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Late Pleistocene echimyid rodents (Rodentia, Hystricognathi) from northern Brazil

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ABSTRACT

Echimyidae (spiny rats, tree rats and the coypu) is the most diverse family of extant South American hystricognath rodents (caviomorphs). Today, they live in tropical forests (Amazonian, coastal and Andean forests), occasionally in more open xeric habitats in the Cerrado and Caatinga of northern South America, and open areas across the southern portion of the continent (*Myocastor*). The Quaternary fossil record of this family remains poorly studied. Here, we describe the fossil echimyids found in karst deposits from southern Tocantins, northern Brazil. The analyzed specimens are assigned to *Thrichomys* sp., *Makalata* cf. *didelphoides* and *Proechimys* sp. This is the first time that a fossil of *Makalata* is reported. The Pleistocene record of echimyids from this area is represented by fragmentary remains, which hinders their determination at specific levels. The data reported here contributes to the understanding of the ancient diversity of rodents of this region, evidenced until now in other groups, such as the artiodactyls, cingulates, carnivores, marsupials, and squamate reptiles.

Key words: Caviomorphs, Echimyidae, fossil record, Quaternary, South America.

INTRODUCTION

The living members of Hystricognathi (Rodentia: Hystricomorpha) include three lineages: the African phiomorphs, represented by four extant families (the three classical families plus Heterocephalidae; Patterson and Upham 2014), the Old World porcupines (Hystricidae) and the New World caviomorphs distributed in 13 families (Huchon and Douzery 2001, Woods and Kilpatrick 2005, Upham and Patterson 2012, Patton 2015a). The Echimyidae (spiny rats, tree rats and the coypu) is the most diverse family of caviomorphs (Emmons 2005, Patton 2015a). These rodents have a small body size (with an exception for *Myocastor* Kerr, 1792) and brachydont or protohypsodont cheek

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teeth (*sensu* Mones 1968). The taxonomic history of the echimyids has been complex, even at the subfamily and genus levels (Patterson and Pascual 1968, Patterson and Wood 1982, Galewski et al. 2005, Emmons 2005, Fabre et al. 2014, Emmons et al. 2015a, Patton 2015a). Recent molecular and morphological phylogenies reveal traditional subfamilies to be non-monophyletic (Leite and Patton 2002, Carvalho and Salles 2004, Galewski et al. 2005, Upham and Patterson 2012, Fabre et al. 2012, Verzi et al. 2014, 2016, Olivares and Verzi 2015).

Echimyids have an extended fossil record, but some controversies remain about the age of the family. Molecular studies date their origin back to the early Miocene (Upham and Patterson 2012, Fabre et al. 2012, Voloch et al. 2013) while the fossil record could be even older (e.g. late Eocene, Frailey and Campbell 2004; late Oligocene, Verzi et al. 2014). It is also worth noting that Paleogene echimyids require cladistic analyses to assess their relationships with modern forms (Carvalho and Salles 2004, Verzi et al. 2014, 2016).

The modern distribution of echimyids includes predominantly tropical forests (i.e. Amazonian, coastal and Andean forests) and occasionally more open and xeric habitats in the Cerrado and Caatinga in northern South America (Hershkovitz 1958, Vucetich and Verzi 1999, Galewski et al. 2005, Upham and Patterson 2012, Olivares and Verzi 2015). *Myocastor* is the only extant echimyid distributed in southern South America (Woods et al. 1992, Patton 2015b). Additionally, part of the history of the family (late Miocene to Pleistocene) took place in open habitats of southern South America (Olivares and Verzi 2015). The youngest fossil echimyids are mostly from the Pleistocene to Holocene of Brazil (Table I; Winge 1887, Ameghino 1907, Paula Couto 1950, Souza-Cunha and Guimarães 1978, Guerin et al. 1993, Emmons and Vucetich 1998, Salles et al. 1999, 2006, Toledo et al. 1999, Rodrigues and Ferigolo 2004, Chahud 2005, Hadler et al. 2008, Roth et al. 2008, Castro and Langer 2011, Ferreira et al. 2012, Oliveira et al. 2013, Kerber et al. 2014, 2016), Bolivia (Marshall and Sempere 1991), and Argentina (Vucetich et al. 1997, Olivares and Verzi 2015). Although this fossil record is impoverished, a sample of the astonishing diversity achieved by this group in the tropical and subtropical areas of lower latitudes of South America (Verzi et al. 2014) provides important data for diversity analyses and paleogeographic and paleoclimatic inferences. We present here the first data on the late Pleistocene diversity of echimyids from the Gruta dos Moura limestone cave in Aurora de Tocantins, low latitudes of South America.

MATERIALS AND METHODS

Locality and Geology

The studied material was collected from a carbonate deposit, which was found in a block at the wall of the main room of the Gruta dos Moura limestone cave in Aurora de Tocantins (12º42’47” S and 46º24’28” W), State of Tocantins, northern Brazil (Figure 1). The carbonate rocks from Aurora do Tocantins are part of the Speleological Province of the Bambuí Group, where numerous caves are located (Zampaulo and Ferreira 2009). The geology of this area is 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 Serviço Geológico do Brasil on the geology of the municipality of Aurora de Tocantins report carbonate and terrigenous deposits (CPRM 2006). The lower portion of area is represented by the Sete Lagoas Formation, which is composed of thick deposits of mudstones, calcareous and dolomites presenting stromatolites. The Sete Lagoas Formation is covered by siltstone and laminate siltstones of the Serra de Santa Helena Formation. This carbonate-terrige-

