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Middle Miocene vertebrates from the Amazonian Madre de Dios Subandean Zone, Perú

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A B S T R A C T

A new middle Miocene vertebrate fauna from Peruvian Amazonia is described. It yields the marsupials *Sipalocyon* sp. (Hathliacynidae) and *Marmosa* (*Micoureus*) cf. *laventica* (Didelphidae), as well as an unidentified glyptodontine xenarthran and the rodents *Guiomys* sp. (Caviidae), “*Scleromys*” sp., cf. *quadrangulatus-schurmanni-colombianus* (Dinomyidae), an unidentified acaremyid, and cf. *Microsteiromys* sp. (Erethizontidae). Apatite Fission Track provides a detrital age (17.1 ± 2.4 Ma) for the locality, slightly older than its inferred biochronological age (Colloncuran-early Laventan South American Land Mammal Ages: ~ 15.6 – 13.0 Ma). Put together, both the mammalian assemblage and lithology of the fossil-bearing level point to a mixture of tropical rainforest environment and more open habitats under a monsoonal-like tropical climate. The fully fluvial origin of the concerned sedimentary sequence suggests that the Amazonian Madre de Dios Subandean Zone was not part of the Pebas mega-wetland System by middle Miocene times. This new assemblage seems to reveal a previously undocumented “spatiotemporal transition” between the late early Miocene assemblages from high latitudes (Patagonia and Southern Chile) and the late middle Miocene faunas of low latitudes (Colombia, Perú, Venezuela, and ?Brazil).

Keywords:

Colloncuran-early Laventan
Marsupialia
Rodentia
Biochronology
Fission track age
Biogeography

1. Introduction

The middle Miocene period is characterised by the last climatic optimum (MMCO, for Middle Miocene Climatic Optimum) before a sustainable deterioration culminating with Pliocene–Pleistocene ice ages (Zachos et al., 2001, 2008). In Northern South America, this MMCO coincides with the emergence of the “Pebas system”, a large wetland with marine influence partly engulfing what is lowland Amazonia today (for review, see Hoorn et al., 2010a,b).

This environment was particularly favourable to biodiversity and it allowed a wide array of organisms, such as molluscs, arthropods, and plants to be fossilised (e.g., Hoorn, 1993; Antoine et al., 2006; Pons and De Franceschi, 2007; Jaramillo et al., 2010; Wesselingh and Ramos, 2010). By contrast, and with the notable

exceptions of La Venta (late middle Miocene, Colombia; Kay et al., 1997) and Fitzcarrald local fauna (eastern Perú; Antoine et al., 2007; Goillot et al., 2011; Pujos et al., in press), middle Miocene mammals are virtually unknown in tropical-equatorial South America (e.g., Negri et al., 2010).

The present work aims to report a new vertebrate locality from the Subandean Zone of Southwestern Peru, designated MD-67 ($S12^{\circ}38.683'$; $W71^{\circ}19.284'$; ~ 428 m Above Sea Level) and documenting the concerned interval. MD-67 was discovered by one of us (MR) nearby Pilcopata (Cusco) in 2007 (Fig. 1). The corresponding results are exposed hereunder in systematic, biostratigraphical, and biogeographical perspectives.

1.1. Geological context

The western Amazon drainage basin extends today from southern Colombia to northern Bolivia (Hoorn et al., 2010a). Since Pliocene times (Espurt et al., 2007, 2010), the Amazonian foreland

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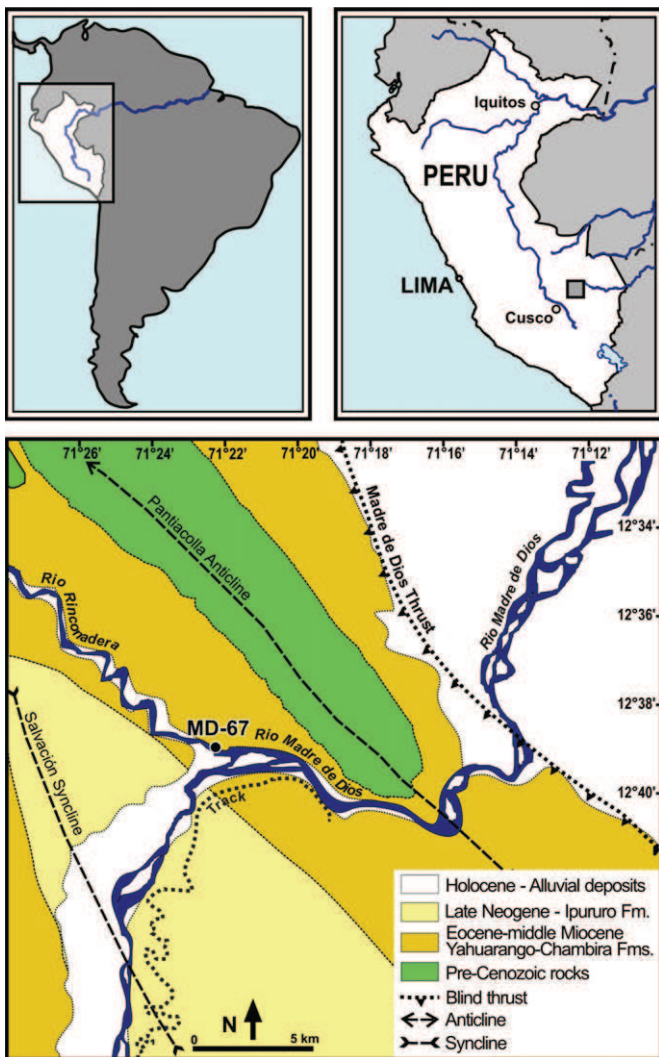


Fig. 1. Location and geological map of the studied area, in the Amazonian Madre de Dios Subandean Zone, Perú; modified after Vargas and Hipólito (1998).

basin has been divided into two foreland basin systems (*sensu* DeCelles and Giles, 1996): the North Amazonian foreland basin system and the South Amazonian foreland basin, separated by the Fitzcarrald Arch (Roddaz et al., 2005). The South Amazonian foreland basin system comprises the Southern Peruvian and Northern Bolivian foreland basins. The Subandean Zone is part of the Madre de Dios foreland basin (Fig. 1). The southernmost part of the Subandean Zone is structured by a syncline (Salvación Syncline) followed by a thrust-related anticline (Pantiacolla Anticline) and the Madre de Dios blind thrust front (Fig. 1).

The fossiliferous outcrop dips 35° SW with a N130 strike (Fig. 2). It crops out in the southern flank of the Pantiacolla anticline and was originally mapped as part of the Paleocene–Eocene Yahuarango Formation, based on sedimentary facies, but without any biostratigraphic constraint (Vargas and Hipólito, 1998). The Yahuarango Formation (northern Perú) is poorly dated and it consists mainly of red siltstones and mudstones forming distal fluvial deposits (see Roddaz et al., 2010 for a review).

The fossiliferous level corresponds to a 1 m-thick sand-and-gravel channel of fluvial origin, with iron-rich pisolites and topped by a ferruginous duricrust (Fig. 2A). These features coincide with a lateritic profile (e.g., Tardy, 1992). The fossiliferous channel developed over paleosol mudstones (Fig. 2A and B).

2. Material and methods

2.1. Paleontology

All the vertebrate fossil remains described here were recovered either by hand-picking on the ferruginous crust topping the MD-67 locality during the exploratory 2007 field trip, or by excavating and by screen-washing of the corresponding sediment during the 2009 field season. In 2009, ca. 200 kg of rough sediment were screen-washed, using a 1 mm mesh. A new survey in 2011 unfortunately showed the fossil-yielding outcrop had been washed away by the Madre de Dios River in the meantime (Fig. 2C).

Fragments of turtle plates and crocodile teeth were also recovered in MD-67. As they do not display diagnostic features, they will not be described here. By contrast, neither fish nor plant remains were unearthed in MD-67.

Among mammalian remains, a mesio-labial fragment of a hypselodont upper tooth referable to a toxodontid notoungulate was recognised in MD-67. This specimen, of poor biochronological and environmental use, is the only remain unambiguously assignable to native ungulates in the concerned locality.

