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ORIGINAL PAPER

Tropical Fossil Caviomorph Rodents from the Southwestern Brazilian Amazonia in the Context of the South American Faunas: Systematics, Biochronology, and Paleobiogeography

Leonardo Kerber[1] · **Francisco Ricardo Negri**[2] · **Ana Maria Ribeiro**[3] · **Norma Nasif**[4] · **Jonas Pereira Souza-Filho**[5] · **Jorge Ferigolo**[3]

Abstract The fossil-bearing stratigraphic sections of the Solimões Formation (southwestern Brazilian Amazonia) are exposed mainly along the Juruá, Purus, and Acre rivers, and in road cuts. These deposits have provided fossils of the four main lineages of Caviomorpha – Cavioidea, Erethizontoidea, Octodontoidea, and Chinchilloidea, contributing to the understanding on the evolution of tropical Neogene rodents. Herein, our knowledge about fossil rodents from this region is reviewed. New specimens are recorded, including taxa mentioned for this region for the first time, such as basal cavioids, Dolichotinae, *Caviodon* (Hydrochoeridae), and *Drytomomys* (Dinomyidae). Unfortunately, the deposits have no absolute ages, and based on palynological data and the biochronology of several taxa (mainly mammals), the encompassed fauna has been constrained to the late Miocene. However, some rodent lineages recorded here seem to be more related to older faunas, from the middle Miocene and Paleogene. Regarding the biogeographic and paleoenvironmental affinities, most of the Neogene rodents from the Acre region show more similarities to those from the Entre Rios, Argentina, and Urumaco, Venezuela, where wet environments were present during Neogene times. An increase in prospecting along southwestern Amazonian rivers looking for rodents (among other vertebrates) associated with methods to better constrain the ages of these faunal assemblages will contribute to a better understanding of the evolution of the tropical rodents as well as the stratigraphy and age of that portion of the basin.

Keywords Caviomorpha · Neogene · Amazonia · Northern South America · Tropical mammals

Introduction

Western Amazonia is one of the world's greatest biodiversity hotspots (Fig. S1). This high diversity of endemic forms is not exclusive to modern times, dating back at least to the Paleogene (Campbell 2004; Antoine et al. 2012, 2014, 2016). The evolution of the biota of this region was highly influenced by the Andean Uplift, and erosion/sedimentation derived from this process, which began in the Paleogene and reached its peak during the Neogene (Hoorn et al. 2010b). Caviomorph rodents underwent an important period of diversification during the Neogene, in particular the middle to late Miocene, with most of the modern groups having their first appearance in this interval of time (Vucetich et al. 1999, 2015). In this regard, the paleontological study of this region

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✉ Leonardo Kerber
leonardokerber@gmail.com

[1] CAPPA - Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, Rua Maximiliano Vizzotto, São João do Polêsine 598, Brazil

[2] Laboratório de Paleontologia, Campus Floresta, Universidade Federal do Acre, Estrada do Canela Fina, Km 12, Cruzeiro do Sul, AC 69.980-000, Brazil

[3] Seção de Paleontologia, Fundação Zoobotânica do Rio Grande do Sul, Museu de Ciências Naturais, Av. Salvador França, 1427, Porto Alegre, RS 90690-000, Brazil

[4] Facultad de Ciencias Naturales e Instituto Miguel Lillo, INSUGEO, Universidad Nacional de Tucumán, Miguel Lillo 205, 4000 San Miguel de Tucumán, Tucumán, Argentina

[5] Laboratório de Paleontologia, Universidade Federal do Acre, Campus Universitário BR 364, Km 04 – Distrito industrial, Rio Branco, AC 69920-900, Brazil

is fundamental for understanding the evolution of life in proto-Amazonia (Tejada-Lara et al. 2015).

Fossil rodents from northern South America have been recovered from Neogene levels (Fig. S1 C), mostly those found in the middle Miocene of La Venta, Colombia (Fields 1957; Walton 1997), Fitzcarrald Local Fauna and upper Madre de Dios, Peru (Antoine et al. 2007, 2013, 2016; Tejada-Lara et al. 2015); the late Miocene of the Urumaco Formation, Venezuela (Linares 2004; Horovitz et al. 2010) and the Solimões Formation, Brazil (see below); and the Pliocene of San Gregorio, Venezuela (Vucetich et al. 2010). In the last few years, Paleogene levels bearing several small rodents have been recognized from the Peruvian Amazonia (Frailey and Campbell 2004; Antoine et al. 2012, 2016) (Fig. S1 C).