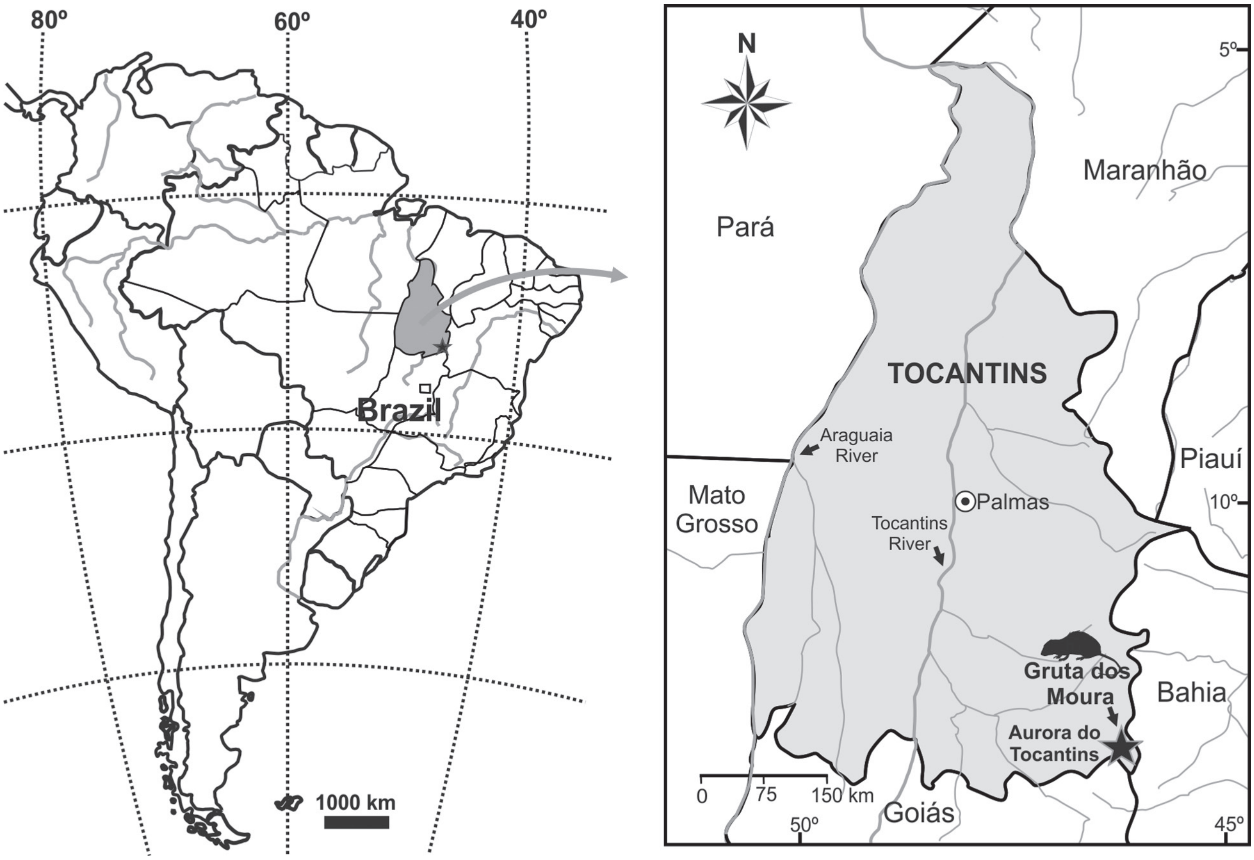

Figure 1 - Location of Aurora de Tocantins, which contains the Gruta dos Moura limestone cave.

nous 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 Urucuia Formation. The caves were developed mainly in the limestones of Lagoa do Jacaré Formation, which consist in 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 (Avilla et al. 2013a). Millimeter- 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 Urucuia sandstones that 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 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 coraloids, showing high 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 that is 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 reduced water flow, causing the precipitation of carbonates and concentrating sediment (Avilla et al. 2013a).

The occurrence of sedimentary deposits covered by carbonate incrustation lenses is also observed in many other caves in the region of Aurora do Tocantins. These sediments may correspond to a large-scale event of increased humidity that caused 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 (i.e. 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 Echimyidae were collected from a block of calcareous rock that was screen-washed by four sieves with meshes of 10 mm, 5 mm, 2.5 mm and 1 mm. Fossil materials and small pieces of rocks kept on the sieves were dried and sorted in the laboratory with the help of a stereomicroscope.

The identification and diagnosis of the specimens from Gruta dos Moura cave were made by direct morphological comparison of molars and dentaries of Echimyidae specimens housed at the Setor de Mastozoologia of the Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MN/UFRJ); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (MACN); Museo de La Plata, La Plata, Argentina (MLP); Museo de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia', Mar del Plata, Argentina (MMP); Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA (MVZ); Museu de Zoologia, Universidade Federal de Bahia, Bahia, Brazil (UFBA); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP); Universidade de Brasília, Brasília, Brazil (UnB) (Appendix); and also by comparisons with descriptions in the literature (Emmons 2005). Dental nomenclature follows Marivaux et al. (2004) and homologies of crests are based on Verzi et al. (2014), Olivares and Verzi (2015).

Abbreviations: MDL, mesiodistal lenght; LLW, Linguolabial width; UNIRIO-PM, Coleção de Paleontologia de Mamíferos da Universidade Federal do Estado do Rio de Janeiro, Brazil.

RESULTS

SYSTEMATIC PALEONTOLOGY

Rodentia Bowdich, 1821
Hystricomorpha Brandt, 1855
Hystricognathi Tullberg, 1899

Octodontoidea Simpson, 1945
Echimyidae Gray, 1825
Thrichomys Trouessart, 1880
***Thrichomys* sp.**

Material: UNIRIO-PM 2753, right dentary with dp4-m2; UNIRIO-PM 2754, left M1 or M2; UNIRIO-PM 2755, left dp4; UNIRIO-PM 2756, left dp4; UNIRIO-PM 4795, right DP4; UNIRIO-PM 4796, left dp4; UNIRIO-PM 4797, left dp4; UNIRIO-PM 4798, left M1 or M2; UNIRIO-PM 4799, left M1 or M2; UNIRIO-PM 4800, left M1 or M2; UNIRIO-PM 4801, left M1 or M2; UNIRIO-PM 4802, left M1 or M2; UNIRIO-PM 4803, left M1 or M2; UNIRIO-PM 4804, left M1 or M2; UNIRIO-PM 4805, right M1 or M2; UNIRIO-PM 4806, right M1 or M2; UNIRIO-PM 4807, right M3; UNIRIO-PM 4808, right m1 or m2; UNIRIO-PM 4809, left m1 or m2; UNIRIO-PM 4810, left m3.

