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Didelphidae marsupials (Mammalia, Didelphimorphia) from the Late Pleistocene deposit of the Gruta dos Moura Cave, northern Brazil

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ABSTRACT

The present study acknowledges the diversity of fossil marsupials from the Gruta dos Moura cave, as well as environmental and climatic aspects during the Quaternary. The results show that this is the largest diversity of Pleistocene marsupials recorded in a single cave: *Didelphis albiventris*, *D. aurita*, *Gracilinanus agilis*, *G. microtarsus*, *Marmosa murina*, *Monodelphis brevicaudata*, *M. domestica* and *Sairadelphys tocantinensis*. Furthermore, the described specimens are also part of the only fossil assemblage unequivocally referable to the late Pleistocene. Paleontological studies suggest an intimate association with dry and open environments with high abundance of water sources. Since most of the identified taxa are characteristic of open forests and gallery forests, this could represent the actual environment around the Gruta dos Moura cave. Recent studies identified sympatric occurrences between species from open and dry environments and species from humid forests that were identified among our material and are characteristic of humid regions. Therefore, these species could inhabit gallery forests and capons, or even ecotones, inside a dry and open environment. Moreover, the extinction of *Sairadelphys* could also indicate that the climatic and environmental conditions changed or that the past environment was more heterogeneous than the current environment of the region.

Key words: mammals, Didelphidae, marsupials, Northern Brazil, Quaternary, Late Pleistocene.

INTRODUCTION

Extant South American marsupials are included in two lineages: Ameridelphia and Australidelphia. While Ameridelphia is highly diverse in this continent, Australidelphia is represented only by the microbiotherid *Dromiciops glioides* (Aplin

and Archer 1987). Ameridelphia is represented by three lineages that diverged during the Paleocene, and has great stratigraphic distribution, large variety of forms, sizes, and feeding habits (Pascual 1980, Oliveira and Goin 2006). In this contribution we studied the family Didelphidae, which contains species from small to medium sizes that are usually arboreal, and of omnivorous, insectivorous,

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piscivorous and frugivorous diets. The first records of didelphid marsupials are from the late Cretaceous of North America, and from the Paleocene of South America (Pascual 1980). During the Miocene the Didelphidae became extinct in North America but reoccupied that continent during the Great American Biotic Interchange (Reig et al. 1987, Marshall et al. 1990).

Many genera of living Didelphidae are also found as fossils at Neogene and Quaternary deposits from Argentina, Brazil and Colombia (Goin 1995). The oldest didelphid taxa with living representatives are recorded in the middle Miocene of La Venta, Colombia, and comprise three species: *Thylamys minutus*, *Thylamys colombianus* and *Micoureus laventicus* (Goin 1995). Another Neogene taxon, the new species *Didelphis solimoensis*, from the late Miocene of Formação Solimões, state of Acre, northern Brazil, is the oldest representative of this genus (Cozzuol et al. 2006).

The diversity of Didelphidae from the Brazilian Quaternary is well represented from karstic caves. Among the Brazilian karstic caves containing Quaternary fossils, the caves from Lagoa Santa, state of Minas Gerais, were studied by a Danish researcher, Peter Wilhelm Lund (Lund 1950). The fossil materials collected by Lund were sent to the Natural History Museum of Denmark, where the marsupial fossils were described by Winge (1893), who identified thirteen species representing the largest association diversity of fossil marsupials found until now (Cartelle 1999). The second largest assemblage of didelphids from the Brazilian Quaternary described in the literature is from Serra da Mesa, state of Goiás (Salles et al. 1999). Eight taxa were described for this region: *Monodelphis domestica*, *Monodelphis kunsii*, *Gracilinanus emiliae*, *Gracilinanus agilis*, *Thylamys* sp., *Micoureus demerarae*, *Didelphis albiventris* and *Philander opossum*. Cartelle (1999) also reported some Pleistocene-Holocene marsupials from several

caves in Bahia, identifying four species: *Didelphis albiventris*, *Gracilinanus agilis*, *Micoureus cinereus* and *Monodelphis domestica*.

The whole record of Didelphidae from the Brazilian Quaternary is represented by living genera, except for the new genus and species recently described, *Sairadelphys tocantinensis*. The specimens representing this new taxon were also collected at a karstic cave located in southeast, state of Tocantins, northern Brazil (Oliveira et al. 2011). In addition to this material, other didelphid taxa were found associated with the specimens of *S. tocantinensis*, which are described here.

MATERIALS AND METHODS

LOCALITY AND GEOLOGY

All studied specimens come from a carbonate deposit which was found in a block at the wall of the main room of the limestone cave, Gruta dos Moura, in Aurora de Tocantins (12°42'47" S and 46°24'28" W), state of Tocantins, northern Brazil. The carbonate rocks of the region of Aurora do Tocantins are part of the Speleological Province of the Bambuí Group, where a large number of caves have been found (Zampaulo and Ferreira 2009). The geology of the studied area is still poorly known. The predominant rocks in the region are rhythmic limestones and siltstones from the Paraopeba Subgroup of Neoproterozoic age, although alluvial deposits might occur locally (Dardene 1978, Dardene and Walde 1979).

The information provided by the Geological Survey of Brazil (CPRM 2006) on the geology of the municipality of Aurora de Tocantins report carbonate and terrigenous deposits. The lower portion of area is represented by the Sete Lagoas Formation, which is composed of thick deposits of mudstones, calcareous and dolomites. The Sete Lagoas Formation is covered by siltstone and laminate siltstones of the Serra de Santa Helena Formation. This carbonate-terrigenous

conjunction of rocks is superimposed by dark calcarenites and marls, with organic material from the Lagoa do Jacaré Formation. Superimposed over the Bambuí Group are the Cretaceous sediments of the Urucua Formation. The caves were developed mainly in the limestones of Lagoa do Jacaré Formation, which consist of slightly weathered dark gray metacalcarenites, massive or with horizontal lamination, with sparry calcite (generally in veins), micritic calcite, ooids and small amounts of silica. In some outcrops there are interbedded metacalcarenites, mudstones and calcilutites. Millimetre- to centimeter-wide whitish gray intraclasts occur throughout the predominant limestones (CPRM 2006).

The limestones often form plateaus that rise from the rest of the terrain and comprise a partially active karst system. Most caves occur above the ground level in high portions of the plateaus. The caves originated during a period of formation of karst relief in which the rocks that now compose the plateaus were below the ground level. The current outcrops were developed not by the uplift of the plateaus, but by the different types of erosion of the limestones and the erosive retraction of the Urucua sandstones which once covered the region and today occur to the east of the study area. Access to the plateaus occurs mainly through vicinal roads and paths that cut the vegetation. Currently, the region is situated mainly within the Cerrado biome.