In the Acre region (AC) of southwestern Brazilian Amazonia (see Cozzuol 2006 for definition), the study of fossil rodents began in the 1940s, when Patterson (1942) described a neoepiblemid, *Phoberomys bordasi* Patterson 1942, from the upper Purus River. Subsequently, several caviomorphs were reported from the Neogene of this region, mainly large forms, such as dinomyids and neoepiblemids (Negri et al. 2010). One of the most remarkable works on rodents from this area was an unpublished Masters dissertation by Sant'Anna-Filho (1994), who studied the caviomorphs from Juruá River collected during the famous expeditions of Simpson/Price in 1956 and Price in 1962 (Ranzi 2008). Although several taxa have been reported over the years, knowledge regarding fossil rodents from southwestern Amazonia is far from being well documented. The fauna includes primarily medium- to large-bodied forms, while the small taxa are still poorly represented. The rodents are represented mainly by isolated teeth and some postcranial elements. More complete remains are rare; nevertheless, Negri and Ferigolo (1999) described an exceptionally well-preserved skull of *Neoepiblema ambrosettianus* (Ameghino, 1889), which is the most complete Neoepiblemidae ever found. As stated by Kay and Cozzuol (2006), most results have been mentioned in brief reports, abstracts, and local scientific journals or in unpublished Masters theses and Ph.D. dissertations, many of them in the Portuguese language. Since the first mentions of vertebrates from Acre (Chandless 1866; Agassiz and Agassiz 1868), peer reviewed articles that include descriptions of fossil rodents have been published (e.g., Patterson 1942; Paula Couto 1978, 1983; Frailey 1986; Mones and Toledo 1989; Bocquentin-Villanueva et al. 1990; Bergqvist et al. 1998; Negri and Ferigolo 1999; Kerber et al. 2016). Nevertheless, they are still few considering the high diversity and abundance of this group in the western Amazonia of Brazil.

In this light, the aim of the present contribution is 1) to provide an overview about the fossil record of caviomorph rodents from the AC, southwestern Brazilian Amazonia; 2) to report new specimens collected during an expedition to the Juruá River in 2008 (Electronic Supplementary Material – ESM 1; Fig. S1) and specimens housed in the UFAC collection (ESMs 1–2); and 3) to provide discussions about morphology, systematics, biochronology, paleobiogeography, and future prospects. Material and methods, and geological setting are available in ESM 1.

Institutional Abbreviations

AMNH, paleontological collection of the American Museum of Natural History, New York, United States of America; **DMG,** paleontological collection of the Departamento Nacional de Produção Mineral (DNPM), Rio de Janeiro, Brazil; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, United States of America; **UFAC**, paleontological collection of the Universidade Federal do Acre (Campus Rio Branco), Rio Branco, Brazil. **UFAC-CS**, paleontological collection of the Universidade Federal do Acre (Campus Floresta/Cruzeiro do Sul), Cruzeiro do Sul, Brazil.

Results and Discussion

Fossil Rodents from Southwestern Brazilian Amazonia, Acre Region – an Overview

Systematic Paleontology

Mammalia Linnaeus, 1758
Euarchontoglires Murphy et al., 2001
Rodentia Bowdich, 1821
Ctenohystrica Huchon et al., 2000
Hystricognathi Tullberg, 1899
Caviomorpha Wood and Patterson (in Wood 1955)
Cavioidea Fischer de Waldheim, 1817
Cavioidea *incertae sedis* (sensu Vucetich et al. 2015)

Eoincamys Frailey and Campbell, 2004

Eoincamys sp.

cf. *Eobranisamys* Frailey and Campbell, 2004

Comments. In 2008, new remains from the upper Juruá River, State of Acre (ESM 1) assigned to the caviomorph cavioids *Eoincamys* (ESM 2; Figs. 1a, S3 A-C) and cf. *Eobranisamys* (ESM 2; Figs. 1b, S3 D) were collected. Unfortunately, these specimens have no stratigraphic context. In spite of this, the biochronologic data available for these taxa suggest that they are Paleogene forms. In this case, these specimens probably come from older levels than those bearing Neogene vertebrates from the Solimões Formation.

Dasyproctidae Smith, 1842

Dasyproctidae indet.