Description: This taxon is the most abundant in our sample. *Thrichomys* sp. is represented by 19 upper and lower teeth with distinct wear stages and a dentary with dp4-m2 corresponding to a juvenile specimen (m2 unworn and unerupted m3).

The upper cheek teeth show distinct wear stages. Right DP4 (UNIRIO-PM 4795: Figure 2 c) shows little wear (juvenile specimen *sensu* Neves and Pessôa 2011) and it is trilophodont, but the union between of the last loph and the hypocone is wide, evidencing the coalescence of the mesolophule with the posteroloph + metaloph. The enamel layer of the anterior face of this loph is oblique and antero-posteriorly wide as in *Thrichomys pachyurus* (Wagner, 1845) (see Neves and Pessôa 2011: fig. 2A, B). There is no evidence of a fossette in the last loph, distinguish it from *Thrichomys inermis* Pictet, 1841, in which the mesolophule appears as

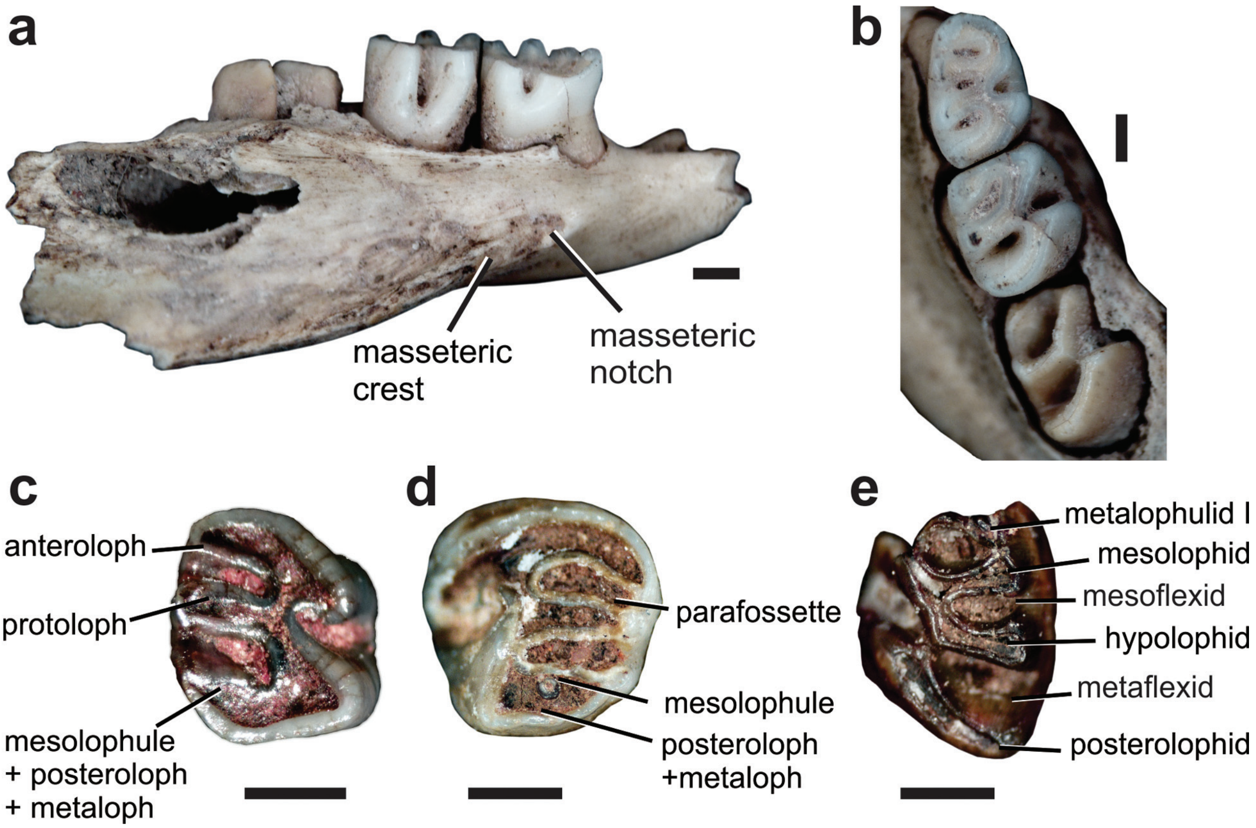

Figure 2 - *Thrichomys* sp. from the late Pleistocene of Tocantins. **a-b**, Right dentary with the dp4-m2 series (UNIRIO-PM 2753) in lateral (**a**) and occlusal views (**b**). **c**, Right DP4 (UNIRIO-PM 4795) in occlusal view. **d**, Left M1 or M2 (UNIRIO-PM 2754) in occlusal view. **e**, Left dp4 (UNIRIO-PM 2756) in occlusal view. Scale bar: 1 mm. (See the colors in the online version).

an independent crest in juvenile specimens (Neves and Pessôa 2011: fig. 3A-C).

The M1 or M2 correspond to sub-adults and adults with distinct wear stages. The sub-adult specimens (*sensu* Neves and Pessôa 2011) resemble *T. pachyurus*, *Thrichomys laurentius* Thomas, 1904 and *Thrichomys* sp. from Tocantins (Rocha et al. 2011: fig. 19), in which the protoloph is uniformly wide, and differ from the other species where the labial portion of this loph is wider than the medial portion (M1-M2 of *T. pachyurus* in Neves and Pessôa [2011: fig. 2F] compared to Figure 2d). In these molars, all lophs are of similar length compared to *T. laurentius*, *Thrichomys apereoides* (Lund, 1839) and *Thrichomys* sp. (Rocha et al. 2011: fig. 19) but not in *T. pachyurus* and *T. inermis* in which the protoloph is slightly longer (Neves and Pessôa 2011). The tetralophodont molars of the sample could correspond to the M2 because they are longer than wide. These preserve the metafossette in advanced wear stages (molars with para- and mesofossette), such as in the *T. inermis* and *T. pachyurus* (Neves and Pessôa 2011: figs. 2G and 3G).