The Gruta dos Moura cave is an epigenic, solutional, ramiform to network cave with some branchwork passages (*sensu* Palmer 1991) and has great vertical and horizontal development. The entire length of the cave has not yet been completely mapped. The Gruta dos Moura cave originated in a phreatic zone and was later invaded and enlarged by vadose water. There is a notable difference between the upper and lower levels of the cave. The higher levels show galleries and fissures with many speleothems, including travertines, draperies, stalactites, stalagmites and coralloids,

showing a higher activity of vadose waters. The fossils were found in the lower levels, which consist of phreatic passages and rooms with few speleothems. Slightly consolidated sedimentary deposits outcrop at these levels, composed of massive, very fine to coarse, immature and poorly sorted sands with clayey matrix. In some parts of the cave a relict carbonate precipitation layer can be seen having a rich in millimeter- to centimeter-sized fragments of bones and teeth. This layer seems to have covered the sedimentary deposits in a period of decreased sedimentation and stagnation of water flow, causing the precipitation of carbonates and concentrating sediment.

The occurrence of sedimentary deposits covered by carbonate incrustation lenses is also observed in many other caves in the region of Aurora do Tocantins, possibly corresponding to a large scale event of increased humidity, causing changes in the pattern of recharge from the land surface and consequently in the entire environment. Similar occurrences were studied by Auler et al. (2009), who identified three processes (clastic sediment input, erosion and calcite deposition) that are linked to distinct palaeoenvironmental and climatic conditions.

The episodes of clastic input would be related to a drier climate, sparse vegetation and intense sediment yield due to runoff, while the precipitation of calcite would be related to wetter conditions (Auler and Farrant 1999, Brain 1995, Brook et al. 1997). Sediment erosion inside those caves can be interpreted as cause of intermediate climatic conditions, which were not humid enough for speleothem deposition and not dry enough to allow transportation of sediment into the caves (Auler et al. 2009).

METHODOLOGY

The fossil remains of Didelphidae were collected from a block of calcareous rock that was water-washed and sieved (screenwashing). The screenwashing

was made with four sieves with meshes of 10mm, 5mm, 2.5mm and 1mm. The material kept on the sieves was dried and, later, selected in laboratory using a stereoscopic microscope.

The identification and diagnosis of the specimens from Gruta dos Moura cave were made by morphological comparison of cranial and mandible elements of Didelphidae specimens housed at the following institutions: Fossil Mammal collection of the Mammalogy Laboratory, Universidade Federal do Estado do Rio de Janeiro (UNIRIO); Mammalogy collection of the Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MN/UFRJ); Mammalogy Laboratory, Zoology Department, Universidade Federal de Pernambuco, Pernambuco, Brazil (UFPE); Universidade Federal do Espírito Santo, Espírito Santo, Brazil (UFES); and Museo de La Plata, La Plata, Argentina (MLP).

The dental nomenclature followed Goin and Candela (2004) (Fig. 1). The post-protocrest can be seen on *Gracilinanus microtarsus* but was not named on figure 1 of Goin and Candela (2004). The acronyms M1, M2, M3 and M4 are used to address the first, second, third and fourth upper molars, respectively; and the acronyms m1, m2, m3 and m4 refer to the first, second, third and fourth lower molars, respectively. The deciduous molars are referred to as “dp”.

RESULTS

The methodology described here allowed the recovering of 57 cranio-mandibular specimens with preserved teeth (upper and lower molars) that, after careful identification, revealed five genera and eight species of Didelphimorphia. Therefore, the diversity presented here is comparable to the diversity of didelphids from Serra da Mesa and Lagoa Santa localities, considered the largest records on diversity of didelphids to South America (Salles et al. 1999, Winge 1893). However, it is worth noting that the material studied here

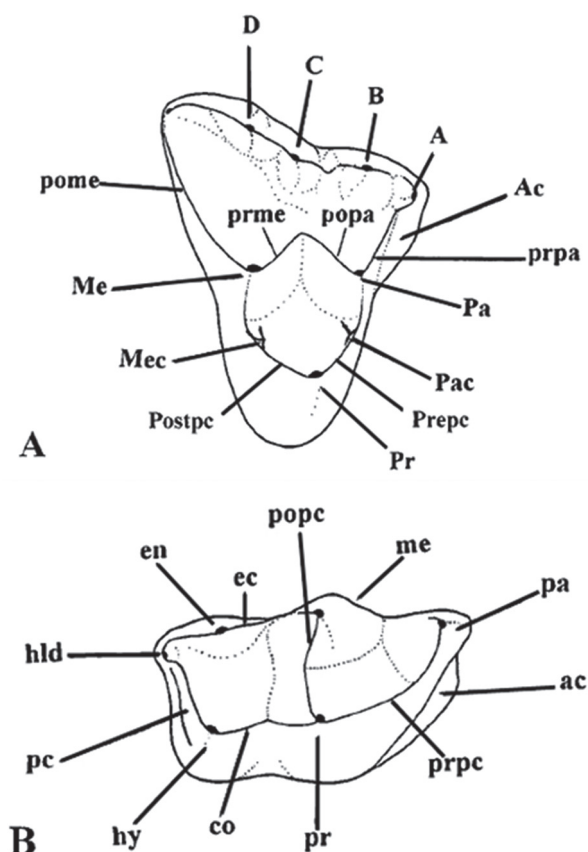


Figure 1 - Nomenclature for didelphimorph molar (modified from Goin and Candela 2004). A. Upper right molar; B. Lower right molar. Abbreviations for upper molars: A, B, C, D: stylar cusps A, B, C, and D, respectively; Ac: anterior cingulum; Me: metacone; Mec: metaconule; Pa: paracone; Pac: paraconule; pome: postmetacrista; popa: postparacrista; Postpc: postprotocrista; Pr: protocone; Prepc: preprotocrista; prme: premetacrista; prpa: preparacrista. Abbreviations for lower molars: ac: anterior cingulum; co: cristid obliqua; ec: entocristid; en: entoconid; hld: hypoconulid; hy: hypoconid; me: metaconid; pa: paraconid; pc: postcingulum; popc: postprotocristid; pr: protoconid; prpc: preprotocristid.

comes from a single cave, while the Didelphidae diversity from Serra da Mesa and Lagoa Santa were recovered from several caves on each respective locality (Winge 1893, Salles et al. 1999).