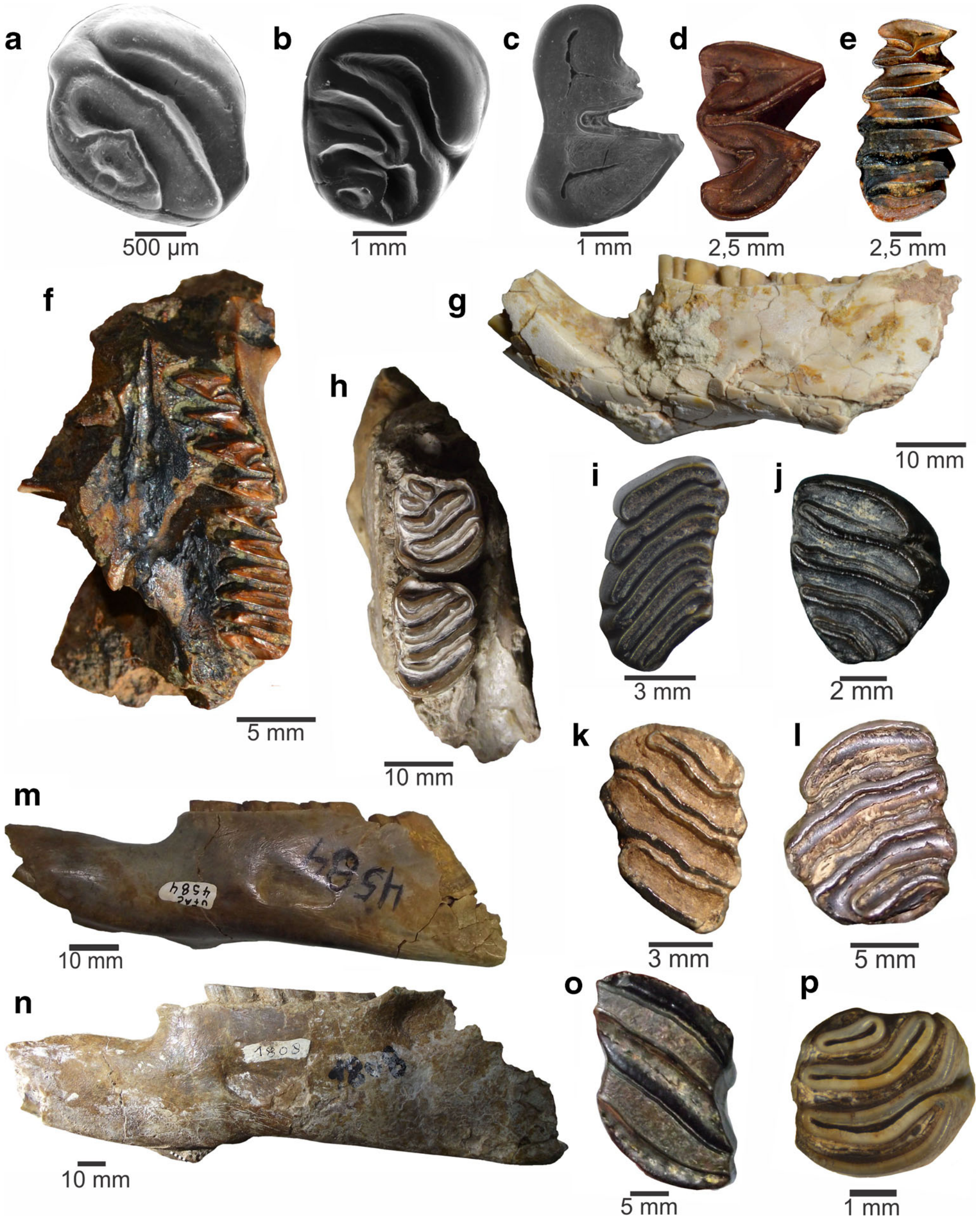

Fig. 1 Fossils of caviomorph rodents from Acre region. **a** Right upper premolar of *Eoincamys* sp. (DP4?/UFAC-CS 016) from upper Juruá River, in occlusal view; **b** Right M1 of cf. *Eobranisamys* sp. (UFAC-CS 048) from upper Juruá River, in occlusal view; **c** Left p4 (UFAC 5468) of Dolichotinae indet. from Patos locality, Acre River, in occlusal view; **d** Right M1 or M2 (UFAC 5465) of *Caviodon* from Patos locality, in occlusal view; **e**, Right M3 (UFAC 4761) of *Cardiatherium* sp. from Cachoeira do Bandeira locality, in occlusal view; **f** Palatal portion with left M2–M3 (UFAC 4681) of *Cardiatherium* sp. from Cachoeira do Bandeira locality, in occlusal view; **g** Left dentary (UFAC-CS 043) of *Potamarchus* cf. *adamiae* from Morro do Careca, in lateral view; **h** Right dentary with m2–m3 of *Drytomomys* sp. (UFAC 2742) from Talismã locality, in occlusal; **i** Left M1? (UFAC 5467) of cf. *Pseudopotamarchus villanuevai* from Patos locality, in occlusal view; **j** Right M3 (UFAC-CS 059) of Potamarchinae indet. from Belfort locality, Juruá River; **k** Left lower molar (m1 or m2) of *Tetrastylus* sp. (UFAC-CS 062) from Belfort locality, Juruá River, in occlusal view; **l** P4 (UFAC 039) of *Telicomys amazonensis* from upper Juruá River, in occlusal view; **m** Left dentary (UFAC 4584) of *Neoepiblema horridula* from Talismã locality, in lateral view; **n** left dentary (UFAC 1808) of *Neoepiblema ambrosettianus* from Niterói locality, in lateral view; **o** Left lower molar (m1 or m2 – UFAC 1817) of *Phoberomys* sp. from Patos locality, in oclusal view; **p** Lower molar of "*Scleromys*" cf. *colombianus* (UFAC-CS 070) from upper Juruá River, in occlusal. Additional images are available in the Electronic Supplementary Material (ESM)

