it is only weakly deformed by dorso-ventral compression. It is similar to the skull of *B. urumaquensis* but more elongate. In lateral view there is a convexity at the nasal level that ends behind the level of the maxillary zygomatic root. In front of this root, a strong narrowing of the rostrum precedes the protruding alveolus of the caniniform, which is very curved and diverges distally

in anterior view. The occipital region is not significantly deformed and is rounded in outline, not subtriangular as in *B. urumaquensis*. A conspicuous protuberance can be seen on the upper part of the occipital plane, which is absent in *B. urumaquensis*.

In palatal view, the dental series diverges anteriorly, describing an open arch that is laterally concave. The molariform series is continuous and the diastema separating it from the caniniform is shorter and more laterally positioned than in *B. urumaquensis*. Dentition is not preserved. However, to judge from the alveoli shape it may be assumed that the caniniform was subtriangular with well rounded edges and that the molariforms were more simple in shape. Molariforms 1 to 3 were probably subelliptical in shape, with the greatest diameter being diagonal with respect to the sagittal plane; the M4 is smoothly bilobate with the posterior lobe smaller than the anterior as in *B. urumaquensis*.

DISCUSSION

The diversity of tardigrades in the middle Miocene to Early Pleistocene of Northern Venezuela is noteworthy. The Socorro, Urumaco and Codore formations together have yielded two species of Megatheriinae Gray, 1821, (see Carlini *et al.*, 2006, this volume), six species of other Megatherioidea Gray, 1821 and the six Mylodontoidea discussed in this paper. The taxa from the Urumaco Formation may not have been contemporaneous, since different fossiliferous levels have been recognised in this unit (Díaz de Gamero & Linares 1989).

Almost all the recorded species are large, ranging from as large as *Glossotherium robustum* (Owen, 1842), to slightly smaller than *Lestodon trigonidens* Gervais, 1873. This suggests that either the 'faunas' were composed only of large-sized tardigrades (which would be unique for South American Tertiary vertebrate faunas), or that the small- and medium-sized taxa are absent due to taphonomic reasons. If the latter, then tardigrade diversity in the Neogene of Venezuela must have been even higher than currently estimated.

There are three separate clades of Mylodontoidea in the Socorro, Urumaco and Codore formations:

- (1) *Mirandabradys*, a genus closely related to *Pseudopreotherium* (based on shared derived features of the skull), is represented by three successive species: *M. socorrensis*, *M. urumaquensis* and *M. zabasi*. *Mirandabradys socorrensis* seems to be more derived than *Pseudopreotherium*, based on the proximal and distal immobilisation of the fibula on the tibia.
- (2) *Urumacotherium garciai*, which stands clearly apart from the other mylodontoids because of its distinctive dentition (molariforms very wide and short, almost laminar) and the shape and relative size of its femur and tibia (femur length/tibia length = 2.47). Negri & Ferigolo (2004) included this species and *U. campbelli* (Frailey 1986) in their new subfamily Urumacotheriinae.
- (3) The Lestodontinae (Mylodontidae) represented by the two species of *Bolivatherium*. These are characterised by their low, long and straight skull, large caniniform, divergent molariform series and femur that has a wide and massive proximal third with a conspicuous third trochanter.