The upper molars of this sample are similar to the material recently described from the late Quaternary of Ceará and Piauí (Oliveira et al. 2013, Kerber et al. 2016). However, the anteroloph of the DP4 of Ceará (Oliveira et al. 2013: fig. 6) is more transversely oriented than in the DP4 of the sample of Tocantins. The upper molars of Ceará correspond to a juvenile (*sensu* Neves and Pessôa 2011), whereas in the sample of Tocantins there is only one DP4 and molars belong to sub-adults and adults, which difficult their comparison.

Lower cheek teeth are mostly of juvenile specimens, as seen in UNIRIO-PM 2753 (Figure 2a, b), in which the tetralophodont dp4 shows little wear and preserves the lophids and flexids or newly formed fossettids (UNIRIO-PM 2756; Figure 2e). All labial flexids of dp4 are similar in length, which is different from *T. laurentius* and the material of the Quaternary of Ceará (Oliveira et al. 2013: fig. 6B) in which the mesoflexid is shorter. The dentary is slender and the notch for the tendon of the infraorbital part of the medial masseter muscle (i.e. masseteric notch) is a semicircular step at level of dp4, incorporated into the origin of the masseteric crest as in the remaining species of the genus (Olivares and Verzi 2015). The dental measurements among species of *Thrichomys* are very similar. However, *T. pachyurus* is slightly larger than *T. inermis* and *T. apereoides* (Oliveira et al. 2013: table 4). The material described here, in some cases, is still a little bigger than *T. pachyurus*.

Measurements: See Table II.

Commentaries: *Thrichomys* has cursorial habits and lives in open areas from Caatinga, Cerrado and Pantanal (Oliveira and Bonvicino 2006). The alfa taxonomy of this genus is not well known (see Pessôa et al. 2004, Reis and Pessôa 2004, Oliveira and Bonvicino 2006). Four species are recognized: *Thrichomys apereoides* (Lund, 1839), *T. inermis* (Pictet, 1843), *T. pachyurus* (Wagner, 1845), and *T. laurentius* Thomas, 1904 (Pessôa et al. 2015). In a recent study, the morphological distinctions among *T. laurentius*, *T. inermis* and *T. pachyurus* have been recognized (Neves and Pessôa 2011). D'Elía and Myers (2014) recognized the validity of *Thrichomys fosteri* Thomas, 1903 for populations from Paraguay and Mato Grosso do Sul. Rocha et al. (2011) identified a distinct species in the western region of Tocantins, different from *T. inermis* and *T. pachyurus* (see also Braggio and Bonvicino 2004). The materials recovered from the caves are more similar to *T. pachyurus*, *T. inermis* and *Thrichomys* sp., of the western region of State of Tocantins (Rocha et al. 2011) than the remaining living species of the genus. Currently, *T. pachyurus* is distributed to the east and south of the studied area, while *T.* aff. *inermis* is found to the north (Nascimento et al. 2013). Fossils of *Thrichomys* have been found in the intertropical region of Brazil (Table I), including the late Quaternary of the States of Mato Grosso do Sul (Salles et al.

TABLE I

Quaternary fossil records of Echimyidae from Brazil. Abbreviations: BA, Bahia; CE, Ceará; GO, Goiás; MG, Minas Gerais; MS, Mato Grosso do Sul; PA, Pará; PE, Pernambuco; PI, Piauí; RS, Rio Grande do Sul; SP, São Paulo; TO, Tocantins; †, extinct taxon.

Taxa	Provenance	Age	Reference
Carterodon sulcidens (Lund, 1841)	G.A. da Lapa Vermelha Emperaire (P.L), MG	Holocene	Souza-Cunha and Guimarães (1978)
Carterodon sulcidens (Lund, 1841)	Serra da Bodoquena/MS	Quaternary	Salles et al. (2006)
Carterodon sulcidens (Lund, 1841)	Serra da Mesa/GO	Quaternary	Salles et al. (1999)
Carterodon sulcidens (Lund, 1841)	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
Proechimys J. A. Allen, 1899	Serra da Mesa/GO	Quaternary	Salles et al. (1999)
Proechimys J. A. Allen, 1899	Serra dos Carajás/PA	Holocene	Toledo et al. (1999)
Proechimys J. A. Allen, 1899	Gruta dos Moura/TO	Late Pleistocene	This work
Echimys Cuvier, 1809	Serra dos Carajás/PA	Holocene	Toledo et al. (1999)
Makalata cf. *didelphoides* (Desmarest, 1817)	Gruta dos Moura/TO	Late Pleistocene	This work
Dactylomys dactilynus (Desmarest, 1817)	Serra dos Carajás/PA	Holocene	Toledo et al. (1999)
Kannabateomys amblyonyx (Wagner, 1845)	Grutas de Iporanga, Iporanga/SP	Quaternary	Ameghino (1907)
Kannabateomys amblyonyx (Wagner, 1845)	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
Kannabateomys Jentink, 1891	Abismo Ponta de Flecha/SP	Quaternary	Chahud (2005)
Kannabateomys Jentink, 1891	Abismo Ponta de Flecha/SP	Quaternary	Castro and Langer (2011)
Phyllomys brasiliensis (Lund, 1840)	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
Phyllomys Lund, 1839	G.A. da Lapa Vermelha Emperaire (P.L)	Holocene	Souza-Cunha and Guimarães (1978)
Phyllomys Lund, 1839	Sítios Sangão and Garivaldino/RS	Holocene	Hadler et al. (2008)
Phyllomys Lund, 1839	Sítio Deobaldino Marques/RS	Holocene	Roth et al. (2008)
Phyllomys Lund, 1839	Abismo Ponta de Flecha/SP	Quaternary	Castro and Langer (2011)
Phyllomys Lund, 1839	Sítio Alcobaça, Buíque/PE	Holocene	Ferreira et al. (2012)
Phyllomys Lund, 1839	Serra da Capivara/PI	Late Pleistocene/Holocene	Kerber et al. (2016)
Trinomys setosus (Desmarest, 1821)	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
Trinomys Thomas, 1921	Abismo Ponta de Flecha/SP	Quaternary	Castro and Langer (2011)
†*Euryzygomatomys mordax* (Winge, 1887)	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
†*Euryzygomatomys mordax* (Winge, 1887)	Sítio Garivaldino/RS	Holocene	Hadler et al. (2008)
Euryzygomatomys spinosus (G. Fisher, 1814)	Grutas de Iporanga, Iporanga/SP	Quaternary	Ameghino (1907)
Euryzygomatomys Goeldi, 1901	Sítio Deobaldino Marques/RS	Holocene	Roth et al. (2008)
Clyomys laticeps (Thomas, 1909)	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
†*Clyomys riograndensis* Hadler et al. 2008	Sítio Garivaldino/RS	Holocene	Hadler et al. (2008)