Comments. The fossil record of dasyproctids (or related forms) is scarce in southwestern Amazonia. Frailey (1986) reported isolated teeth of Dasyproctidae indet., from the Acre VI locality (= Patos locality; Cozzuol 2006), Acre River. Sant'Anna-Filho (1994) also reported isolated teeth of Dasyproctidae indet. from the Juruá River. According to

Campbell et al. (2006), the material reported by Frailey (1986) is most likely "*Neoreomys*" *huilensis* Fields, 1957, from La Venta. The specimen LACM 117577 from Acre River resembles the right m2 of a juvenile individual reported by Walton (1997: fig. 24.3 A) from Colombia. According to Vucetich and Verzi (2002), the lower molar reported by Sant'Anna-Filho (1994) could be related to *Dasyprocta* Illiger, 1811. Sant'Anna-Filho (1994) suggested that this dasyproctid material could be from one of the most ancient forms related to the modern forms. However, see the discussion below on the rodents from the upper Juruá River.

Caviidae G. Fischer, 1817
Dolichotinae Pocock, 1922

Dolichotinae indet.

Comments. In the AC, the fossil record of caviids is scarce, but here we report for the first time the occurrence of a dolichotine from sediments of the Patos locality, Acre River (ESM 2, Figs. 1c, S4).

Hydrochoerinae Gray, 1825

Caviodon Ameghino, 1885

Caviodon sp.

Comments. Frailey (1986) reported fragments of cheek teeth from the Acre River assigned to Cardiomyinae. However, according to Vucetich et al. (2010), none of the specimens assigned by Frailey (1986) are cardiomyines. Frailey's genus and species indeterminate A is a caviid, but not a cardiomyine, and the genus and species B is probably a neoepiblemid (Vucetich et al. 2010). Here, we report the first reliable record of this group from Brazil, represented by an isolated tooth of *Caviodon* from the Patos locality (ESM 2, Figs. 1d, S5 A). This taxon was also recently reported from the Pliocene of northern South America (Vucetich et al. 2010).

Cardiatherium Ameghino, 1883

Cardiatherium sp.

Comments. Neogene capybaras have been reviewed in the last few years (e.g., Vucetich et al. 2005, 2012, 2014; Deschamps et al. 2007, 2013) reducing their diversity to four species of a single genus: *Cardiatherium chasicoense* (Pascual and Bondesio, 1968), *Cardiatherium patagonicum* Vucetich et al., 2005, *Cardiatherium paranaense* (Ameghino, 1883), and *Cardiatherium orientalis* (Francis and Mones, 1965). In the AC, the first remains of hydrochoerids were described by Frailey (1986) who reported remains of *C. orientalis* (= *Kiyutherium orientalis* Francis and Mones, 1965) based on isolated cheek teeth from the Acre River. Subsequently, Sant'Anna-Filho (1994) assigned fragments of cheek teeth from the Juruá River to Hydrochoeridae indet. Deschamps et al. (2013) considered the specimens reported by Frailey (1986) and Sant'Anna-Filho (1994) as *Cardiatherium* sp. They also suggested that the specimen DGM 537 M reported by Sant'Anna-Filho (1994) resembles the teeth of *Cardiatherium talicei* (Francis and Mones, 1965) and *Cardiatherium isseli* Rovereto, 1914, both species with dubious validity (Vucetich et al. 2014).

Here, we report material of *Cardiatherium* from the Patos and Cachoeira do Bandeira localities, Acre River (ESM 2, Figs. 1e-f, S5 B-G). The specimens have an M3 with six prisms. Considering the evolutionary context in which the number of prisms increases in cavioids with time (Deschamps et al. 2007), the specimens here reported seem to show more plesiomorphic traits than *C. paranaense* and *C. orientalis* (7–8 prisms), and *C. patagonicum* (10–11 prisms), resembling *C. chasicoense* (6 prisms) as diagnosed by Deschamps et al. (2007). In this sense, these specimens have more affinities with *C. chasicoense,* the oldest species of this genus, than with other previously described species. Notwithstanding, an M3 reported by Frailey (1986) has seven prisms, plus an incipient one. This suggests possible intraspecific variation in the number of prisms on the M3 in the species from southwestern Amazonia, or the presence of more than one species in this region.

Erethizontoidea Simpson, 1945
Erethizontidae Thomas, 1897

Erethizontidae indet.

Comments. The fossil record of Erethizontidae from southwestern Amazonia is very scarce, represented only by isolated teeth. Frailey (1986) described an upper molar from the Acre River that is more related to modern forms than to other earlier erethizontids. Campbell et al. (2006) mentioned the existence of several isolated teeth of Erethizontidae, some of them assigned to a larger form, and other smaller ones with more affinities to *Microsteiromys* Walton, 1997, from the middle Miocene of Colombia than to other known taxa. Here, we examine a new specimen of a small erethizontid from the Juruá River (ESM 2, Fig. S6 A), which is not identified at generic/specific level.

Octodontoidea Simpson, 1945

Octodontoidea indet.

Comments. The new fossil of an octodontoid reported here is poorly informative, and it is regarded as Octodontoidea indet. (ESM 2, Fig. S6 B).