The nomenclature used for marsupial dentition is adapted from that of Goin and Candela (2004). Morphological features of the cavioid rodent are described and diagnosed following the terminology and phylogenetic characters proposed by Pérez (2010). For dental features of the dinomyid, octodontoid, and erethizontid rodents, we follow the nomenclature of Wood and Wilson (1936), as modified by Antoine et al. (2012).

Except when mentioned, dimensions are given in mm.

2.2. Apatite fission track analysis (AFTA)

Apatite grains were mounted and polished for etching to several the natural spontaneous fission tracks. Apatites were etched using 5 N HNO₃ at 20 °C for 20 s. Etched grain mounts were packed with mica external detectors and corning glass (CN5) dosimeters and irradiated in the FRM 11 thermal neutron facility at the University of Munich in Germany. Following irradiation the external detectors were etched using 48% HF at 20 °C for 25 min. Analyses were carried out on a Zeiss Axioplan microscope at a magnification of ×1250, using a dry (×100) objective. Confined track length measurements were made using a drawing tube and digitising tablet, calibrated against a stage micrometre. Single-grain AFT ages were calculated using the external detector method and the zeta calibration approach, as recommended by the I.U.G.S. Subcommittee on Geochronology (Hurford, 1990). Track length measurements were restricted to confined tracks parallel to the c-crystallographic axis.

2.3. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; IGM, Ingeominas (Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Museo Geológico, Bogotá, Colombia; ISE-M, Institut des Sciences de l'Évolution, Montpellier, France; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MLP, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Perú; UCMF, Universidad Nacional Museum of Paleontology, Berkeley, USA; UFAC, Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Rio Branco, Brazil.



Fig. 2. Middle Miocene vertebrate locality MD-67, in the Amazonian Madre de Dios Subandean Zone, Perú. A. Detail of the fossil-yielding red sand-and-gravel channel, developing over red clays (paleosol), as discovered in October 2007. Note the dipping of the topping surface (ferruginous duricrust). Picture by Patrice Baby. B. Detail of the transition between the underlying red clays (top) and the gravel channel, with iron-rich pisolites (black balls, at the bottom). Picture by Patrice Baby (same day as in Fig. 2A). C. The same area in August 2011. The fossil-yielding channel (denoted by the white dotted line) had been washed away by the Madre de Dios River in the meantime. Picture by Laurent Marivaux. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Other abbreviations

dist., distal; est., estimated; FAD, First Appearance Datum; *H*, height; HI, Hypsodonty Index ($=H/MDL$); *L*, length; max, maximal; LLO, Last Local Occurrence; MDL, mesio-distal length; mes, mesial; SALMA, South American Land Mammal Age; *W*, width.

3. Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
 Cohort MARSUPIALIA Illiger, 1811
 Order DIDELPHIMORPHIA Gill, 1872
 Suborder SPARASSODONTA Ameghino, 1894
 Superfamily BORHYAENOIDEA Ameghino, 1894
 Subfamily HATHLIACYNIDAE Ameghino, 1894
Sipalocyon Ameghino, 1887
Sipalocyon sp.

MUSM 1967 is a much worn and eroded tooth, with a tribosphenic bunodont pattern and three broken roots (one lingual and two labial ones). Following the work of Forasiepi et al. (2006), this tooth is interpreted as a right M3 of a carnivorous marsupial. It is roughly triangular in occlusal view, with a straight mesial side (mes $W = 5.10$), a long and bilobed distolingual border (max $L = 6.69$), and a concave labial side ($MDL = 4.67$). Crown height equals 3.24 mm. The paracone and the metacone have their bases twinned, thus determining a very short premetacrista. Even if its tip is broken away and eroded, the paracone was low, with a faint pre-paraconule; the most prominent cusp is the metacone, which occupies a central position in occlusal view (Fig. 3A and B). The paraconule and the metaconule are equally developed, and closely appressed to the paracone and metacone, respectively (Fig. 3A and

B). The protocone is bulbous, much lower than the latter cusps, and widely remote from them, which further determines a wide triangular basin which is bordered by a faint preprotocrista and a low postprotocrista. The postmetacrista is strongly developed and distally convex, with a flat and high vertical wear facet but without carnassial notch (Fig. 3B). The styler shelf is smooth and reduced, with faint or absent cusps. Yet, a rounded crest surrounds the mesiolabial corner of the tooth, which was either interpreted as an ectocingulum or a “Cusp B” (Marshall, 1978; Forasiepi et al., 2006).

The main morphological features of this tooth (tribospheny, reduced protocone, paracone and metacone closely appressed, and reduced styler shelf and cusps) point to a carnivorous marsupial, as defined by Muizon (1999: 502). The presence of a thick and low protocone, and of equally developed paraconule and metaconule allow referring it as to a medium-sized hathliacynid borhyaenoid (Forasiepi et al., 2006). Accordingly, comparison was made with *Cladosictis* Ameghino, 1887 (early Miocene of Argentina and Chile; Flynn et al., 2002) *Sipalocyon* Ameghino, 1887 (Colhuehuapian-Santacrucian of Patagonia; Marshall, 1981), *Acyon* Ameghino, 1887 (middle Miocene of Southern Bolivia; Forasiepi et al., 2006), and *Notogale* Loomis, 1914 (Deseadan of Bolivia and Argentina; Muizon, 1999). A similar large-sized lingual basin is only observed in *Notogale mitis* (Ameghino, 1897), as illustrated by Marshall (1981: Figs. 54 and 55). Based on compatible proportions/size and on the presence of an ectocingulum, MUSM 1967 shows the closest affinities with the M3 of *Sipalocyon gracilis* Ameghino, 1887 (AMNH 107401-001; FM 9254-001; Santacrucian) and *Sipalocyon externa* (Ameghino, 1902) (Colhuehuapian; Marshall, 1981). It differs from *S. externa* in having a lower and smoother protocone, a very wide lingual basin, labially-displaced paracone and metacone, and in showing a more developed paraconule and metaconule (Marshall, 1981), but closely resembles the M3 of *S. gracilis* from “Rio Coyle” (maxilla MNHN SCZ 122,