TABLE I (continuation)

Taxa	Provenance	Age	Reference
Clyomys Thomas, 1916	Serra da Bodoquena/MS	Quaternary	Salles et al. (2006)
Thrichomys apereoides (Lund, 1839)	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
Thrichomys apereoides (Lund, 1839)	Serra da Mesa/GO	Quaternary	Salles et al. (1999)
Thrichomys apereoides (Lund, 1839)	Serra da Bodoquena/MS	Quaternary	Salles et al. (2006)
Thrichomys apereoides (Lund, 1839)	Serra da Capivara/PI	Late Pleistocene/Holocene	Guerin et al. (1993)
Thrichomys Trouessart, 1880	Sítio Alcobaça, Buíque/PE	Holocene	Ferreira et al. (2012)
Thrichomys Trouessart, 1880	G.A. Lapa Vermelha Emperaire (P.L)/MG	Holocene	Souza-Cunha and Guimarães (1978)
Thrichomys Trouessart, 1880	Parque Nacional de Ubajara, Ubajara/CE	Holocene	Oliveira et al. (2013)
Thrichomys Trouessart, 1880	Serra da Capivara/PI	Late Pleistocene/Holocene	Kerber et al. (2016)
Thrichomys Trouessart, 1880	Gruta dos Moura/TO	Late Pleistocene	This work
†*Dicolpomys fossor* Winge, 1887	Grutas de Lagoa Santa/MG	Quaternary	Paula Couto (1950)
†*Dicolpomys fossor* Winge, 1887	Sítios Sangão and Garivaldino/RS	Holocene	Hadler et al. (2008)
†*Dicolpomys fossor* Winge, 1887	Grutas de Iporanga /SP	Quaternary	Ameghino (1907)
†*Dicolpomys* aff. *fossor* Winge, 1887	Sítio Deobaldino Marques/RS	Holocene	Roth et al. (2008)
Callistomys Emmons and Vucetich, 1998	Lapa do Capão Seco, Lagoa Santa/MG	Quaternary	Emmons and Vucetich (1998)
Myocastor coypus (Molina, 1782)	Cavernas de Lagoa Santa/MG	Quaternary	Winge (1887); Kerber et al. (2014)
Myocastor coypus (Molina, 1782)	Toca do Ossos/BA	Quaternary	Kerber et al. (2014)
Myocastor coypus (Molina, 1782)	Plataforma continental, B. Hermenegildo/RS	Pleistocene	Rodrigues and Ferigolo (2004)
Myocastor coypus (Molina, 1782)	Sítio Sangão/RS	Holocene	Hadler et al. (2008)
Myocastor coypus (Molina, 1782)	Arroio Touro Passo /RS	Late Pleistocene	Kerber et al. (2014)
Myocastor coypus (Molina, 1782)	Sanga da Cruz /RS	Late Pleistocene	Kerber et al. (2014)
Myocastor coypus (Molina, 1782)	Arroio Chuí /RS	Late Pleistocene	Kerber et al. (2014)
cf. *Myocastor* Kerr, 1792	Serra da Capivara/PI	Late Pleistocene/Holocene	Kerber et al. (2016)
Eumysopinae indet.	Plataforma continental, B. Hermenegildo/RS	Pleistocene	Rodrigues and Ferigolo (2004)

2006), Goiás (Salles et al. 1999), Minas Gerais (Paula Couto 1950, Souza-Cunha and Guimarães 1978), Piauí (Kerber et al. 2016), Ceará (Oliveira et al. 2013) and Pernambuco (Ferreira et al. 2012).

Proechimys Allen, 1899

***Proechimys* sp.**

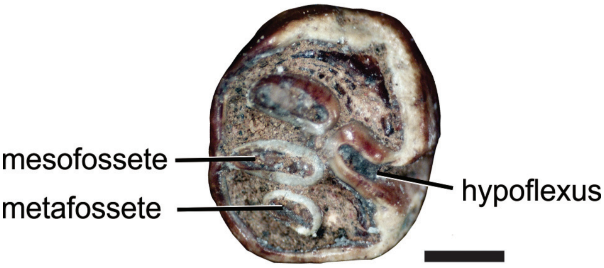

Figure 3 - *Proechimys* sp. from the late Pleistocene of Tocantins. Right M1 or M2 (UNIRIO-PM 2757) in occlusal view. Scale bar: 1 mm. (See the colors in the online version).

Material: UNIRIO-PM 2757, right M1 or M2.