Echimyidae Gray, 1825

Echimyidae indet.

Comments. The diversity of the Echimyidae in the fossil record of the Brazilian Amazonia is low, being recognized only by the remains of "Heteropsomyinae" indet., from the Acre River (Frailey 1986) and "Eumysopinae" indet., from the Juruá River (Sant'Anna-Filho 1994). Nevertheless, this possibly reflects problems in the fossil collecting methodology.

Chinchilloidea Kraglievich, 1940
Dinomyidae Alston, 1876

Potamarchus Burmeister, 1885

Potamarchus murinus Burmeister, 1885

Comments. *Potamarchus murinus* was first mentioned from southwestern Amazonia by Frailey (1986), who reported specimens from the Acre River. After that, Sant'Anna-Filho (1994) reported new specimens from the upper Juruá River. More recently, Kerber et al. (2016), based on new remains, reviewed the potamarchine rodents from the Solimões Formation and reported a dentary of *P. murinus* from the Patos locality, Acre River (late Miocene; Cozzuol 2006).

Potamarchus sigmodon Ameghino, 1891

Comments. *Potamarchus sigmodon* was mentioned by Sant'Anna-Filho (1994), based on isolated cheek teeth from the upper Juruá River. This species was originally described from Entre Rios (Ameghino 1891), based on scarce material. Although problematic, Nasif et al. (2013) stated that this species seems to be valid, due to the absence of crenulations (present in *P. murinus* and *P. adamiae*), a narrow masseteric fossa and a short symphysis.

Potamarchus adamiae Kerber et al., 2016

Comments. *Potamarchus adamiae* was recently proposed by Kerber et al. (2016), based on a palate with M1–M3 from the Cantagalo locality, upper Juruá River. Herein, new specimens assigned to *Potamarchus* cf. *adamiae* are reported (ESM 2; Figs. 1h, S7 A-D). One of them is a dentary with the premolar–m3 series. It is noteworthy that the crenulation is present in the worn cheek teeth (premolar–m2) but not in the m3, which has less wear (Fig. S7 B). This observation suggests that the appearance of crenulation in potamarchines is associated with the acquisition of total tooth functionality. Variation in the presence/absence of crenulations was reported on isolated cheek teeth from southwestern Amazonia (Frailey 1986; Kerber et al. 2016). Nevertheless, here this variation is present in the same specimen, which allows suggesting an ontogenetic origin for this character (Fig. S7 B).

Pseudopotamarchus Kerber et al., 2016

Pseudopotamarchus villanuevai Kerber et al., 2016

Comments. *Pseudopotamarchus villanuevai* is a taxon recently erected by Kerber et al. (2016) based on an incomplete maxilla from the Cachoeira do Bandeira locality, Acre River, Solimões Formation. Herein, a new specimen with affinities to this taxon from the Patos locality, Acre River, is reported (ESM 2; Figs. 1f, S7 E).

Simplimus Ameghino, 1904

Simplimus sp.

Comments. *Simplimus* sp. was reported from the upper Juruá River by Sant'Anna-Filho (1994) based on isolated teeth. This taxon was originally described from the "Friasian" beds, middle Miocene of Argentina, also based on isolated teeth (see Ameghino 1904; Kraglievich 1930; Vucetich 1984).

Drytomomys Anthony, 1922

Drytomomys sp.

Comments. Specimens from the Talismã locality, Purus River are assigned to *Drytomomys* (ESM 2; Figs. 1i, S9-S10), based on their similarity to the material described from Ecuador and La Venta (Anthony 1922; Fields 1957). Nevertheless, UFAC 2742 has thinner enamel on the leading edges than the trailing edges, differing from *Drytomomys aequatorialis* Anthony, 1922, in which the thickness of the enamel on the leading and trailing edges is more homogeneous (ESM 2, S9). The differences between specimen UFAC 2742, *D. aequatorialis,* and "*Olenopsis*" spp. from La Venta, suggest the presence of a new species of *Drytomomys* from the AC. But considering that Walton (1997) remarked on the difficulty of identifying species among the La Venta specimens because of their wide variability in size, relative size of the incisors, crown height and shape, and enamel unfolding at different wear degrees (Walton 1997: fig. 24.3.I-K), we assign the dentary UFAC 2742 to the generic level only. With the unresolved taxonomic problems exposed in Walton (1997), Candela and Nasif (2006), and herein, it is clear that *Drytomomys* plus the "*Olenopsis*" specimens from Colombia need to be reviewed.

This further review will clarify this generic problem and furnish data to test our assignment of the AC material.

Eumegamyinae Kraglievich, 1926

Eumegamys Kraglievich, 1926

Eumegamys paranensis Kraglievich, 1926

Comments. *Eumegamys paranensis* was reported from the upper Juruá deposits by Sant'Anna-Filho (1994), based on isolated cheek teeth. *Eumegamys* was described originally from the Mesopotamian of Argentina (Kraglievich 1926). It is also recorded in Urumaco (Horovitz et al. 2010).