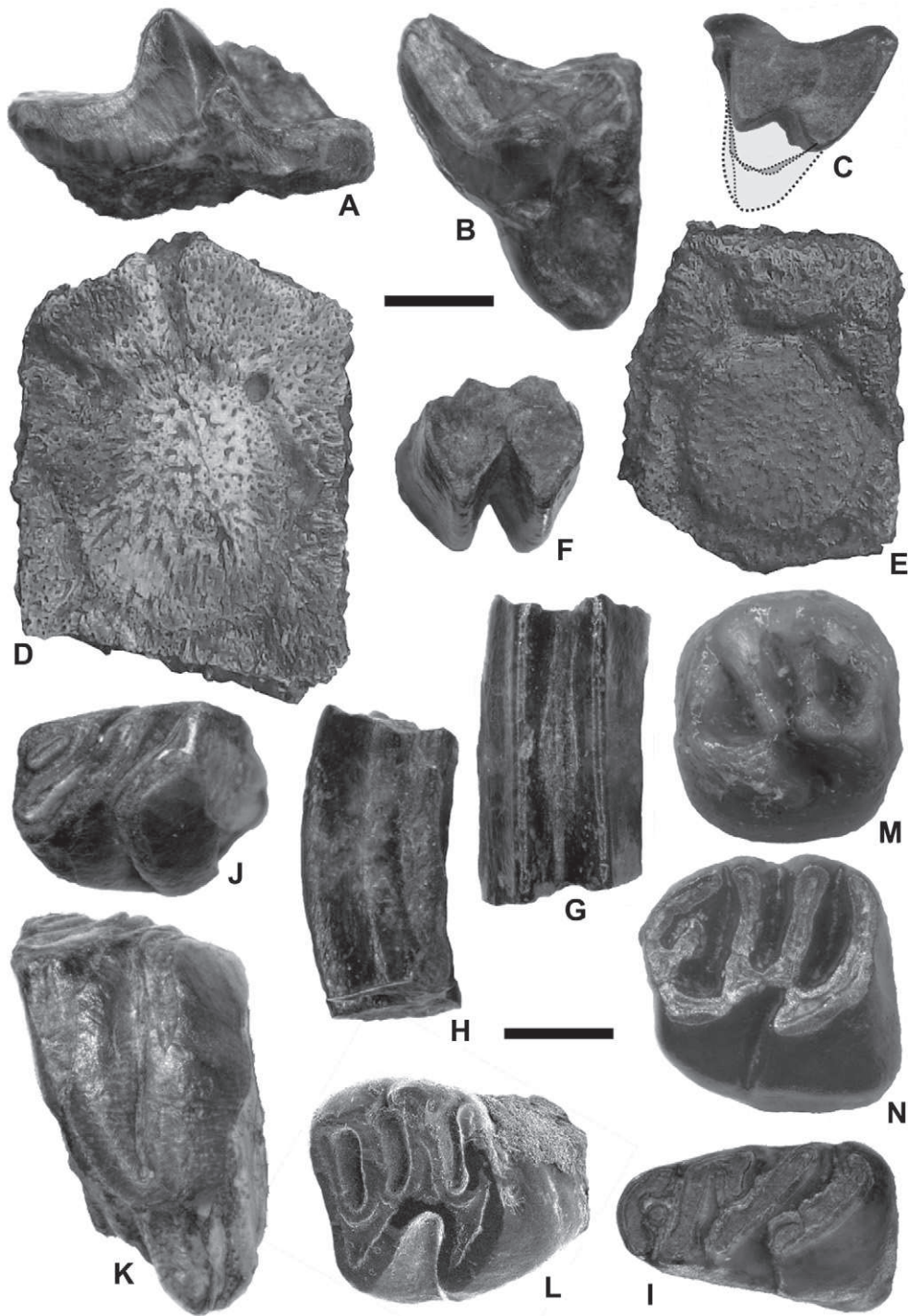


Fig. 3. Fossil mammal remains from the MD-67 locality, middle Miocene of the Amazonian Madre de Dios Subandean Zone, Perú. A–B. *Sipalocyon* sp., right M3 (MUSM 1967) in labial (A) and occlusal views (B). C. *Marmosa (Micoureus)* cf. *laventica*, left M3 lacking the protocone (MUSM 1968). Reconstructed areas appear in grey (reconstruction based on Marshall, 1976: text-Fig. 2). D–E. Glyptodontinae indet., isolated osteoderms in external view. D, MUSM 1720; E, MUSM 1585. F–H. *Guiomya* sp., left M1/2 (MUSM 1970) in occlusal (F), labial (G), and mesial views (H). I–K. “*Scleromys*” sp., gr. *quadrangulatus-schurmanni-colombianus*. Left d4 (MUSM 1971) in occlusal view (I). Left m1 (MUSM 1972) in occlusal (J) and labial views (K). L. *Acaremyidae* indet., left m1/2 (MUSM 1973) in occlusal view. M–N, cf. *Microsteiromys* sp. Left P4 (MUSM 1974) in occlusal view (M). Right ?M3 (MUSM 1975) in occlusal view (N). Scale bar = 2 mm (A–B, F–K), 5 mm (D–E), or 1 mm (C, L–N).

Tournouër Collection; Santa Cruz Formation, Patagonia) in all these aspects. *Sipalocyon* has a Colhuehuapian–Friasian range, so far restricted to middle and high latitudes (37.5–48°S; Marshall, 1981; Flynn et al., 2008). Recognition of a hathliacynid closely allied to *Sipalocyon*, here referred as to *Sipalocyon* sp., widely extends northward the geographical range of the genus.

Superfamily DIDEIPHOIDEA Gray, 1821
 Family DIDEIPHIDAE Gray, 1821
 Subfamily DIDEIPHINAE Gray, 1821
 Tribe MARMOSINI Reig, Kirsch and Marshall in Reig, 1981
 Genus *Marmosa* Gray, 1821

Subgenus *Micoureus* Lesson, 1842 *sensu* Voss, and Jansa, 2009: 101

Marmosa (Micoureus) cf. laventica Marshall, 1976

MUSM 1968 is a left upper molariform tooth, the protocone of which was broken away. This tooth has a dilambdodont tribosphenic pattern, a large stylar shelf, and four stylar cusps (termed A–D). It bears one lingual and two labial roots. The tooth is almost unworn and its dimensions are very small (MDL = 1.75; est $W = 1.8$). The metacone is much larger and higher than the paracone. There was neither paraconule nor metaconule. All these features point to a marmosine didelphid rather than to a microbiothere (Marshall, 1976). MUSM 1968 was compared to the M1–M3 series UCMP 108563 of “*M. laventica* Marshall, 1976” from the middle Miocene of La Venta, Colombia, described and illustrated by Marshall (1976: text-Fig. 2), as well as to the isolated M1 IGM 251011 and M3 IGM 250278 of the same species and area, as described and figured under the name “*M. laventicus*” by Goin (1997: Fig. 11.2). Its isometric proportions, moderate dissymmetry (with a lingual part slightly mesially displaced), and concave labial border in occlusal view allow identifying it as an M3. The missing part of the tooth was virtually reconstructed, based on available illustrations of *M. (Mi.) laventica* (Fig. 3C). There was neither junction between the preprotocrista and the paracone nor between the postprotocrista and the metacone. The stylar cusp A is disconnected from the paracone and from the preparacrista. The stylar cusp B appears as the strongest cusp, as it does in fresh teeth of most marmosines (Rossi et al., 2010: 22). There is a deep mesiolabial notch for the metastyle of M2, but neither labial, nor distal cingulum, as in *M. (Mi.) laventica* (Marshall, 1976) and the living species *M. (Mi.) demerarae* Thomas, 1905 (ISE-M V-1590). A thick cingulum, running along the labial half of the mesial side, was connecting the stylar cusp A and the protocone through the preprotocrista, as in the isolated M3 IGM 250278 of *M. (Mi.) laventica* (Goin, 1997). This cingulum is much stronger and the tooth ca. 30% smaller than in *M. (Mi.) demerarae*. Even if their overall size is comparable, the stylar cusps are much stronger and the notch for the metastyle of M2 is much deeper in MUSM 1968 than in the M3s of the living *Marmosa (Marmosa) murina* Linnaeus, 1758 (Linnaeus’s Mouse Opossum; ISE-M V-1109).

Basically, the size, proportions, and morphological features of MUSM 1968 closely match those of the M3 of *M. (Mi.) laventica* from La Venta area, Colombia, i.e., the only fossil species described and named for this genus so far (Goin, 1997). The stratigraphical range of *M. (Mi.) laventica* spans the La Victoria Fm. and the base of the Baraya Mb. of the overlying Villavieja Fm. in La Venta region, Colombia (~13.5–13.0 Ma; Goin, 1997; Madden et al., 1997: 511; Gradstein et al., 2005). If the close affinities of MUSM 1968 with *Marmosa (Micoureus)* are confirmed, this would be the second fossil occurrence of this living (sub-) genus (Goin, 1997).

Infraclass EUTHERIA Gill, 1872

Order XENARTHRA Cope, 1889

Suborder CINGULATA Illiger, 1911

Superfamily GLYPTODONTOIDEA Gray, 1869

Family GLYPTODONTIDAE Gray, 1869

Subfamily GLYPTODONTINAE Gray, 1869

Genus and species indet.

Two isolated carapace osteoderms were found. They are small (MUSM 1720: $W = 16$, preserved $L = 22$; MUSM 1585: $W = 13$, $L = 17$), quadrangular to pentagonal in shape, with large round principal figures near the posterior edge. In both osteoderms, the principal figure is completely surrounded by peripheral ones – eight in MUSM 1720 (Fig. 3D) and six in MUSM 1585 (Fig. 3E) – , although medial,

lateral, and posterior figures are reduced in size. The principal figure is slightly convex on MUSM 1720, while it is flat on MUSM 1585. Osteoderms are thin (MUSM 1720: 3.5 mm; MUSM 1585: 4.8 mm), with a punctuated surface, and serrated edges. The principal and radial sulci are wide and shallow. Piliferous pits are large and located in some intersections of the principal sulcus and the radial sulci (Fig. 3D–E).