Description: The specimen is a right M1 or M2 with advanced stage of wear. All labial flexi are closed to form fossettes, and the hypoflexus is still open. The presence of three fossettes equally penetrating in the occlusal surface differentiate UNIRIO-PM 2757 from *Trinomys* Thomas, 1921, *Mesomys* Wagner, 1845 and *Isothrix* Wagner, 1845, in which the mesoflexus (and the corresponding mesofossette) is less penetrating than the remaining flexi (fossettes). UNIRIO-PM 2757 shows a well-developed metafossette (Figure 3); this feature differentiates it from *Thrichomys*, which in a similar wear stage has the metafossette more reduced or absent. Among the variation in lophs pattern showed by *Proechimys*, an occlusal design of M1-2 with four lophs as that in UNIRIO-PM 2757, is the most frequent (Patton 1987).

Measurements: See Table II.

Commentaries: *Proechimys* is the most speciose living echimyid with more than twenty species recognized across a wide geographic range (Patton 1987, Patton and Leite 2015). This genus occupies diverse environments in Amazonian forest and Cerrado. In the living fauna of Tocantins, *P. roberti* is recorded (Weksler and Bonvicino 2010, Rocha et al. 2011). Although the material described herein is similar to this species (see Rocha et al. 2011: fig. 17), the information of a single molar is limited to differentiate it from the other species.

The fossil record of *Proechimys* includes materials assigned to *Proechimys* sp. from the Plio-Pleistocene of Venezuela (Rincón et al. 2009), Holocene of Pará (Toledo et al. 1999) and Quaternary of Goiás (Salles et al. 1999) (Table I). The assignment of "*Eumysops*" *ponderosus*, from the Late Miocene of Argentina, to *Proechimys* (see Bond 1977) is contingent on a revision (Reig 1989).

TABLE II

Measurements (in mm) of the late Pleistocene equimyids from Tocantins. MDL, mesiodistal length; LLW, labiolabial width.

Taxon/specimen	MDL	LLW
***Thrichomys* sp.**		
UNIRIO-PM 4795 - DP4	1.81	2.18
UNIRIO-PM 2754 - M1 or M2	3.36	2.30
UNIRIO-PM 4798 - M1 or M2	2.31	2.03
UNIRIO-PM 4799 - M1 or M2	2.65	2.35
UNIRIO-PM 4800 - M1 or M2	2.23	2.02
UNIRIO-PM 4801 - M1 or M2	2.73	2.00
UNIRIO-PM 4802 - M1 or M2	2.05	1.94
UNIRIO-PM 4803 - M1 or M2	1.75	1.70
UNIRIO-PM 4804 - M1 or M2	2.38	1.66
UNIRIO-PM 4805 - M1 or M2	2.16	1.80
UNIRIO-PM 4806 - M1 or M2	2.22	2.22
UNIRIO-PM 4807 - M3	2.07	2.40
UNIRIO-PM 2755 - dp4	2.84	1.58
UNIRIO-PM 2756 - dp4	2.50	1.83
UNIRIO-PM 4796 - dp4	1.45	2.25
UNIRIO-PM 4797 - dp4	1.40	1.78
UNIRIO-PM 4808 - m1 or m2	2.25	2.49
UNIRIO-PM 4809 - m1 or m2	2.23	2.27
UNIRIO-PM 4810 - m3	1.55	1.84
UNIRIO-PM 2753 - dp-m2 series	8.11	2.61
***Proechimys* sp.**		
UNIRIO-PM 2757- M1 or M2	2.76	2.51
Makalata* cf. *didelphoides		
UNIRIO-PM 2751 - dp4	3.53	2.03
UNIRIO-PM 2752 - M1	3.16	2.33

Makalata Husson, 1978

Makalata* cf. *didelphoides (Desmarest, 1817)

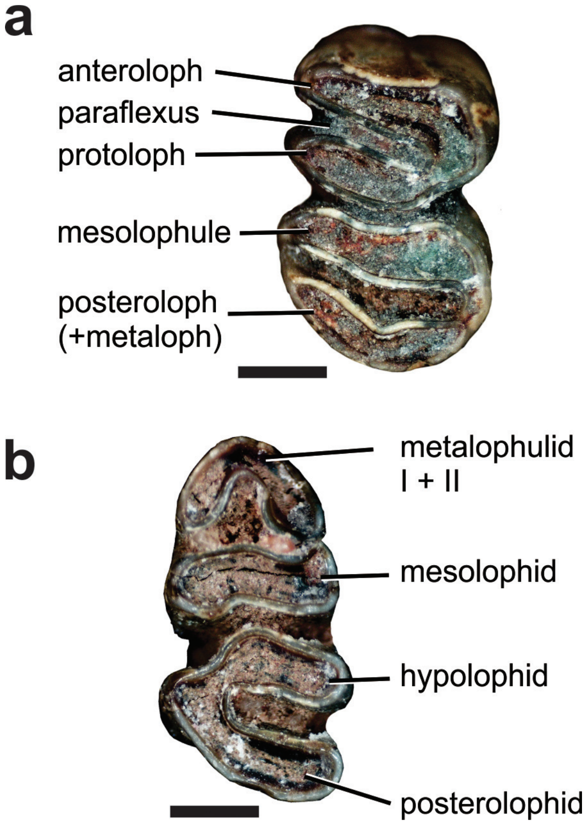

Figure 4 - *Makalata* cf. *didelphoides* from the late Pleistocene of Tocantins. **a**, Right M1 (UNIRIO-PM 2752) in occlusal view. **b**, Left dp4 (UNIRIO-PM 2751) in occlusal view. Scale bar: 1mm. (See the colors in the online version).

Material: UNIRIO-PM 2751, left dp4; UNIRIO-PM 2752, right M1.

Description: UNIRIO-PM 2752 (Figure 4a) is a right M1. The anteroloph and the protoloph are lingually connected and there is no indication of mure, as it occurs in the anterior part of M1 of *Makalata didelphoides* and *Santamartamys rufodorsalis* (J.A. Allen, 1899). As in M1 of the latter two species, these lophs (and the paraflexus) are slightly anterolabially oriented while mesolophule and posteroloph (and mesoflexus) are more transverse. The metaflexus is more penetrating than the paraflexus and is open only labially. As in *Makalata didelphoides* (e.g. MN/UFRJ 21499, IP 267), the lingual margin of protocone area is straight, and the entire area of protocone plus protoloph is shaped like a triangle, and the anterior side of posteroloph has a slight medial convexity (cf. Fig. 4a and Iack-Ximenes 2005, fig. 11D). The stage of UNIRIO-PM 2751 indicates that is not an adult individual because this pattern is similar to specimens of *Makalata* with unerupted or scarcely worn M3 (e.g. MN/UFRJ 21499, IP 267).