SYSTEMATICS

MAMMALIA Linnaeus, 1758

DIDELPHIMORPHIA Gill, 1872

DIDELPHIDAE Gray, 1821

Didelphis Linnaeus, 1758

Didelphis aurita (Wied-Neuwied, 1826)

(Fig.2 C-E)

Referred material: UNIRIO-PM1206, left dp3; UNIRIO-PM1207, right dp3; UNIRIO-PM1208, left dp3.

Description and comments: The deciduous molars are broad on its middle-distal portion, labio-lingually compressed, and having inflated cusps. The trigone basin is deep, and the ectoflexus is absent. The most developed styler cusps are StB and StD. The paracone is very small, and it is fused with the StB. The specimens differ from *Didelphis albiventris* in having smaller molars. Compared to the deciduous molars of *D. marsupialis*, the paracone is not as coalesced to the StB as in *D. aurita*. On *Philander*, the paracone is aligned with the metacone.

Fossil record in South America: This is the first record of the taxon to the continente (Fig. 2).

Remarks: *Didelphis aurita* is found in eastern Brazil in the Tropical Atlantic Forest and in the *Araucaria* Forest domains. Populations of black-eared opossums still occur in the remnants of the Atlantic Forest of Alagoas and Pernambuco, but are considered to be rare (Gardner 2008).

Didelphis albiventris (Lund, 1840)

(Fig.2 A-B)

Referred material: UNIRIO-PM1209, left dentary.

Description: The m1 is worn. The metaconid is the largest cusp of the trigonid; it is tall, labially displaced, with slender edges. The protoconid is the smallest cusp of the trigonid, and has slender and straight edges. The entoconid and the hypoconulid are very close, and both are distally displaced. The post-hypocristid is rectilinear. The hypoconid is broad and labially displaced. The m2 is worn on the trigonid, the hypoconid is well developed and distally displaced, and the anterior cingulum is well developed. The m4 has developed anterior cingulum.

Comments: The lower molars have a shallow talonid, well developed anterocingulid, and hypoconulid distally displaced. The specimen differs from *Didelphis aurita*, which has the entoconid more set apart from the hypoconulid, and the entoconid is not distally placed. This is particularly evident on the m4. The material is also distinct from *Didelphis marsupialis*, since this species has larger molars. The m4 of *D. marsupialis* has the entoconid coalesced to the hypoconulid, and in the m3 the entoconid is much more developed. The dentary is very thick, a feature unusual in living specimens of *D. albiventris*, and has a straight ventral edge. Fossil record in South America: late Pleistocene of Mar Del Plata and Holocene of Córdoba, Argentina; Pleistocene of Lagoa Santa, Minas Gerais and Bahia; Quaternary of Serra da Mesa, Goiás, Brazil (Winge 1893, Salles et al. 1999, Cartelle 1999) (Fig. 2).

Remarks: *Didelphis albiventris* inhabits open and deciduous forest areas, including areas of low and irregular rainfall such as the Caatinga and Monte Desert (Gardner 2008).

Gracilinanus Gardner & Creighton, 1989

Gracilinanus agilis (Burmeister, 1854)

(Fig.3 A-E)

Referred material: UNIRIO-PM1116, left M1; UNIRIO-PM1117, left M2; UNIRIO-PM1118, left M2; UNIRIO-PM1119; UNIRIO-PM1210, right M1; UNIRIO-PM1211, right M2; UNIRIO-PM1212, left M2; UNIRIO-PM1213, left M3; UNIRIO-PM1214, left M3; UNIRIO-PM1215, right maxillary with M2 and M3; UNIRIO-PM1216, left maxillary with M1-4; UNIRIO-PM1217, left maxillary with M3 and M4, right M2; UNIRIO-PM1225, left M3; UNIRIO-PM1226, left M3; UNIRIO-PM1227, right M1; UNIRIO-PM1228, left M1.

Description: The M1 and M2 are broader mesiodistally than the M3. The M1 has a well developed preparacrista connected to the StB. The