The concerned osteoderms cannot be confidently identified at genus or species level because their characteristics are widely distributed in several clades. However, they are likely to document a single small and unknown taxon within the Glyptodontinae (smaller than the oldest glyptodontine genus known so far, *Boreostemma* from Laventan SALMA), because of the combination of the following characters: (i) osteoderms flat or smoothly convex, (ii) surface punctuated, (iii) principal figure completely surrounded by peripheral figures, and (iv) quadrangular “U”-shaped cross section of the sulci. The latter feature has been suggested as a noncranial character that differentiates Glyptodontinae from Propalaeohoplophorinae within Glyptodontidae (Carlini et al., 2008). As a consequence, a reduced size – almost twice smaller than the corresponding osteoderms in *Boreostemma* – and the presence of thin osteoderms might represent a plesiomorphic condition for the Glyptodontinae. On the other hand, the posteriorly displaced position of the principal figure, as well as the reduction in size of posterior, medial, and lateral peripheral figures, appear as tied to the location of the osteoderms in the carapace (i.e., submarginal), instead of representing a plesiomorphic trait (i.e., principal figure close to the posterior margin), as seen on glyptatelines and *Parapalaeohoplophorus* (see Croft et al., 2007).

Order RODENTIA Bowdich, 1821

Infraorder HYSTRICOGNATHI Tullberg, 1899

Parvorder CAVIOMORPHA Wood, 1955

Superfamily CAVIOIDEA Fischer de Waldheim, 1817

Family CAVIIDAE Fischer de Waldheim, 1817

Guimys sp.

MUSM 1970 is a very small tooth ($L = 2.93$; $W = 2.61$), hypselodont (i.e., “euhypsodont” following Pérez, 2010), preserving the occlusal surface, but the basal most part of which crown is broken away (Fig. 3G–H). This tooth is interpreted as a left M1 or M2. It is bilobed, with lozenge-shaped lobes connected by a thick labial bridge; the mesial lobe is slightly smaller than the distal one (Fig. 3F). The occlusal surface of both lobes lacks any fossette and the apex of each lobe is not constricted at the current wear stage. The hypoflexus is transversely developed (reaching c. 80% of the transverse width of the crown) and funnel-shaped; cement is filling the bottom of the hypoflexus, which is pointing distally and labially. A shallow furrow faces the tip of the hypoflexus. There is no transverse dentine crest crossing each lobe (Fig. 3F). Enamel is present all around the crown but interrupted on the labial most part of each lobe.

The bilobed pattern of this molar is characteristic of cavioid caviomorph rodents (Pérez, 2010; Croft et al., 2011). Among Cavioidae, the hypselodont pattern of this tooth impedes its referral to *Asteromys*, *Luantus*, *Chubutomys*, and *Phanomys* (Pérez, 2010). The funnel-shaped hypoflexus points to the clade including *Eocardia robusta*, *Guimys unica*, and crown cavioids (Pérez, 2010). The absence of transverse dentine crest on each lobe discards referring this tooth as to *Prodolichotis pridianae* or *Orthomyctera chapadmalense*, while the funnel-shaped hypoflexus further distinguishes MUSM 1970 from *P. pridianae* (Walton, 1997; Pérez, 2010). The presence of a single labial furrow makes it distinct from upper molars of *E. robusta*. To sum up, the morphology of this specimen points to a stem cavioid and, together with its small size, it is only

consistent with *Guiomys* Pérez, 2010, the smallest and earliest caviid known so far, from the middle Miocene of Patagonia (?Collocuran and Laventan SALMAs; Pérez, 2010; Pérez and Vucetich, 2011) and the Laventan of Quebrada Honda, Bolivia (Croft et al., 2011). This left molar is provisionally referred to as *Guiomys* sp., as it is 15–20% smaller than the teeth of the type and only species of the latter genus (Pérez, 2010; Croft et al., 2011).

Superfamily CHINCHILLOIDEA Kraglievich, 1940

Family DINOMYIDAE Peters, 1873

Subfamily POTAMARCHINAE Kraglievich, 1926

Scleromys sp., gr. *quadrangulatus-schurmanni-colombianus*

MUSM 1971 is a left d4. It is low-crowned and elongate mesiodistally, with a trapezoid occlusal outline, widening distally (MDL = 5.04; W = 2.81; H = 3.10; HI = 0.62). It has an “F-Γ-I-I” lophid pattern, with distinctive features such as taeniodonty (see Antoine et al., 2012), elongate cristids connected distolingually to the anterolophid and the metalophid, a circular supernumerary cuspid mediolabial to the anterolophid, and a short transverse supernumerary lingual lophid distal to the metalophid (Fig. 3I). The hypolophid and the posterolophid are straight, oblique, distinct, and parallel one to another. The hypolophid displays a small mesiolabial spur. The enamel band is crenulated on the mesial side of the posterolophid. Such crenulations occur frequently in potamarchine teeth (especially in *Potamarchus murinus*; Sant’Anna Filho, 1994). This tooth is twice smaller than d4s of “*Olenopsis*”/“*Drytomomys*” from the Middle Miocene of La Venta (Colombia; Fields, 1957: 330, Fig. 18; Candela and Nasif, 2006) and of Fitzcarrald (Perú; Antoine et al., 2007). In addition, MUSM 1971 is quite distinct from the d4 of *P. murinus* from the middle to late Miocene of the Upper Juruá, Brazil (AMNH 58535; Sant’Anna Filho, 1994), in having a trapezoid occlusal outline and in being tetralophodont, instead of being quadrangular and pentalophodont, respectively. MUSM 1971 is tetralophodont, half the size of, and much less hypsodont (HI = 0.62) than the pentalophodont p4s referred to *Simplimus indivisus* (MLP 15-244a: HI ~ 2.92; Laguna Blanca/Río Fénix, Friasian SALMA, Patagonia; Vucetich, 1984) and to *Simplimus* sp. (UFAC DGM 533M: HI ~ 2.88; Upper Juruá, middle-late Miocene, Brazil; Sant’Anna Filho, 1994). On the other hand, its size and proportions recall those of d4s of “*S.*” *schurmanni* from La Venta, Colombia, as illustrated by Fields (1957: 285, Fig. 5). The pattern is quite similar, especially for the distal lophids. Yet, the occlusal pattern of mesial lophids and cuspids observed in MUSM 1971 prevents from referring it to “*S.*” *schurmanni*. Teeth of “*S.*” *colombianus* (La Venta; Fields, 1957; Walton, 1997) are ca. 20% larger than both “*S.*” *schurmanni* and MUSM 1971.

MUSM 1972 is a left lower molariform and hypsodont tooth, with a quadrangulate occlusal contour and a straight anterior border (Fig. 3J). It is high, elongate mesiodistally and at an early stage of wear (MDL = 4.14; W = 3.72; H = 8.4; HI = 2.03). The mesiodistal and labiolingual lengths of the tooth diminish and increase strongly with wear, respectively, which allows interpreting it as an m1 at “stage of wear n°2”, by comparison with serial sections of molariform teeth of “*S.*” *colombianus* as proposed by Fields (1957: 318–319, Fig. 14). Roots are still developed and the neck is well-marked (Fig. 3K). This tooth is tetralophodont and taeniodont, with oblique and large lophids. The short metalophulid I and the longer metalophulid II are connected at both lingual and labial ends. The hypolophid and the posterolophid (damaged in its distolingual part) are not connected lingually at the current stage of wear, but they would join in later stages. Contrary to other lophids, the posterolophid is curved and concave mesiolingually in occlusal view, joining a thick and mesially-displaced hypoconid.