Tetrastylus Ameghino, 1886

Tetrastylus sp.

Comments. Material assigned to *Tetrastylus* sp. was previously reported by Frailey (1986), from the Acre River. Here, a euhypsodont and tetralophodont isolated left lower molar from the Juruá River is assigned to *Tetrastylus* sp. (ESM 2; Figs. 1k, S11 A) based on its lophid occlusal design and its smaller size compared to *Telicomys* Kraglievich 1926, and *Carlesia* Kraglievich 1926 (Nasif 2009) (ESM 2). The specific identity of this specimen is not possible due to the scarce morphological evidence available. Several species of *Tetrastylus* have been described from the late Miocene/Pliocene and maybe Pleistocene, but problems concerning its alpha taxonomy are being revaluated (Nasif 2009; Nasif et al. 2013).

Telicomys Kraglievich, 1926

Telicomys amazonensis Frailey, 1986

Comments. *Telicomys* includes giant dinomyids with euhypsodont molars that tend to tetralophodonty with the progress of wear and narrow flexi separating lophs (Nasif 2009). *Telicomys amazonensis* was described by Frailey (1986) based on a partial skull collected in the Acre River. This species represents the FAD of this genus because other records are restricted to the Pliocene (Montehermosan and Chapadmalalan) of Argentina (see Pascual 1967). Herein, new specimens from the upper Juruá River are assigned to this taxon (ESM 2; Figs. 1l, S11 B-C). The general morphology of these teeth resembles *T. amazonensis* described by Frailey (1986). In size, the material is more similar to *T. amazonensis* than to *Telicomys giganteus* (Ameghino 1904), which is the larger species of this genus (Frailey 1986). *Telicomys amazonensis* was considered distinct from *T. giganteus* mainly in its smaller size, having a narrower occiput, and P4 and M3 being of the same size, but larger than M1 and M2, which are of a similar size. This last characteristic (P4 larger than M1) is observed in the new specimens reported here. So far, this species appears to be endemic to the Western Amazonia.

cf. *Gyriabrus* Ameghino, 1883

Comments. cf. *Gyriabrus* was reported by Paula Couto (1983), who assigned a single isolated left p4 (AMNH 55825) from the upper Juruá River to this taxon. We agree with the assignment of Paula Couto on the basis of the illustration of the tooth (Paula Couto 1983: 120). The size and general morphology are similar to the type of *G. holmbergi* (Ameghino, 1885) (Kraglievich 1930) (type species of this genus), but the occlusal pattern presents more oblique lophids and more convex anterior margins of the lophids in comparison to the p4 of this species. *Gyriabrus* comprises eight nominated species from the Argentine Mesopotamian that need revision (Nasif et al. 2013).

Neoepiblemidae Kraglievich, 1926

Neoepiblema Ameghino, 1889

Neoepiblema horridula (Ameghino, 1886)

Neoepiblema ambrosettianus (Ameghino, 1889)

Comments. In the AC deposits, specimens assigned to *Neoepiblema* are very common. This genus was first reported by Mones and Toledo (1989), who reported mandibular remains of *Neoepiblema* (= *Euphilus*) cf. *ambrosettianus* from the Niterói locality, Acre River. In the following year, Bocquentin-Villanueva et al. (1990) described a new species for this genus from the AC – *N. acreensis.* Bocquentin-Villanueva and Negri (1993) reported the presence of *N. horridula* from the Talismã locality. Later, Negri and Ferigolo (1999) described the most complete material of this group, represented by a skull of *N. ambrosettianus* from the Niterói locality, Acre River. Negri and Ferigolo (1999) also revised the taxonomy of *Neoepiblema*, and reduced the number of species to *N. ambrosettianus* (including *N. acreensis* and the material assigned to *Euphilus* cf. *ambrosettianus* reported by Mones and Toledo 1989) and *N. horridula*.

The largest associations of fossils documenting *Neoepiblema* from the AC are from two outcrops: Talismã, Purus River and Niterói, Acre River. The material from the Talismã locality is assigned to *N. horridula*, while only *N. ambrosettianus* is reported from the Niteroi locality. Negri (2004) discussed this peculiar pattern advocating the possibility of diachronism in these deposits (see below).

These two species reported for the AC deposits were proposed based on specimens from the upper Miocene beds of Entre Rios ("Conglomerado Osífero") (Ameghino 1886, 1889; Kraglievich 1926). Recently, Carrillo and Sánchez-Villagra (2015) maintained that both species are valid taxa.

Herein, we present some preliminary data from a review in progress about these rodents (L.K., personal communication). The analysis of the material of *Neoepiblema* is in accordance with previous interpretations that the material from the AC is included in two species (*N. horridula* and *N. ambrosettianus*, although further comparative analyses with the material from other localities are required) (ESM 2; Figs. 1m-n, S 12–13) and has reinforced what was expressed by Negri (2004) about differences in the fossil content between Niterói and Talismã, especially regarding neoepiblemids. The analyzed material of *Neoepiblema* comes from four localities (ESM 2), and the most significant fossil-bearing localities are the two formerly referred (see Cozzuol 2006; Latrubesse et al. 2010). In addition to the specimens from Talismã and Niterói, the material from the Cachoeira do Bandeira locality is assigned to *N. horridula* (ESM 2) and that from Morro do Careca to *Neoepiblema* sp.