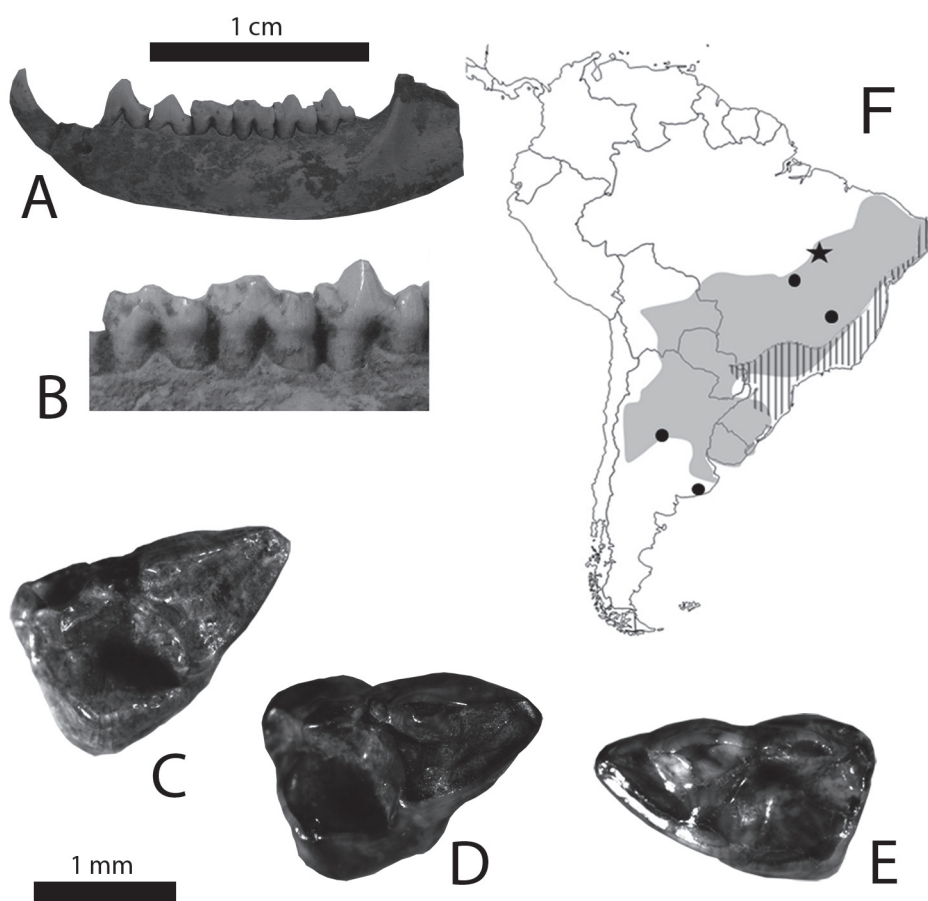


Figure 2 - Selected specimens of *Didelphis* from Gruta dos Moura and its revised geographic distribution for the Pleistocene. **A.** An almost complete left dentary of *Didelphis* cf. *albiventris* (UNIRIO-PM1209) in labial view. **B.** A detail view of molar series of the left dentary of *Didelphis* cf. *albiventris* (UNIRIO-PM1209) in labial view. Note the great wear mainly in the m1 and m2. Scale: 1cm. **C.** Left dp3 of *Didelphis* cf. *aurita* (UNIRIO-PM1206) in occlusal view; **D.** Left dp3 of *Didelphis* cf. *aurita* (UNIRIO-PM1208) in occlusal view; **E.** Right dp3 of *Didelphis* cf. *aurita* (UNIRIO-PM1207) in occlusal view. Scale 1mm. Geographic **F.** Distribution of *Didelphis aurita* and *D. albiventris*. Gray area is the geographic distribution of the extant *Didelphis albiventris*. Area with vertical lines is the geographic distribution of the extant *Didelphis aurita*. Black star marks the Gruta dos Moura cave locality. Black circles mark Pleistocene records of *Didelphis albiventris*. (Gardner 2008, Winge 1893, Salles et al. 1999, Cartelle 1999).

StB is well developed, and similar in height to the paracone. The M3 is more mesiodistally compressed than the M2. The protocone of the M3 is also very compressed, and the ectoflexus is deep. The M1 has a poorly developed ectoflexus, and the M2 has a moderately developed ectoflexus. The styler shelf is moderately developed. A small StC is present.

Comments: The material is characterized by the presence of upper molars mesiodistally compressed, small styler cusps, StC that may or may not be present, and metacone larger than the paracone. The species differs from *Gracilinanus microtarsus* because the latter has the posprotocrista extended beyond the base of the metacone. This feature is not observed in *G. agilis*.

Fossil Record in South America: Pleistocene of Lagoa Santa, Minas Gerais; Quaternary of Serra da Mesa, Goiás and Rio Grande do Sul; Pleistocene of Bahia (Winge 1893, Salles et al. 1999, Cartelle 1999, Hadler et al. 2009) (Fig. 3).

Remarks: Living specimens were trapped in disturbed cloud forest characterized by a bamboo (*Chusquea* sp.) understory and a mossy ground cover. Salazar-Bravo et al. (2002) mentioned trapping a specimen in a habitat consisting of a mixture of pajonales, sphagnum bogs, mixed-species forest, and *Polylepis* forest on a “blocky” limestone substrate.

Gracilinanus cf. microtarsus (J.A. Wagner, 1842) (Fig. 3 F-H)

Referred material: UNIRIO-PM1218, right M3; UNIRIO-PM1219, right M2.; UNIRIO-PM1220, left M2

Description: The metacone is much larger than the paracone. The stylar shelf and the trigon basin are similar in size. The M2 and M3 have the postprotocrista extended to beyond the base of the metacone. The anterior cingulum is narrow, and it is connected to the preprotocrista. The StC is present. The left M2 has StD, StB and StC of similar sizes. The protocone is mesiodistally broader. The first upper molars have the protocone labio-lingually compressed.

Comments: Molar teeth are characterized by the postprotocrista extended to beyond the lingual limit of the metacone. This feature is only observed in *G. microtarsus*, which distinguishes it from other species of *Gracilinanus*. Some molars have the anterior cingulum connected to the preprotocrista. The material studied differs from *Marmosa*, which presents more developed anterior cingulum, and has little difference in size between the paracone and the metacone. It is also different from *Micoureus*, which presents a more conspicuous size difference between the paracone and the metacone. In addition, the molars of *Micoureus* are labio-

lingually compressed, making it broader. Finally, *G. microtarsus* differs from *Thylamys*, because the latter has the postprotocrista labially extended.

Fossil Record in South America: Pleistocene of Lagoa Santa, Minas Gerais, Quaternary of Rio Grande do Sul. Brazil (Winge 1893, Salles et al. 1999, Cartelle 1999, Hadler et al. 2009)

Marmosa Gray, 1821

Marmosa murina (Linnaeus, 1758)

(Fig. 4)

Referred material: UNIRIO-PM1093, left maxillary with M1-2; UNIRIO-PM1094, right maxillary with M2-3; UNIRIO-PM1219, fragment of right maxillary with M1; UNIRIO-PM1221, right M2; UNIRIO-PM1222, right M3; UNIRIO-PM1223, left maxillary with M3-4; UNIRIO-PM1224, left M2.

Description: The M3 have individualized StB and StD, subdivided StC, marked ectoflexus; paracone and metacone of similar sizes; wide trigone and stylar shelf labio-lingually compressed, well developed protocone anterior cingulum connected with the preprotocrista. At the M1-M2 the StB is individualized. A vestigial metaconule is present (Fig. 4A and 4B).

Comments: The molar teeth are characterized by the presence of small and separated StB and StD; subequal paracone and metacone, well developed ectoflexus and vestigial metaconule eventually present. *M. murina* differs from *Micoureus*, which has less developed cingulum, especially at the M4, and also has a more conspicuous difference between the paracone and the metacone. It differs from *Gracilinanus*, because the latter has molars that are mesiodistally broader, which makes the stylar shelf broader than the trigone. Furthermore, the protocone of *Gracilinanus* is more compressed. Lastly, *Thylamys* differs from *M. murina*, in having labio-lingually compressed molars.

Fossil Record in South America: This is the first fossil record of *M. murina* (Fig. 4).