These two lower teeth have a typical dinomyid occlusal pattern (i.e., high-crowned, tetralophodont, taeniodont, with oblique

lophids, and a posterolophid isolated before wear). By their dimensions and pattern, they are provisionally thought to document a single taxon. *Scleromys* Ameghino, 1887 is the earliest representative of Dinomyidae (Horovitz et al., 2006). The high crown, mesiodistal elongation, quadrangular contour, large and persistent fossettids, and straight aspect of the mesial border of MUSM 1972 discard any referral to the typical Santacrucian species of *Scleromys*, i.e., the type species *Scleromys angustus* Ameghino, 1887 and *Scleromys osbornianus* Ameghino 1894 (Argentinian Patagonia). The present specimen seems to be somewhat closer to *S. quadrangulatus* (pre-Santacrucian “Pinturan” age, Patagonia, Argentina; Kramarz, 2006) and to *Scleromys* sp. (Mariño Formation, ?early Santacrucian, Mendoza, Argentina; Cerdeño and Vucetich, 2007) in sharing both a small size and a quadrangular contour. MUSM 1972 further resembles *S. quadrangulatus* in having a straight mesial border, and a mesiodistal elongation. However, the lower molars referred to *S. quadrangulatus* are lower-crowned than MUSM 1972 and they lack persistent fossettids. The latter feature is so far only observed in *S.* sp. from the Mariño Formation (Cerdeño and Vucetich, 2007), “*S.*” *schurmanni* Stehlin, 1940 and “*S.*” *colombianus* Fields, 1957, from the Laventan of Colombia and Peru (Fields, 1957; Walton, 1997; Antoine et al., 2007). Similarly, in the Patagonian species of *Scleromys*, the metalophulid II is typically reduced, being shorter than the metalophulid I. In that aspect, MUSM 1972 seems to be closer to the Laventan species from Colombia in having a larger metalophulid II. Nevertheless, in the latter taxa (the generic assignment of which is challenged by most authors; e.g., Patterson and Wood, 1982; Walton, 1997), teeth are noticeably larger, higher-crowned and wider labiolingually than in MD-67. Regardless of the lingual hypolophid–posterolophid junction (not yet occurring in MUSM 1972), the MD-67 specimen matches an m3 referred to “*Scleromys* cf. *S. schurmanni*” from the Laventan Fitzcarrald local fauna of Peruvian Amazonia (MUSM 1566; Antoine et al., 2007; Negri et al., 2010), being only narrower labiolingually and lower-crowned. In addition, this lower molar has similar proportions and lophid pattern as an m2 from the middle to late Miocene of the Upper Juruá, Brazil (UFAC DGM 582M; Sant’Anna Filho, 1994) referred to “*S.*” *colombianus*, by reference to specimens from La Venta, Colombia. However, the tooth from MD-67 is distinctly smaller, lower-crowned, and less prismatic.

To sum up, the dental pattern and the occlusal contour of MUSM 1972 match those of several species referred to *Scleromys sensu lato*, either of pre-Santacrucian (*S. quadrangulatus*) or of Laventan ages (“*S.*” *colombianus* and “*S.*” *schurmanni*; Fields, 1957). These taxa are likely to form a “lineage” distinctive from the typical Santacrucian *Scleromys* cluster, as hypothesised by Kramarz (2006: 59). Following that scheme, the crown height, proportions, and fossettid development of MUSM 1972 shall coincide with a “transitional evolutionary stage” between *S. quadrangulatus* from the early Miocene of Argentina and the representatives of “*Scleromys*” from the late middle Miocene of Northern South America (Fields, 1957; Sant’Anna Filho, 1994; Walton, 1997; Kramarz, 2006; Antoine et al., 2007; Cerdeño and Vucetich, 2007). As such, these specimens, provisionally referred to as “*Scleromys*” sp., may document a “Friasian” to Collocuran morphological grade for potamarchine dinomyids.

Superfamily OCTODONTOIDEA Waterhouse, 1839

Family ACAREMYIDAE Ameghino, 1902

Genus and species indet.

MUSM 1973 is a diminutive lower molar (MDL = 1.72; W = 2.10), roughly square in occlusal view, and with a rather high crown (“mesodont” *sensu* Vucetich and Kramarz, 2003). It is interpreted as a left m1 or m2. This tooth has a tetralophodont pattern, with bulky lophids and no cuspid well individualised (Fig. 3L). Enamel is thick,

especially on the labial half of the molar. In occlusal view, the mesial margin is straight and the distal one convex. The lophids are thick, transversely oriented, and separate by deep and wide flexids. The hypoflexid is deep (it almost reaches the lingual half of the tooth), nearly transverse, and “U-shaped” in occlusal view. The talonid is narrower than the “trigonid”, due to the weak lingual development of the posterolophid, thus providing a trapezoid shape to the occlusal contour of the tooth. The metalophulid I is complete and straight, with a thick mesiolabial projection, pointing linguodistally and joining the metalophulid II. The metalophulid II is long, and it also joins the metalophulid I at the lingual margin of the tooth, determining a mesial fossettid, oval and elongate transversely (closed anteroflexid). The junction between both metalophulids is somewhat constricted lingually, mesial to the mesostylid. The ectolophid is distinct and oblique. The hypolophid is transverse, and it connects lingually a smoothly constricted entoconid. The mesoflexid is open lingually until a late stage of wear. The metaflexid is also open lingually, and it would not get closed even with heavy wear. The posterolophid is curved, with a strong hypoconid and a short lingual arm (getting longer with wear).

Both the tetralophodont pattern and small size of MUSM 1973 allow attributing it to an early diverging octodontoid. The absence of an eight-shaped-pattern due to the lingual opening of the metaflexid discards referring this tooth to the Octodontidae (Vucetich and Kramarz, 2003). Among Echimyidae, the transverse orientation of the lophids impedes any referral to Adelphomyiinae, while tetralophodonty distinguishes it from Echimyinae (Vucetich et al., 1993; Kramarz, 2001). MUSM 1973 resembles *Protacaremys* (Collhuehupian–Colloncuran SALMAs of Patagonia and Chile; Flynn et al., 2008) in having deep, transversely elongate and persistent fossettids/flexids (notably the antero-fossettid/-flexid), but differs from it in the absence of pinched and cuspidate lophids, in the U-shaped, transversely oriented and smooth hypoflexid, in the complete and early lingual junction between the metalophulids I and II (anterolophid and mesolophid *sensu* Vucetich and Kramarz, 2003), and in lacking a figure-eight occlusal pattern (Kramarz, 2001).

On the other hand, the dental pattern of MUSM 1973 is strongly reminiscent of Acaremyidae (*Acaremys*, *Sciamys*, and *Galileomys*; Vucetich and Kramarz, 2003). It differs from the m1s and m2s of *Galileomys* in a marked mesodonty, the presence of transverse lophids, flexids, and fossettids, a stronger transverse development of the U-shaped hypoflexid, and in the lingual connection between the two mesial lophids (Vucetich and Kramarz, 2003; Kramarz, 2004). It resembles more *Sciamys* and *Acaremys*. Nevertheless, it can be distinguished from *Sciamys*, as illustrated by Arnal and Vucetich (2011), by the quadrangular occlusal contour (more elongate mesiodistally in *Sciamys*), by a shorter labial arm of the posterolophid, and by smaller dimensions. It differs from known species of *Acaremys* in having a mesolophid reaching the lingual wall and determining a transversely elongate anterofossettid persistent until late stages of wear, two features which are only observed in *Sciamys* among acaremyids (Vucetich and Kramarz, 2003). It further differs from *Acaremys* in having a much smaller metaconid, a narrower and transversally longer mesoflexid, a less penetrating hypoflexid, and a posterolophid narrower mesiodistally. As a result, MUSM 1973 is likely to document a late representative of Acaremyidae with closer affinities to *Sciamys* and *Acaremys* than to *Galileomys*, provisionally identified as “Acaremyidae indet”.

Superfamily ERETHIZONTOIDEA Thomas, 1897
 Family ERETHIZONTIDAE Thomas, 1897
 cf. *Microsteiromys* sp.

Two upper molariform teeth are assigned to a small erethizontid.