The specimen UNIRIO-PM 2751 (Fig. 4b) is a left dp4 with a general occlusal morphology similar to that of *Makalata*, *Echimys* Cuvier, 1809 and *Toromys* Iack-Ximenes, Vivo and Percequillo, 2005. The metalophulid I (or anterolophid) and metalophulid II (e.g. MN/UFRJ 21499, 21494) form a curved lamina (Emmons 2005) that is in contact with the mesolophid lingually. This lamina has a strong posterior fold because of the metalophulid II is interrupted leaving the anterior fossette opened backwards. The mesolophid is slightly sigmoid, different to that of *Echimys* and *Toromys*, which is straight. The presence of a shallow fold in the anterior margin of this lophid, combined with the curved morphology of the anterior lamina, is shared with specimens of *Makalata didelphoides*. The last two lophids, hypolophid and posterolophid, are labially connected. UNIRIO-PM 2751 (Table II) is similar in size to the dp4 of *Makalata* (MDL – 3.45 mm), and smaller than those of *Echimys* (MDL – 4.43 mm) and *Toromys* (MDL – 4.95 mm). Detailed complementary morphology of UNIRIO-PM 2751 and UNIRIO-PM 2752 is equivalent to that observed in the specimen *Makalata didelphoides* MZUSP 899 (Iack-Ximenes et al. 2005, fig. 11D).

Measurements: See Table II.

Commentaries: The specimens reported here have laminar cheek teeth with a morphology distinctive of Echimyinae (Emmons 2005). This group within Echimyidae, as defined by Emmons (2005), includes *Echimys*, *Phyllomys* Lund, 1839, *Makalata*, *Diplomys* Thomas, 1916, *Callistomys* Emmons and Vucetich, 1998, *Pattonomys*

Emmons, 2005, and *Santamartamys* Emmons, 2005. *Toromys* was recently included within this subfamily (Emmons et al. 2015a).

Makalata includes arboreal echimyids that are restricted to the Amazon region where they occupy areas near bodies of water (Emmons 2005, Oliveira and Bonvicino 2006). The taxonomic status of living *Makalata* species has been in state of flux. At least eight species were recognized by Woods and Kilpatrick (2005). According to Emmons (2005), living representantives are divided into two groups: "*didelphoides* group" and "*grandis* group". The IUCN redlist recognizes at least four valid species - *Makalata didelphoides, Makalata macrura* (Wagner, 1842), *Makalata rhipidura* (Thomas, 1928) and *Makalata obscura* (Wagner, 1840) - (Patton et al. 2008a, b, c, Zeballos et al. 2008). Iack-Ximenes et al. (2005) assigned one of the species of "*grandis* group" to a genus of its own, *Toromys*, i.e. *Toromys grandis. M. rhipidura* is considered *Toromys rhipidurus*, but this is pending a more thorough review (Emmons et al. 2015b). Accordingly, *Makalata* is restricted only to "*didelphoides* group" (i.e. *M. didelphoides*, *M. macrura* and *M. obscura*; Emmons and Patton 2015).

The presence of *Makalata* in Gruta dos Moura implies the first mention of this genus in the fossil record (Table I). As noted above, the occlusal morphology of the recovered teeth resembles *M. didelphoides*, the living representative of the genus currently inhabiting Tocantins (Patton et al. 2008a). This species is distributed in the islands of Trinidad and Tobago, Venezuela, French Guiana, Suriname, Guyana, southwest to northeastern of Bolivia and Brazil (States of Amazonas, Roraima, Pará, Amapá, Mato Grosso and Tocantins) (e.g. Emmons and Patton 2015).

DISCUSSION

Brazil hosts the largest diversity of living echimyids. Both in this key area and other zones within the current distribution of this family, the fossil record is scarce and its alpha taxonomy and chronology remains poorly understood. Most of Brazilian records are from Quaternary sediments of caves (Table I) and have limited temporal resolution. The fossils material derived from old collections, such as the classic fauna of Lagoa Santa, clearly need a review. In this sense, the collection of new specimens with stratigraphic control associated to numerical ages is important to understand the past diversity of the group and how such diversity was affected by Pleistocene climatic oscillations.

Based on the stratigraphic control of the material described herein, we can reliably assume that specimens from Gruta dos Moura cave represent a synchronous sample. The calcareous block where the echimyid fossil remains were found belongs to the same stratigraphic level found throughout one of the secondary tunnels of Gruta dos Moura cave. The sedimentological features, such as color and granulometry, also suggest that the calcareous blocks had the same genesis (Avilla et al. 2013a).

Disaggregation of the block revealed that there was a taphonomic selection by size, where only fragments of small vertebrates, especially mammals such as marsupials (Villa Nova et al. 2015), bats and rodents, were preserved. The only exception was a fragment of a maxillary bone with an almost complete upper tooth row of the tayassuid *Catagonus stenocephalus* (Lund in Reinhardt, 1880), an extinct mammal from the South American Pleistocene which dated by ESR (Electron Spin Resonance) to 20.000 (± 2000) years before present (YBP; Avilla et al. 2013a). In accordance, we consider here that this dating applies to the entire fossil assemblage found in the calcareous blocks of the secondary tunnel of Gruta dos Moura cave. Thus, the diversity of echimyids described here, considering that *Makalata* is recorded as a fossil also for the first time, 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 approximately