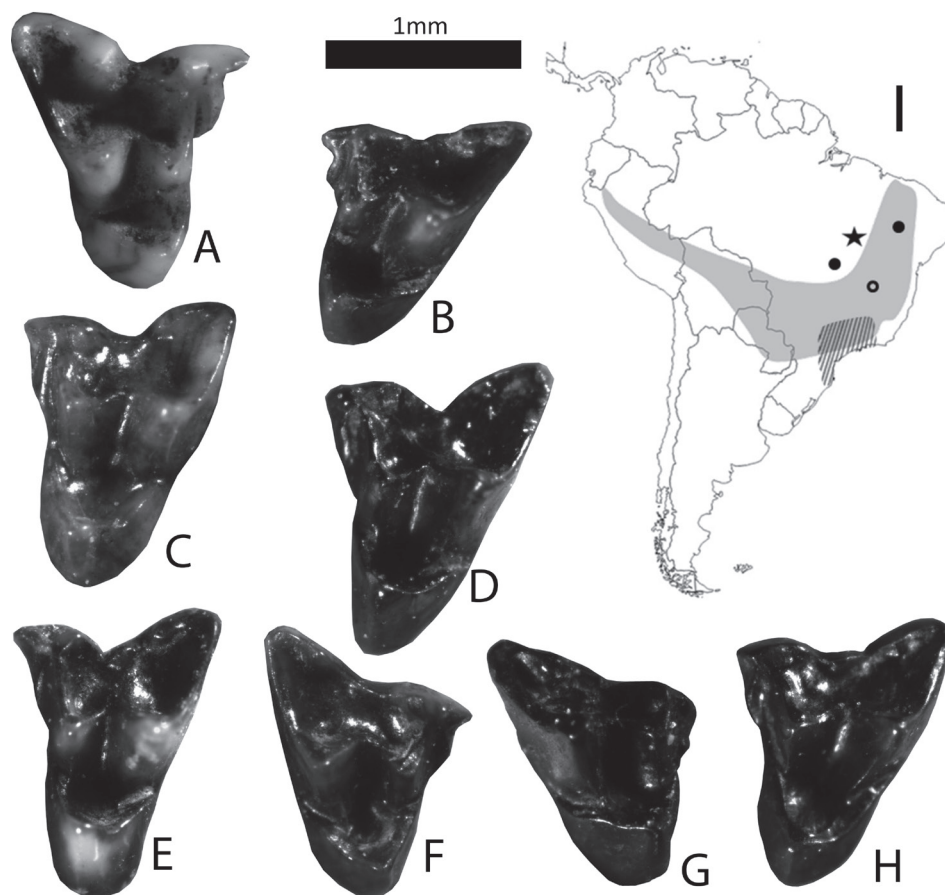


Figure 3 - Selected specimens of *Gracilinanus* from Gruta dos Moura and its revised geographic distribution for the Pleistocene. **A.** *Gracilinanus agilis* right M2 (UNIRIO-PM1211) in occlusal view; **B.** *G. agilis* left M2 (UNIRIO-PM1118) in occlusal view; **C.** *G. agilis* left M2 (UNIRIO-PM1212) in occlusal view; **D.** *G. agilis* left M3 (UNIRIO-PM1214) in occlusal view; **E.** *G. agilis* left M3 (UNIRIO-PM1213) in occlusal view. **F.** *Gracilinanus* cf. *microtarsus* right M2 (UNIRIO-PM1219) in occlusal view; **G.** *G. microtarsus* right M3 (UNIRIO-PM1218) in occlusal view; **H.** *G. microtarsus* left M2 (UNIRIO-PM1220) in occlusal view. Scale 1mm. **I.** Geographic distribution of *G. agilis* and *G. microtarsus*. Gray area is the geographic distribution of the extant *G. agilis*. Area with vertical lines is the geographic distribution of the extant *G. microtarsus*. Black star marks the Gruta dos Moura cave locality. Black circles mark Pleistocene records of *G. agilis*. Open circle mark Pleistocene records for both *G. agilis* and *G. microtarsus*. (Gardner 2008, Winge 1893, Salles et al. 1999, Cartelle 1999, Hadler et al. 2009).

Monodelphis Burnett, 1830

Monodelphis brevicaudata (Erxleben, 1777)
(Fig.5 A-D)

Referred material: UNIRIO-PM1095, right M1; UNIRIO-PM1096, left M1; UNIRIO-PM1097, left M1; UNIRIO-PM1098, right M1; UNIRIO-PM1099, left maxillary with M1-2; UNIRIO-

PM1229, left maxillary with M1-3; UNIRIO-PM1230, left M2; UNIRIO-PM1231, left M1; UNIRIO-PM1232, left M1.

Description: The M1 has a labio-lingually compressed protocone while the M3 presents a mesio-distally compressed protocone. The StD is the largest cusp in all molars. The ectoflexus is

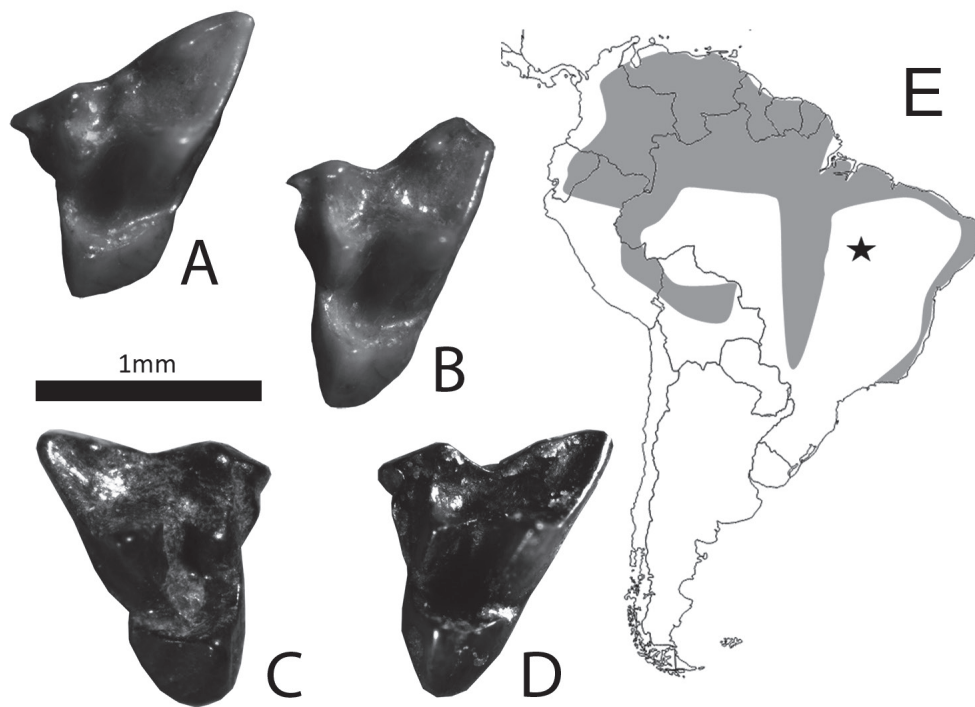


Figure 4 - Selected specimens of *Marmosa murina* from Gruta dos Moura and its revised geographic distribution for the Pleistocene. **A.** Left M1 (UNIRIO-PM1093) in occlusal view; **B.** Left M2 (UNIRIO-PM1093) in occlusal view; **C.** Right M3 (UNIRIO-PM1222) in occlusal view; **D.** Left M2 (UNIRIO-PM1224) in occlusal view. Scale 1mm. **E.** Geographic Distribution of *Marmosa murina*. Gray area is its extant geographic distribution. Black star marks the Gruta dos Moura cave locality. (Gardner 2008, Winge 1893, Salles et al. 1999, Cartelle 1999).

shallow and displaced anteriorly. The preparacrista is very elongated. The metacone is much larger than the paracone. The anterior cingulum is very narrow. The StE is poorly developed in some specimens but evident in others, and the StA is conspicuous. The StB is small. There is also evidence of a vestigial metaconule. The centrocrista is V-shaped.