MUSM 1974 is a left P4 with a circular occlusal outline ($L = 2.14$; $W = 2.20$). It is preserved at a very early stage of wear (just erupted). Accordingly, there is no wear facet due to the contact with a mesial or a distal tooth (Fig. 3M). The crown is much higher lingually than labially. The tooth was biradicate, with lingual and labial roots mesiodistally elongate. The occlusal pattern is restricted to the apical-most part of the crown, with distinct cusps. The tooth is tetralophodont, with a thin but complete anteroloph, curved distolingually, with a prominent protocone. The paraflexus is triangular in occlusal view, and open both lingually and labially at the current stage of wear. The protoloph is oblique, short lingually, and independent from adjacent lophids at both ends; the lingual protoloph is a low and constricted crest. The paracone is distinct and bulky. The hypoflexus is deep and wide (i.e., there is no endoloph). The lingual cusps, still distinct at the current stage of wear, would be coalescent after a smooth wear. The mesoflexus is open lingually and medially; the mure is low and constricted, interrupted at the current stage of wear. The third loph is very short, restricted to the centro-distal part of the crown, and interpreted as a mesolophule; it is connected lingually to the anterior arm of the hypocone and labially, to the mesoloph. The posteroloph is thin, with a hypocone and a metacone distinct and bulky. It extends mesiolabially to the metacone until a faint cusp, interpreted as a mesostyle and facing the paracone. The posteroflexus, still open mesiolabially, would be quadrate at later stages of wear.

A right pentalophodont molar (MUSM 1975; $L = 2.44$ mm; $W = 2.11$ mm) has three broken roots, with two labial roots (circular cross section) and a mesiodistally elongate lingual one, which point to an upper molar (Fig. 3N). A contact facet is visible on the mesial side of the crown, but not on the distal side. Given the stage of occlusal wear, it allows identifying this tooth as a probable M3, even if the tooth is only slightly tapering distally (as in M2s) and if the hypocone is also located as in an M2, i.e., lingually displaced with respect to what is generally observed in M3s. The occlusal pattern is longer than wide, with a “EUJ”-shaped occlusal design. All the lophids are moderately worn, with slight constrictions, and a low obliquity. The anteroloph is the most developed loph, and it connects a labiolingually compressed and oblique paracone. The paraflexus is oval, elongate transversely, open labially but closed lingually by a low and constricted lingual protoloph. The protoloph is straight, slightly oblique, and it connects a strong paracone, labially. It joins the mesolophule lingually, through a strong but very short mure, oriented sagittally. The mesostyle and the paracone are remote and the mesoflexus is wide and U-shaped in occlusal view (open labially). The mesolophule is transversely oriented and S-shaped, with a labiodistally-oriented mesostyle. The metaflexus is wide, comma-shaped, still labially open at this stage of wear, and closed lingually by a labiolingually compressed hypocone and its strong anterior arm. The posteroloph is short, but it extends mesiolabially until the metacone, thus forming a distolabial wall. The posteroloph is somewhat constricted labially to the hypocone and lingually to the metaloph. The latter is short, oriented mesiolabially, connected to the mid-posteroloph and disconnected to both the distolabial wall and the metacone, thus forming a small posterofossette joined labially to the metaflexus.

The pentalophodont pattern of the upper molar, the low loph-obliquity, and the circular occlusal outline of the P4, as well as the low crown and thick enamel of both teeth, point to erethizontids. Given their compatible size and pattern, both teeth are assumed to document a single diminutive taxon. The fossil record of Erethizontidae ranges from the Late Oligocene up to Recent times (Vucetich et al., 1999; Candela and Morrone, 2003). Accordingly and whenever possible, these teeth were compared to those of

Protosteiomys (Deseadan, Patagonia; Wood and Patterson, 1959), of *Eosteiomys* Ameghino, 1902, *Hypsosteiomys* Patterson, 1958, *Parasteiomys* Ameghino, 1903, and *Branisamyopsis* Candela, 2003 (Colhuehuapian, Argentina; Patterson, 1958; Candela, 1999, 2003; Dozo et al., 2004; Kramarz, 2004; Kramarz and Bellosi, 2005; Vucetich et al., 2010), of *Steiomys* Ameghino, 1887 (Santacrucian-?Laventan; Patagonia, ?Colombia; Fields, 1957; Walton, 1997; Candela, 1999), of *Neosteiomys* Rovereto, 1914 (?Colloncuran-Huayquerian; Northwestern Argentina; Candela, 1999, 2004), of *Microsteiomys* Walton, 1997 (Laventan; Colombia; Walton, 1997), and of *Erethizon* Cuvier, 1823 (Recent; Candela, 1999).

The teeth from MD-67 are half the size of than those of all known Recent and fossil Erethizontidae but *Microsteiomys jacobsi* Walton, 1997, of compatible size (Walton, 1997). No P4 is described from any Deseadan erethizontid. The P4 from MD-67 differs from all known Recent and fossil Erethizontidae but *Eosteiomys homogenidens* Ameghino, 1902, in having a labially-displaced hypocone. A circular occlusal outline is only observed in *E. homogenidens* (holotype MACN A-52-165) and ?*Steiomys* from La Venta (Walton, 1997). Tetralophodonty and low loph obliquity also characterises the P4 of *Eosteiomys*, ?*Steiomys*, and *Steiomys detentus* Ameghino, 1887 (MLP 15–17). MUSM 1974 further differs from the dP4 of *Parasteiomys uniformis* (Ameghino, 1903) in having a marked mure, and in bearing flexi labiolingually compressed (Candela, 1999). Its paraflexus, which is closed labially, makes it distinct from the P4 of *Branisamyopsis praesigmoides* Kramarz, 2004 and *S. detentus* (Kramarz, 2004: 14, Fig. 7). It also differs from the P4 of *Neosteiomys bombifrons* Rovereto, 1914 in having no lingual wall (Candela, 2004: 61, Fig. 3).

The upper molar from MD-67 differs from all known erethizontids in its labially-interrupted metaloph and in its mesiodistal elongation (e.g., Candela, 1999, 2004; Vucetich et al., 2010). Its size is also very distinctive, as it is twice smaller than in all known taxa, except *M. jacobsi*, of similar dimensions (Walton, 1997). The pentalophodont pattern makes it distinct from *Protosteiomys medianus*, *Hypsosteiomys axiculus*, and *Steiomys* (Patterson, 1958; Wood and Patterson, 1959; Candela, 1999; Dozo et al., 2004). The presence of a mure and the late labial closure of the paraflexus discard any referral to *Parasteiomys* or *Neosteiomys* (Candela, 1999).

The presence of a distal constriction labially to the hypocone and lingually to the metaloph is only observed in *Parasteiomys friantae* Candela, 1999 (but not in *P. uniformis*; Candela, 1999: Fig. 2), *E. homogenidens* (type, MACN A-52–165) and *E. cf. homogenidens* (Kramarz, 2004). However, all these taxa are characterised by lower-crowned teeth, a much larger size, and a complete metaloph, i.e., reaching the labial side of the tooth.

To sum up, the pattern and morphological features of the P4 and of the upper molar from MD-67 show certain affinities with *E. homogenidens* (Colhuehuapian), and *Steiomys* (Santacrucian-?Laventan) to a lesser extent, while size is only compatible with *Microsteiomys* (Walton, 1997). *Microsteiomys* Walton, 1997 is the smallest known representative of New World porcupines, with a geographic and stratigraphic range thus far restricted to the Baraya Member of the Villavieja Fm. of Colombia (c. 13–12.5 Ma, middle Laventan; Madden et al., 1997; Candela and Morrone, 2003). This diminutive monotypic genus is only known by two mandibles, which makes it impossible to compare with the available teeth from MD-67 (Walton, 1997). However, we assume that these teeth are likely to document a close ally of *Microsteiomys* Walton, 1997, here referred to as cf. *Microsteiomys* sp. Given their morphological affinities with taxa spanning the early and middle Miocene interval, these specimens cannot be used with much confidence in a biochronological perspective.