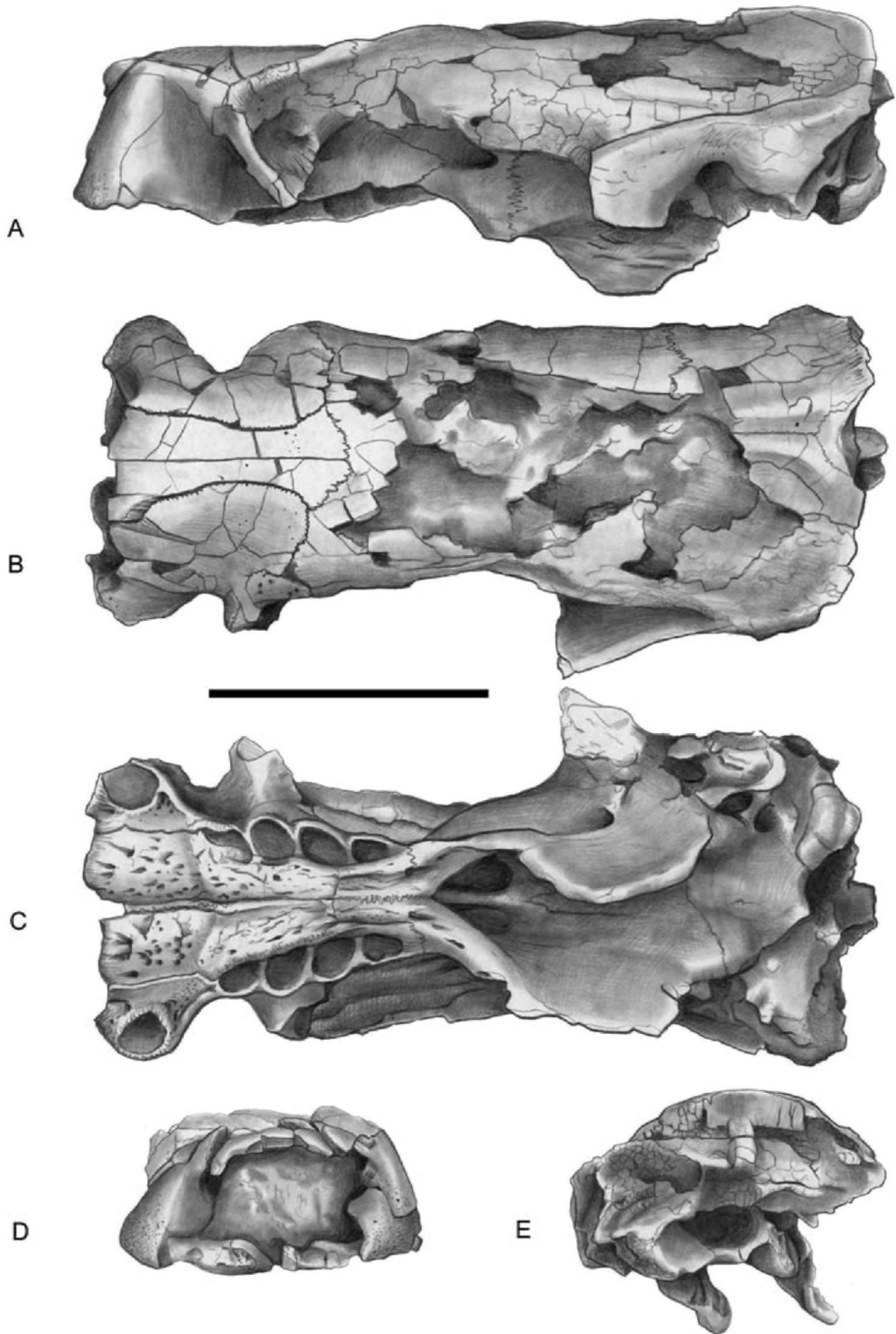


Figure 5 *Bolivartherium codorensis* (Linares, 2004), AMU-CURS 130 (holotype). Skull, in: (A) left lateral, (B) dorsal, (C) palatal, (D) anterior and (E) occipital views. Scale bar = 10 cm.

Palaeobiogeography

The oldest mylodontoids come from the Late Oligocene of Patagonia and Bolivia (Hoffstetter 1954, 1956, 1969). Mylodontoids later became more widespread diversifying into the Octodontobradynae (Late Miocene–Early Pliocene of Brazil; Santos *et al.* 1993), a group comprising *Orophodon*, *Pseudopreotherium* and *Mirandabradys* (Late Oligocene–Pliocene), and the Urumacotheriinae (Late Miocene–Pliocene).

Urumacotherium is the strangest of the Mylodontoidea from the Late Miocene of North Venezuela. This genus has also been reported from the Late Miocene–Pliocene of Acre (Brazil: Bocquentin & Guilherme 1999; Negri & Ferigolo 2004). Consequently, the Urumacotheriinae appear to have been restricted to the northern half of South America.

Pseudopreotherium Hoffstetter is known from the Mio–Pliocene of Venezuela (Collins 1934; Hoffstetter 1961), the Middle Miocene of La Venta, Colombia (Hirschfeld 1985) and the Late Miocene–Pliocene of Acre (Bocquentin & Guilherme 1999) and is also, thus, restricted to tropical regions.

Orophodon, *Octodontotherium* and *Chubutherium* inhabited Patagonia during the Oligocene, but neither they nor their descendants are known from younger strata in that region. This pattern of the disappearance of certain lineages from southern areas of South America and their persistence in more northern areas is also exemplified by the Glyptatelineae (Glyptodontidae). Glyptatelineae inhabited Patagonia during the Mustersan and Deseadan, but is found later only in the Laventan (Middle Miocene) of Colombia (see Carlini *et al.* 1997).

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