Comments: The upper molars have more well-developed StD than the living specimens. The postmetacrista is well-developed. The metacone is much larger than the paracone. Some molar teeth have a small StC. The metaconule may be present. When compared with *Didelphis*, *M. brevicaudata* has less inflated cusps and well developed styles. Compared

with *Marmosa*, the preparacrista is proportionally larger. The StD and StB are better developed. It differs from *Micoureus*, which do not has the antero-labial cingulum connected to the preprotocrista, and by the conspicuous difference between the paracone and the metacone. It differs from *Thylamys* because the latter has mesio-distally quite compressed molars and has less developed styler cusps.

Fossil Record in South America: This is the first fossil record of *M. brevicaudata* (Fig. 5).

Ecology: *M. brevicaudata* is more abundant in multistratal evergreen forests than in dry deciduous forest, but may be found in edge habitats around clearings (Gardner 2008).

Monodelphis domestica (J. A. Wagner, 1842)

(Fig. 5 E-H)

Referred material: UNIRIO-PM1100, right M1; UNIRIO-PM1101, right M1; UNIRIO-PM1102, left M1; UNIRIO-PM1103, left M1; UNIRIO-PM1104, left M1; UNIRIO-PM1105, left M1; UNIRIO-PM1106, right M2; UNIRIO-PM1107, left M2; UNIRIO-PM1108, left M2; UNIRIO-PM1109, left M1; UNIRIO-PM1110, right M1; UNIRIO-PM1111, right maxillary with M2; UNIRIO-PM1112, left maxillary with M1-2; UNIRIO-PM1113, left maxillary with M1; UNIRIO-PM1114, left maxillary with M1; UNIRIO-PM1115, left maxillary with M2; UNIRIO-PM1233, right maxillary with M2-3; UNIRIO-PM1234, right M1; UNIRIO-PM1235, right M1; UNIRIO-PM1236, right M1.

Description: Upper molar with a quite developed and conical StD; in some molars, it is larger than the metacone. It is important to point out this feature, since this stylar cusp is much better developed when compared to living specimens. The M1 is smaller than the M2 and M3, and much more labio-lingually compressed. The ectoflexus is marked but shallow. The preparacrista is very long. The metacone is much larger than the paracone. The anterior cingulum is present. The StE is poorly developed in some specimens but evident in others; the StA is conspicuous. The StB is similar in size to paracone. The M1 also presents a vestigial metaconule. The protocone of the M1 is mesio-distally broader when compared with the M3 and M2. The centrocrista is V-shaped.

Comments: Upper molar teeth with broad protocone, paracone and metacone fairly separated and considerably different in size, where the paracone is very small. The StB and the StD are well developed at the M1-3. The StD is the largest cusp, and is very tall and conical. The upper molars are a little antero-posteriorly compressed and do not have the preprotocrista connected to the anterior cingulum. The StC is absent or much reduced. The

postmetacrasta is well developed and the stylar shelf is broad and deep. The ectoflexus is marked. Compared with *Didelphis*, it has less inflated cusps and styles B and D more developed. Compared with *Marmosa*, the preparacrista is proportionally larger. The StD is larger. It differs from *Micoureus* in the absence of the anterior cingulum connected to the preprotocrista, and for the great difference in size between the paracone and the metacone. *M. domestica* differs from *Thylamys*, which presents molars mesio-distally compressed, and less developed stylar cusps. It differs from *M. glirina*, because the latter has the StD of the M3 slightly smaller and with round border, and the StE is less evident. *M. touan* has smaller StD and StB. The trigone basin is less deep. *M. iheringi* presents smaller molars when compared with *M. domestica*. The StD and StB have similar sizes and are smaller when compared with *M. domestica*. *M. emiliae* has StB and D of similar sizes. The StB is the largest cusp of the M2 and M3. *M. americana* has a smaller masticatory apparatus when compared with *M. domestica*. The StB and StD are developed and of similar sizes. The StB is the largest cusp at the M2 and M3. *M. domestica* differs from *M. theresa* for having larger molars. The StD and B are poorly developed. *M. scalops* is smaller and has mesio-distally broader molars. *M. brevicaudata* has the StD subdivided in two cusps. *M. umbistrick* is smaller. The StD and StB have similar sizes. *M. dimidiata* has smaller molars when compared with *M. domestica*. The StD is smaller than the StB at the M3. *M. kunsii* has StB larger than the StD.

Fossil Record in South America: Pleistocene of Lagoa Santa, Minas Gerais and Bahia; Quaternary of Serra da Mesa, Goiás, Brazil (Winge 1893, Salles et al. 1999, Cartelle 1999) (Fig. 5).

Remarks: *Monodelphis domestica* is most abundant in Paraguay, Bolivia, and in Mato Grosso and northeast of Brazil, with only scattered records in central Brazil.