Phoberomys Kraglievich, 1926

Phoberomys sp.

Comments. As we mentioned in the introduction, *Phoberomys bordasi* was the first rodent described from the AC by Patterson (1942), who described this endemic taxon based on lower cheek teeth from the upper Purus River. According to Patterson (1942), *P. bordasi* is characterized by its smaller size and in having an m1 with a less distally concave and transversely narrower anterior lophid than in *Phoberomys burmeisteri* Kraglievich, 1926 (from the Ituzaingó Formation, Entre Rios, Argentina). Of note, the holotype of this species is almost the same size as *Neoepiblema*. In addition, Patterson (1942) mentioned in the diagnosis that the first three lophids are labially united as in *P. praecursor*. Nevertheless, in the figured holotype (Patterson 1942: fig. 1), which is a drawn reconstruction, it is not possible to assess the presence of the fourth anterior lophid, as diagnosed for *Phoberomys* by Bondesio and Bocquentin-Villanueva (1988). In this regard, the morphology of the p4, with three lophids, is more similar to *Neoepiblema*. In the linear regression analysis of Carrillo and Sánchez-Villagra (2015), *P. bordasi* is included in the variation of *N. ambrosettianus*. Hence, the taxonomic validity of *P. bordasi* is dubious and it is possible that the material referred by Patterson (1942) could be a *Neoepiblema* specimen.

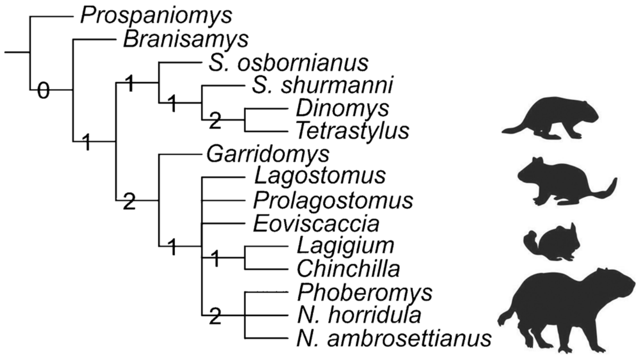

Fig. 2 Strict consensus of four most parsimonious trees (Length 83; CI: 0.55; RI: 0.68) showing the phylogenetical relationships of neoepiblemids and other chinchilloids, using the matrix of Kramarz et al. (2013). Numbers indicate the Bremer support (Bremer 1994)

Other records of *Phoberomys* are present in the works of Paula Couto (1978) and Sant'Anna-Filho (1994). Paula Couto (1978) described a fragment of a lower tooth and a femur from the Juruá River, which were assigned to *P. burmeisteri*. Sant'Anna-Filho (1994) reported isolated cheek teeth of *Phoberomys minima* Kraglievich 1940, from the Juruá River. Herein, a new specimen of *Phoberomys* sp. recovered from the Patos locality is reported (ESM 2; Figs. 1o, S14).

All the specimens from the AC assigned to *Phoberomys* have few diagnostic characters and their assignation to a species is dubious. Therefore, we prefer to use *Phoberomys* sp. to include the specimens reported by Paula Couto (1978) and Sant'Anna-Filho (1994), as well as the specimen UFAC 1817, at least until a complete revision of these specimens is performed. Besides, a recent review (Carrillo and Sánchez-Villagra 2015) proposed that *Phoberomys* is less diverse and that many alleged species might be ontogenetic stages of a single or a few taxa.

Kretzoi and Vöros (1989) described a new large rodent – *Perumys gyulavarii* – collected from the Upper Pisqui, a tributary of the Ucayali River, Peruvian Amazonia. The material was limited to the holotype (an isolated tooth), which was identified as an m2. However, the tooth mentioned by the authors (Kretzoi and Vöros 1989: pl. I) is an upper tooth, possibly a P4 because the second loph is slightly more developed lingually than the other ones, and its lingual extremity is turned distally. This unique tooth corresponds to the typical morphology of neoepiblemid upper teeth, and judging from its large size (MDL: 23.10 mm, LLW, on the mesial portion: 23.20 mm, LLW, on the distal portion: 21.40 mm), it is probably *Phoberomys*.