20.000 YBP, and represents the coldest and drier climatic period of South America of the last million years. The presence of *Catagonus stenocephalus* in these sediments indicates the development of relatively open and dry environments. The ancestral limits of the Chacoan subregion could be traced analyzing its fossil record and other taxa with similar ecological requirements (e.g. *Reithrodon auritus* G. Fisher, 1814 - Tobelém et al. 2013, Avilla et al. 2013a). Remarkably, the taxonomic composition of the echimyids fossil samples from Gruta dos Moura is similar, at least at generic level, to the current assemblage from the Mid-Araguaia River basin in the west of State of Tocantins (Rocha et al. 2011). The last area represents an ecotone between Cerrado and Amazonia in which the typical Cerrado's echimyid *Thrichomys* sp. coexists with the Amazonian *Makalata didelphoides* (Rocha et al. 2011). The other representative of this community, *Proechimys*, is the most widely distributed echimyid genus inhabiting lowland rainforest habitats in Central America, cis- and trans- Amazonia, dry forest in Bolivia and Paraguay, and the Cerrado of central Brazil (Patton and Leite 2015). The Gruta dos Moura cave is located in the current Cerrado, farther east than Mid-Araguaia River basin.

The fossil record of Echimyidae in Brazil during the Quaternary is represented, on the one hand, by typical Amazonian genera recorded at Serra dos Carajás in the Holocene of Pará (Toledo et al. 1999) and typical Cerrado genera registered at Serra da Bodoquena (Salles et al. 2006), and on the other hand, it is represented by both Cerrado (e.g. *Thrichomys* and *Clyomys* Thomas, 1916) (and Caatinga – *Thrichomys*) and Atlantic forest genera (*Phyllomys* and *Callistomys*) recorded together at sites such as Lagoa Santa (Winge, 1887, Emmons and Vucetich 1998), Sangão and Garivaldino (Hadler et al. 2008), Sítio Alcobaça (Ferreira et al. 2012), and Serra da Capivara (Kerber et al. 2016). The fossil echimyid assemblage studied herein includes genera from Cerrado (*Thrichomys*) and Amazonia (*Makalata*) recorded together for the first time (Table I). Similarly, some fossil didelphids of Gruta dos Moura are associated with open and deciduous forest areas and others with humid forest (Villa Nova et al. 2015). Such an interaction could result from the presence of gallery forests, which act as dispersal corridors for rainforest mammals (e.g. Redford and Fonseca 1986, Mares et al. 1989, Costa 2003), or by the presence of ecotones between these biomes (e.g. Rocha et al. 2011). Alternately, this pattern, which includes taxa with distinct environmental affinities absent at present in the region of Gruta dos Moura, could be associated with oscillations of the climatic pulses that occurred in the past during the interval recorded in this region. In any case, the presence of Amazonian species could help in understanding the dynamics of ecotones or dispersal corridors between Amazonian and Cerrado.

The data here reported contributes to the understanding of the ancient diversity of vertebrates of that region, evidenced until now in other groups, such as the artiodactyls, cingulates, carnivores, cervids, marsupials and squamates (e.g. Avilla et al. 2013a, b, Castro et al. 2013, Hsiou et al. 2013, Rodrigues et al. 2014, Villa Nova et al. 2015).

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RESUMO

Echimyidae (ratos-espinhos e ratão-do-banhado) é a família mais diversificada de roedores histricognatos da América do Sul (caviomorfos). Atualmente, equimídeos habitam florestas tropicais (Amazônia, Mata Atlântica e porções florestais andinas), ocasionalmente ambientes mais abertos e secos no Cerrado e Caatinga no norte da América do Sul e ambientes abertos no sul do continente (*Myocastor*). O registro fóssil desta família durante o Quaternário ainda é pouco estudado. Nesse trabalho, descrevemos fósseis de roedores equimídeos provenientes de sistemas cársticos do sul do estado do Tocantins, norte do Brasil. Os espécimes analisados foram atribuídos aos táxons *Thrichomys* sp., *Makalata* cf. *didelphoides* e *Proechimys* sp. Esta é a primeira vez que um fóssil de *Makalata* é reportado. O registro pleistocênico de equimídeos desta área é representado por espécimes bastante fragmentados, o que dificulta a determinação em nível específico. Os dados apresentados contribuem para a compreensão sobre a fauna pretérita de roedores desta região, já evidenciada até o momento em outros grupos, como artiodáctilos, cingulados, carnívoros, marsupiais, lagartos e serpentes.

Palavras-chave: Caviomorfos, Echimyidae, registro fóssil, Quaternário, América do Sul.

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APPENDIX - COMPARATIVE SPECIMENS

Echimys spp. MACN 31158, 31160 (*E. saturnus*); MN/UFRJ 3847, 21505, 60538.

Isothrix MN/UFRJ 56811; MVZ 190629; MZUSP 23789.

Makalata, *M. didelpoides* MN/UFRJ 6152, 10394, 21494, 21495, 21499, IP 267.

Mesomys sp. MN/UFRJ 27956; *M. hispidus* MVZ 190653.

Toromys grandis MN/UFRJ 11924, 11925, 60538.

Trinomys, *T. dimidiatus* UnB 723, 739; MN-UFRJ 62273, 62275, 62278; *T. yonenagae* UFBA 00467 – 00473.

Proechimys, *P. brevicauda* MVZ 153623; *P. cuvieri* MZUSP 21257; *P. goeldii* MZUSP 26621; *P. poliopus* MLP 22.II.00.8, 22.II.00.7; *P. roberti* MVZ 197578, UnB 316, 326; *P. semispinosus* MZUSP 2002; *Proechimys* sp. MZUSP 27551.

Thrichomys, *T. apereoides* UnB 188 – 190, *T. inermis* MMP 1242 – 1245, 1295, 1296, *T. laurentius* MMP 1246, 1293, 1294, 1297, MN/UFRJ 14511, 13664, 42505, 42411, 42395,42403, 42451, 42483, 42458, 42446, 42386, 42457, *T. pachyurus* MN/UFRJ 46896; 616599 (*T. fosteri*?), *Thrichomys* sp. MMP USB 542, MMP 1247, 1292, 150, MN/UFRJ 34406.