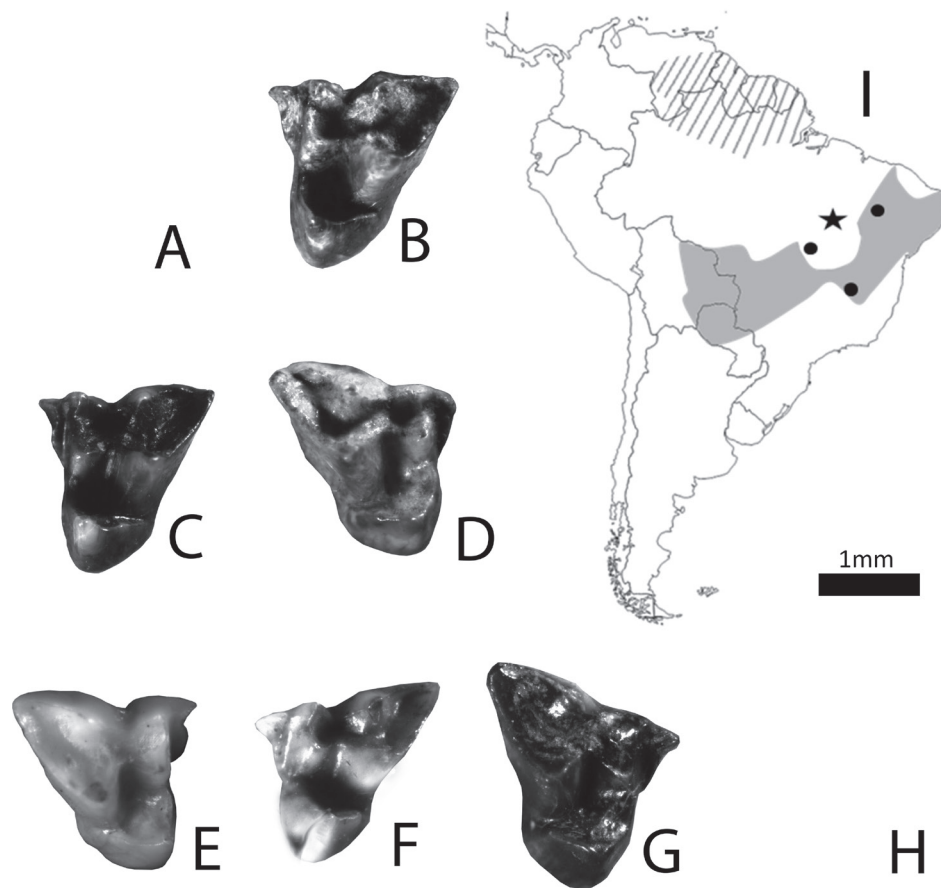


Figure 5 - Selected specimens of *Monodelphis* from Gruta dos Moura and its revised geographic distribution for the Pleistocene. **A.** *Monodelphis brevicaudata* left M2 (UNIRIO-PM1099) in occlusal view; **B.** *M. brevicaudata* left M1 (UNIRIO-PM1097) in occlusal view; **C.** *M. brevicaudata* left M2 (UNIRIO-PM1230) in occlusal view; **D.** *M. brevicaudata* right M1 (UNIRIO-PM1098) in occlusal view; **E.** *Monodelphis domestica* right M3 (UNIRIO-PM1233) in occlusal view; **F.** *M. domestica* left M1 (UNIRIO-PM1102) in occlusal view; **G.** *M. domestica* right M1 (UNIRIO-PM1101) in occlusal view; **H.** *M. domestica* right M1 (UNIRIO-PM1110) in occlusal view. Scale 1mm. **I.** Geographic distribution of *M. brevicaudata* and *M. domestica*. Gray area is the geographic distribution of the extant *M. domestica*. Area with vertical lines is the geographic distribution of the extant *M. brevicaudata*. Black star marks the Gruta dos Moura cave locality. Black circles mark Pleistocene records of *M. domestica*. (Gardner 2008, Winge 1893, Salles et al. 1999, Cartelle 1999).

Sairadelphys Oliveira, Villa Nova, Goin & Avilla, 2011

Sairadelphys tocantinensis Oliveira, Villa Nova, Goin & Avilla, 2011

Hypodygm: DGEO-UFPE 6745, incomplete left maxillary with M2-4; DGEO-UFPE 6746, left m1.

Diagnosis: Very small Didelphidae, slightly larger than *Hyladelphys*. The stilar cusps are reduced in

number and size. The M2 is subequal or slightly larger than the M3. The first inferior molar has well-developed pre-fossid. *S. tocantinensis* differs from *Hyladelphys* for having more bunodont teeth, deeper ectoflex at the M2, paracone and metacone of similar sizes at the M2-3, very short and eccentric protocone, anterior cingulum absent, great reduction in number and size of the stilar cusps forte, and small M4.

Description: the M2 is the largest known molar (the M1 is unknown); $M2 > M3 > M4$. The ectoflex is well developed and symmetrical, so that the parastilar and metastilar regions are very conspicuous. The cusps of the trigone are short and bunodonts. The stylar shelf is taller than the basin of the trigone. The stylar cups are absent; there is only a vestige of StD at the M2. The preparacrista is short and poorly developed. The postmetacrista is slightly longer than the preparacrista. The left m1 has low, slightly inflated cusps. The trigonid is similar in length to the talonid. The protoconid is the largest cusp of the trigonid. The metaconid is labio-lingually compressed. It has a well developed pre-fossid.

Remarks: *Sairadelphys tocantinensis* was a very small marsupial comparable in dental dimensions to some of the smallest living didelphimorphians such as *Hyladelphys* and *Gracilinanus*. The upper molar morphology of *Sairadelphys* includes relatively low crowns, reduced M4, absence of shearing cristae and reduction of protocones. These features are suggestive of insectivorous-frugivorous feeding habits. *Hyladelphys* has more developed posmetacristae than *Sairadelphys*, which is suggestive of a more insectivorous diet (Oliveira et al. 2011).

DISCUSSION

The stratigraphically controlled survey of the described material ensures that all the specimens from Gruta dos Moura cave partially represents the diversity of didelphids that synchronously inhabited the area nearby the cave. We assume that this is a partial diversity because there are few paleontological studies which could certify that the assemblage of a given cave represents the mammal diversity of a region, since the fossilization is a rare process which depends on several factors, especially the taphonomic factors. Therefore, the calcareous block where the marsupial fossil remains were found, belongs to the same stratigraphic level throughout one of the secondary tunnels of Gruta

dos Moura cave. The sedimentological features, such as color and granulometry, also suggests that the calcareous blocks had the same genesis (Avilla et al. 2013). Furthermore, the disintegration of the block revealed that there was a taphonomic selection by size, where only fragments of small vertebrates, especially mammals, including rodents (Tobelem et al. 2013), bats (Avilla et al. 2013) and marsupials (Villa Nova and Avilla 2013), were preserved. The only exception was a fragment of a maxillary bone with an almost complete tooththrow of a tayassuid *Catagonus stenocephalus*, an extinct species from the South American Pleistocene which dates from 22.000 years before present (YBP; Eletron Spin Ressonance; Avilla et al. 2013) which was found in association with the marsupial assemblage studied here. In accordance, we also believe here that this dating is suitable to all the fossil found in the calcareous blocks of the secondary tunnel of Gruta dos Moura cave. Thus, the diversity of didelphids described here represents part of the fauna that inhabited the region around the Gruta dos Moura cave during the Last Glacial Maximum (LGM). The LGM occurred at approximatedly 22.000 YBP, and represents the coldest and drier period of South America of the last million years.

The total diversity of marsupials of Gruta dos Moura cave represents eight taxa which is the largest diversity of this group from a single Brazilian cave (Table I). Here we report the first fossil record of the following species: *Didelphis aurita*, *Marmosa murina* and *Monodelphis brevicaudata*. Moreover, our material is the only assemblage that securely belongs to the late Pleistocene. The other Brazilian fossil assemblages (Table I) were recovered from several caves that do not have absolute datings, preventing us from comparing those assemblages with our study.