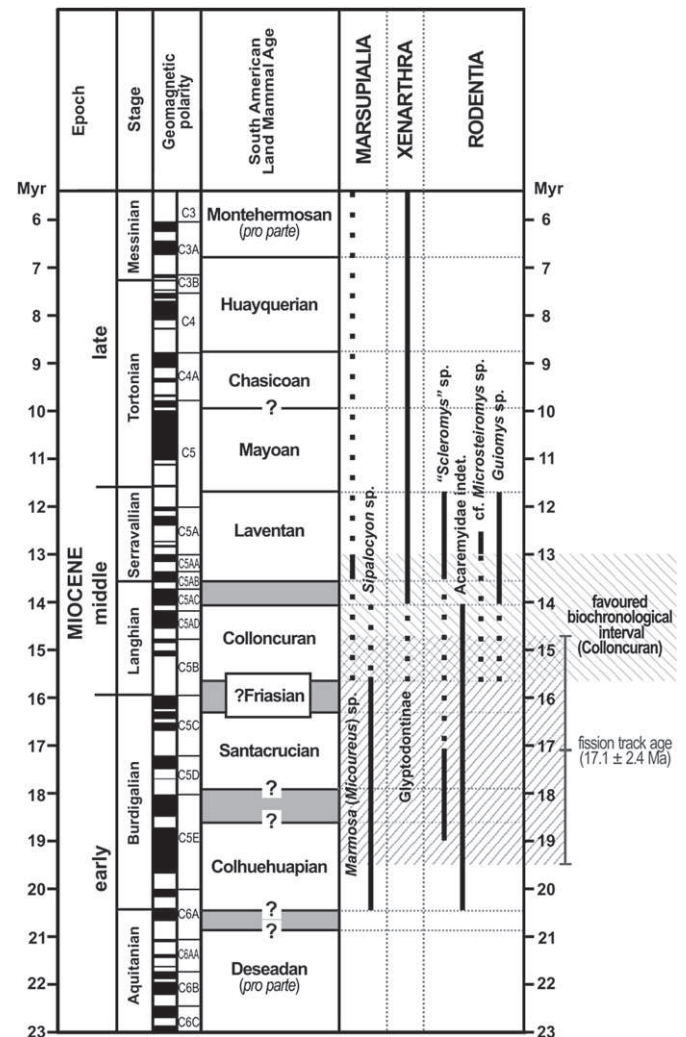
4. Discussion

4.1. Biochronological age

Glyptodontid xenarthrans are of poor biochronological interest, especially when identified above genus level. Caviomorph rodents are the most diverse group in MD-67, with four taxa encompassing four superfamilies (Octodontoidea, Erethizontoidea, Cavoidea, and Chinchilloidea; Vucetich et al., 1999). Caviidae have their FAD in the latest (or post-) Colloncuran of Patagonia, with *Guiomys* (Pérez, 2010; Pérez and Vucetich, 2011), a genus which is recognised at MD-67 (Fig. 3F–H; Table 1). Acaremyidae had a Colhuehuapian-Colloncuran stratigraphical range (Vucetich and Kramarz, 2003) while the hathliacynid marsupial *Sipalocyon* had only an early Miocene record so far (Colhuehuapian-Santacrucian; Marshall, 1981). As such, MD-67 might extend upward the known range of both taxa, and thus represent their Last Local Occurrence (Table 1). On the other hand, the recognition of *Marmosa* (*Micoureus*) and of a *Microsteiomys*-like dwarf porcupine in MD-67 predates the previous FAD of both taxa, formerly restricted to the Laventan

Table 1

Stratigraphic range of the middle Miocene vertebrate locality MD-67 as inferred by mammalian biochronology and fission track datings (see Supplementary Data). Data from Walton (1997), Vucetich et al. (1993, 2010), Vucetich and Kramarz (2003), Kramarz (2004, 2006), Gradstein et al. (2005), Kramarz and Bellosi (2005), Cerdeño and Vucetich (2007), Croft et al. (2011), and Pérez and Vucetich (2011).



SALMA in the La Venta area of Colombia (Table 1; Marshall, 1976; Goin, 1997; Madden et al., 1997; Walton, 1997).

At first sight, the biochronological age for MD-67 is middle Miocene, i.e., Colloncuran-Laventan (~15.6–11.6 Ma; Kay et al., 1997; Madden et al., 1997), but the occurrence of a typical early Miocene genus such as *Sipalocyon* and the potentially “plesiomorphic evolutionary stage” of “*Scleromys*” with respect to its Laventan counterparts (Walton, 1997) would tend to favour a Colloncuran-early Laventan age for this new locality (~15.6–13.0 Ma; Table 1).

4.2. Apatite fission track age of MD-67: 17.1 ± 2.4 Ma

A fission track age was calculated on 11 apatite grains. The corresponding results are detailed in the Supplementary Data. The χ^2 test (Galbraith, 1981; Green, 1981) is currently used to discriminate between concordant ($P(\chi^2) > 5\%$) and discordant ($P(\chi^2) < 5\%$) grain-age distributions. The MD 67 sample passes the χ^2 test ($P(\chi^2) > 5\%$) indicating that the apatite grains display a concordant population and that they are derived from homogeneous sources (Galbraith, 1981; Green, 1981).

The central age (17.1 ± 2.4 Ma), pointing to a Burdigalian–Langhian age for the concerned grains (Table 1), is only partly in agreement with the faunal content of MD-67, interpreted as documenting a Colloncuran-early Laventan age (~15.6–13.0 Ma; Table 1).

In other words, Apatite Fission Track provides a detrital age (17.1 ± 2.4 Ma) for the vertebrate-yielding locality, slightly older than its inferred biochronological age (Colloncuran-early Laventan South American Land Mammal Ages: ~15.6–13.0 Ma). Be as it may, the middle Miocene age of the concerned outcrop is fully contradictory to its original assignment to the Paleocene-Eocene Yahuarango Formation (Vargas and Hipólito, 1998).

4.3. Paleoenvironment

At regional scale, the concerned area mostly yielded terrestrial habitats of low elevation, with a moist forest assumed as resembling the modern Amazonian rainforest, in terms of composition and biodiversity (Hoorn, 1993; Antoine et al., 2006; Pons and De Franceschi, 2007; Hoorn et al., 2010a,b).

Unfortunately, MD-67 yields no pollen, spores, or plant fossils. Available proxies (dental morphology and habitat preferences of living and fossil mammal analogues; depositional environment) thus provide only indirect information on the environment of the concerned area by the time fossil mammals accumulated.

Most rodents from the current assemblage, including a mesodont acaremyid, a hypsodont dinomyid (“*Scleromys*” sp.), and a hypselodont caviid (*Guiomys* sp.), can be interpreted as an indicator of open and dusty environments under a quite dry and windy climate (Candela and Vucetich, 2002). Yet, the dwarf *Microsteiromys*-like erethizontid of MD-67 was most probably fully arboreal, like all living New World porcupines and their fossil kin, as proposed by Candela and Picasso (2008). Accordingly, all living marmosine marsupials, such as the representatives of the subgenus *Marmosa* (*Micoureus*) are forest dwellers, being either arboreal or ground foragers, in moist habitats related to tropical evergreen or mossy forests (Emmons and Feer, 1997).

The appendicular skeleton of *Sipalocyon* is poorly known, but functional anatomy suggests arboreal and potential grasping capabilities for this carnivorous marsupial (Argot, 2003, 2004). The Santa Cruz Beds of Patagonia, which yield most remains of *Sipalocyon*, are interpreted as originating from a temperate coastal plain (Bown and Fleagle, 1993), with moderate rainfall and a mixture of forested habitats/open areas/bushland as suggested by mammals, pollen, and terrestrial arthropods (Vizcaíno et al., 2010).

Lithology of the fossil-bearing beds (i.e., channel-iron deposits, with Fe-rich pisolite gravels) provides valuable information on the depositional environment and associated diagenetic processes: pisolites might have formed in the ground by alteration and concretion of highly ferruginous groundwater solutions under warm, humid, and seasonally-contrasted conditions (Tardy, 1992). Accordingly, isotopic analyses performed on coeval mollusc shells from the Iquitos area (~1000 km more to the North) show the region was experiencing a seasonal water influx under a monsoonal-like tropical climate by that time (Kaandorp et al., 2006; Wesselingh et al., 2006). Both proxies are therefore in good agreement.