Hitherto, the stratigraphically controlled survey of the fossils from the Gruta dos Moura cave reinforce our paleoclimatic and paleoenvironmental interpretations based on the didelphid fauna.

TABLE I
List of didelphidae species from the Pleistocene-Holocene of Brazil taken from Cartelle (1999), Salles et al. (1999) and Hadler et al. (2009).

Species	TO	BA	CE	MG	GO	RS
<i>Caluromys lanatus</i>				X		
<i>Cryptonanus sp.</i>		X				
<i>Didelphis albiventris</i>	X	X	X	X	X	
<i>Didelphis aurita</i>	X					
<i>Didelphis marsupialis</i>				X		
<i>Gracilinanus agilis</i>	X	X		X	X	X
<i>Gracilinanus emiliae</i>					X	
<i>Gracilinanus microtarsus</i>	X			X		X
<i>Lutrolina crassicaudata</i>				X		
<i>Marmosa grisea</i>				X		
<i>Marmosops incanus</i>				X		
<i>Marmosa murina</i>	X					
<i>Marmosa pusilla</i>				X		
<i>Marmosa velutina</i>				X		
<i>Micoureus cinereus</i>		X		X		
<i>Micoureus demerarae</i>					X	
<i>Monodelphis brevicaudata</i>	X					
<i>Monodelphis americana</i>						X
<i>Monodelphis domestica</i>	X	X		X	X	
<i>Monodelphis kunsii</i>					X	
<i>Philander opossum</i>				X	X	X
<i>Thylamys velutinus</i>						X
<i>Sairadelphys tocantinensis</i>	X					

The association of the described didelphids with a specimen of *Catagonus stenocephalus* suggests a profusion of open areas under a dry climatic regime around the Gruta dos Moura cave (Avilla et al. 2013), different from the humid Cerrado present nowadays (Zampaulo and Ferreira 2009). Peccaries of the genus *Catagonus* have several morphological features associated with cursorial habits in relatively open and dry environments (e.g. orbits located in posterodorsal position and behind the M3 due to elongation of the rostrum, pronounced development of nasal sinuses and chambers, infraorbital foramen located anteriorly to the zygomatic arch, a distinct basicranial flexure, and reduction of the lateral digits of the limbs (Wetzel 1977, Gasparini et al. 2009, 2010). This also corroborates the presence of a dry climate during the LGM, where the didelphids and *C. stenocephalus* inhabited the region around the Gruta dos Moura cave.

Since the described diversity of didelphids are represented mostly of extant taxa, we could also infer paleoenvironmental and paleoclimatic settings for this fossil assemblage. Pleistocene faunas of small mammals, which include fossilized specimens of extant fauna, have been used as an important parameter to infer past environments and climates (Avilla et al. 2007). Therefore, as most of the taxa here identified are characteristic of open forests and gallery forests, this could have been the landscape around the Gruta dos Moura cave during the late Pleistocene. This also includes the taxa typical of humid forests, such as *D. aurita*, *G. microtarsus* and *M. brevicaudata*, since these taxa have been recorded on transition areas and drier regions. The gallery forests and capons from the Cerrado biome might have relict fauna from humid environments (Geise and Astúa 2009, Geise et al. 2013). Furthermore, other paleontological studies performed at the Gruta do Urso cave, nearby Gruta dos Moura cave, have fossil fauna from the same age (with datings of 25,000 to 22,000 YBP). The fauna from Gruta do Urso cave suggests an intimate association with dry open environments with high abundance of water sources (Castro et al. 2013, Hsiou et al. 2013). Among this fauna, we highlight several pampean mammals (Castro et al. 2013), capybaras (*Hydrochoerus hydrochaeris*), alligators (*Caiman* sp.) and anacondas (*Eunectes murinus*, Hsiou et al. 2013). However, the current climatic and environmental conditions (humid Cerrado) of the region are certainly different from those during the LGM, when the didelphid fauna described here inhabited the region. This is also evident from the record of living didelphids in other Brazilian biomes, especially in humid biomes adjacent to the Cerrado, and that are present at the fossil fauna from Gruta dos Moura cave. This is the case of *Gracilinanus microtarsus*, *Monodelphis brevicaudata* and *Didelphis aurita* (Gardner 2008). These taxa suggest a hypothesis opposite to the one inferred here. The fossil didelphids from Gruta dos

Moura cave were synchronic and inhabited an open and dry environment around the Gruta dos Moura cave. Given that those species are associated with humid forests, this would suggest that the material has a temporal mixing. Nevertheless, recent studies identified sympatry between species of dry and open environments and species of humid forests (*Gracilinanus*, *Monodelphis* e *Didelphis*) (Geise and Astúa 2009, Geise et al. 2013). Thus, these species could inhabit gallery forests and capons, or even ecotones, inside a drier and open environment. In addition, the presence of the extinct genus *Sairadelphys* might indicate that the climatic and environmental conditions changed, probably leading this taxon to its extinction.

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RESUMO

Neste estudo pretende-se reconhecer a diversidade de marsupiais fósseis da Gruta dos Moura além dos seus aspectos ambientais e climáticos durante o Quaternário. Constatou-se que esta é a maior diversidade de

marsupiais Pleistocênicos coletados em uma única caverna: *Didelphis albiventris*, *D. aurita*, *Gracilinanus agilis*, *G. microtarsus*, *Marmosa murina*, *Monodelphis brevicaudata*, *M. domestica* e *Sairadelphys tocantinensis*. Além disso, esses marsupiais também reúnem a única assembleia fossilífera que seguramente está associada ao Neopleistoceno. Estudos paleontológicos realizados sugerem uma íntima associação com ambientes secos, abertos e de alta profusão de recursos hídricos. Assim, como a maioria dos táxons identificados são característicos de florestas abertas e matas de galerias, essa poderia ser de fato a paisagem do entorno da Gruta dos Moura. Estudos recentes identificaram simpatria entre espécies de ambientes secos/abertos e de florestas úmidas dos táxons aqui identificados e característicos de regiões úmidas. Assim, essas espécies poderiam habitar matas de galeria e capões, ou até ecótonos, em um ambiente mais seco e aberto. Além disso, a extinção de *Sairadelphys* pode ser outro indício de que as condições climático-ambientais mudaram ou que o ambiente pretérito era mais heterogêneo que o encontrado atualmente na região.

Palavras-chave: mamíferos, Didelphidae, Marsupiais, norte do Brasil, Quaternário, Pleistoceno Superior.

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