One of the striking features of the Miocene of Amazonia is the presence of a large and long-lasting “mega-wetland”. The Amazonian mega-wetland reached its maximum extent during the Middle Miocene (also called “Pebas phase” *sensu* Hoorn et al., 2010a,b) and it consisted of a complex mosaic of lakes, embayments, swamps, rivers, and fluvio-tidal environments (see review in Hoorn et al., 2010a,b). Our data suggest the absence of this megawetland in the Amazonian Madre de Dios Subandean Zone of Perú (Fig. 4), while other coeval localities such as IQ-26 and NA069 (nearby Iquitos; Antoine et al., 2006; Pujos et al., 2009) or the Fitzcarrald Local Fauna (Antoine et al., 2007; Goillot et al., 2011) were under its influence during the same period (Fig. 4). This environmental contrast might in turn have played some role in the faunal discrepancies as observed in middle Miocene times between Northern and Southern South America (Madden et al., 1997).

4.4. Biogeography

The earliest undisputable representatives of Glyptodontinae, referred to *Boreostemma*, originate from middle Miocene Laventan localities of La Venta and Fitzcarrald (Colombia and Perú, respectively; e.g., Antoine et al., 2007). In southern South America, the earliest record occurs much later, with *Glyptodontidium tuberifer* from the late Miocene-Pliocene of NW Argentina (e.g., Oliva et al., 2010), which is most probably tied to environmental reasons (Carlini et al., 2008). If confirmed, the referral of the osteoderms of MD-67 to Glyptodontinae would still extend the gap between the first local occurrences of the group in low and high latitudes.

The cavioid rodent *Guiomys* Pérez, 2010 was so far restricted to the middle Miocene of Patagonia and Southern Bolivia, with a ? Colloncuran (~14 Ma; Patagonia)-Laventan (Patagonia + Southern Bolivia) stratigraphic range (Fig. 4; Pérez, 2010; Croft et al., 2011; Pérez and Vucetich, 2011). Accordingly, *Sipalocyon* was so far restricted to high Southern latitudes, from Patagonia to Southern Chile (51.5–37.5°S; Marshall, 1981; Forasiepi et al., 2006; Flynn et al., 2008). The co-occurrence of this stem caviid and of *Sipalocyon* (37.5–48°S) in Peruvian Amazonia extends the geographical range of ~10° and ~25° more to the North, respectively (Flynn et al., 2008; Croft et al., 2011). On the other hand, the small marmosine *M. (Mi.) laventica* and the diminutive erethizontid *Microsteiromys* were only known in the Huila Department of Colombia during a very short Laventan interval (Fig. 4; Goin, 1997; Walton, 1997), i.e., later and ~15° more to the North than in MD-67.

In other words, the MD-67 assemblage both (i) postdates the formerly known range of taxa of mid- and high latitude affinities (*Sipalocyon*; Acaremyidae) and (ii) predates that of taxa of low latitude affinities (*Marmosa* (*Micoureus*); *Microsteiromys*; Glyptodontinae). This phenomenon is summarised by the spatiotemporal range of the small dinomyid recognised in MD-67 and its kin, if close phylogenetic affinities are confirmed between the representatives of *Scleromys* *sensu stricto* (early Miocene of Patagonia and Southern Chile; Flynn et al., 2008) and those of “*Scleromys*” *sensu* Walton, 1997 (late middle Miocene of Colombia and Peru; Walton, 1997; Antoine et al., 2007). Such assertion may be an artefact tied to the scarce fossil

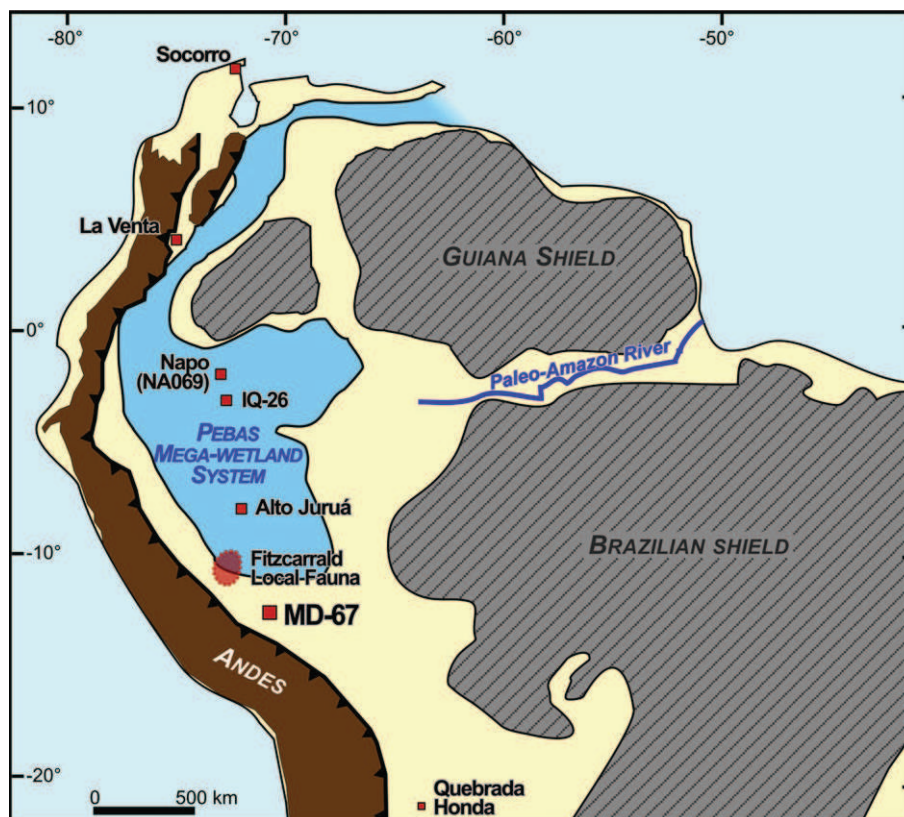


Fig. 4. Palaeogeographic map of Northern South America during middle Miocene times, showing the maximal extension of the Pebas mega-wetland System (deep blue). Modified after Lundberg et al. (1998), Hovikoski et al. (2005, 2010), Roddaz et al. (2006, 2010), Hoorn et al. (2010a,b), Roddaz et al. (2010), and our data. The squares point to vertebrate- and/or arthropod-yielding localities the middle Miocene age of which was discussed in Madden et al. (1997: La Venta), Linares (2004: Socorro), Sánchez-Villagra et al. (2004: Socorro), Antoine et al. (2006, 2007: IQ-26; Fitzcarrald Local Fauna), Croft (2007: Quebrada Honda), Pujos et al. (2009: Napo NA069), Negri et al. (2010: Fitzcarrald), Croft et al. (2011: Quebrada Honda), and Goillot et al. (2011: Fitzcarrald Local Fauna and Alto Juruá). MD-67 (present work) is likely to be the only Colloncuran-early Laventan locality attested in the concerned domain. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

record for the concerned period in South America. Nevertheless, it is likely to reveal a previously undocumented “spatiotemporal transition” between the late early Miocene assemblages as observed in high latitude localities (mostly from Argentina and Chile; Flynn et al., 2008; Vizcaíno et al., 2010) and the late middle Miocene/low latitude faunas (from Colombia, Peru, and Brazil; Kay et al., 1997; Negri et al., 2010). This apparent northward shift of forest-dependent mammals to low latitude areas (where favourable conditions would be maintained, while grassland ecosystems were spreading in higher latitudes) by the end of the Santacrucian (e.g., Vizcaíno et al., 2010), is perfectly exemplified by the platyrrhine primate fossil record, with i) a single post-Santacrucian occurrence and a Colloncuran LLO in Southern South America, and ii) a single Santacrucian occurrence (Madre de Dios, Peru; Marivaux et al., in press) and a much wider Laventan-Recent record in tropical-equatorial South America (for review, see Tejedor, 2008; Marivaux et al., in press).

Yet, faunal affinities with coeval assemblages are difficult to assess, due to the lack of available data for the early middle Miocene interval (Friasian/Colloncuran) all over South America. The fossil record is even scarcer for the early Miocene in low latitudes (e.g., Sánchez-Villagra and Clack, 2004; Goillot et al., 2011; Marivaux et al., in press). In that purpose, a strong effort shall be made in the forthcoming years in order to document the early and middle Miocene period in lowland tropical-equatorial South America.

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Appendix A. Supplementary data

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.jsames.2012.07.008>.

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