Phylogenetic analysis of neoepiblemids. The affinities of neoepiblemids with Chinchilloidea in a phylogenetic context are still poorly explored. Kramarz et al. (2013) presented a cladistic study of chinchilloids including *Neoepiblema*, which nested close to dinomyids. However, in the matrix there were missing data concerning the mandible of this taxon (Kramarz et al. 2013). As a preliminary test, now with more data available, we filled in some of the missing data for *Neoepiblema*, coding *N. horridula*, *N. ambrosettianus*, and *Phoberomys*. In this analysis (Fig. 2), the neoepiblemids emerged as a monophyletic group. In sharp contrast with the original results of Kramarz et al. (2013), these taxa are more closely related to the chinchillids than the dinomyids, as previously suggested by Kraglievich (1940) and Bondesio et al. (1975). A relationship between neoepiblemids and dinomyids was also suggested by the analysis of postcranial remains of *Phoberomys* from Venezuela combined with molecular data derived from living caviomorphs (Sánchez-Villagra et al. 2003; Horovitz et al. 2006). A character shared between neoepiblemids and chinchillids observed here, is the presence of a deep dorsal portion of the masseteric fossa, forming a groove below the coronoid process (character 39). Unexpectedly, Chinchillidae did not emerge as a monophyletic group in all recovered trees, a result different from that found by Kramarz et al. (2013). More characters must be included to elucidate this relation. A more comprehensive phylogenetic analysis, including other chinchilloids, is necessary to understand more precisely the relationships of the neoepiblemids as well as their relationships with the basal radiation of Chinchilloidea.

Caviomorpha *incertae sedis*
“*Scleromys*” Ameghino, 1887

“*Scleromys*” cf. *colombianus* Fields, 1957

Comments. Sant’Anna-Filho (1994) reported an m2 from the upper Juruá River, which exhibits affinities with “*Scleromys*” *colombianus*, in stage 4 of wear (Fields 1957: fig. 14). According to Sant’Anna-Filho (1994), this specimen is comparable in size to the m2 of “*Scleromys*” *schurmanni* Stehlin, 1940, but the occlusal morphology is not compatible with this taxon. One isolated tooth from the upper Juruá River here reported is assigned to “*Scleromys*” (locality PRJ 28) (Fig. 1 P, S16) with affinities to “*S.*” *colombianus*. “*Scleromys*” from northern South America possibly documents another genus distinct from *Scleromys* from the higher latitudes of that landmass (Patterson and Wood 1982; Walton 1997). Corroborating this hypothesis, the phylogenetic analysis of Kramarz et al. (2013) showed that *Scleromys osbornianus* Ameghino, 1894, and “*Scleromys*” *shurmanni* do not form a monophyletic group, but these two taxa appear to be related to dinomyids, a result also found here (Fig. 2). A review of these forms would be necessary, as well as a more comprehensive phylogenetic analysis, inasmuch as Patterson and Wood (1982) stated that “*Scleromys*” from northern South America is more closely related to dinomyids, while the southern form is related to dasyproctids. Recently, Vucetich et al. (2015) included *Scleromys* as Cavioidea *incertae sedis*. As the position of *Scleromys* from higher latitudes and “*Scleromys*” from lower latitudes is not resolved, we prefer to maintain it as a caviomorph *incertae sedis.*

What do the rodents say about the age of the AC deposits?

As stated by Cozzuol (2006), the AC exhibits one of the most diversified faunas of Neogene rodents from northern

Table 1 Updated taxonomic list of the fossil rodents recorded in the Acre region including the taxa identified in this study (ESM 2) and biochronological range of the genera recorded in AC deposits. Ranges of each taxon based in Walton (1997), Vucetich et al. (1999, 2010, 2015, 2016), Frailey and Campbell (2004), Nasif (2009), Antoine et al. (2012), and Tejada-Lara et al. (2015).*Specimens not reviewed by us. **Considering the taxon from northern South America

Mammalia Linnaeus, 1758
Euarchontoglires Murphy et al., 2001
Rodentia Bowdich, 1821
Ctenohystrica Huchon et al., 2000
Hystricognathi Tullberg, 1899
Caviomorpha Wood and Patterson (in Wood 1955)
Cavioidea Fischer de Waldheim, 1817
Caviodea *incertae sedis* (sensu Vucetich et al. 2015)
- *Eoincamys* Frailey and Campbell, 2004 [late Eocene-early Oligocene]
- *Eoincamys* sp.
- cf. *Eobranisamys* Frailey and Campbell, 2004 [middle Eocene-early Oligocene]

Caviidae G. Fisher, 1817
Dolichotinae Pocock, 1922
- Dolichotinae indet.

Hydrochoerinae Gray, 1825
- *Caviodon* Ameghino, 1885 [late Miocene-Pliocene]
- *Caviodon* sp.
- *Cardiatherium* Ameghino, 1883 [late Miocene-?Pliocene]
- *Cardiatherium* sp.

Dasyproctidae Smith, 1842
- Dasyproctidae indet.*

Erethizontoidea Simpson, 1945
Erethizontidae Thomas, 1897
- Erethizontidae indet.

Octodontoidea Simpson, 1945
- Octodontoidea indet.

Echimyidae Gray, 1825
- “Eumysopinae” indet.*
- “Heteropsomyinae” indet.*

Chinchilloidea Kraglievich, 1940
Dinomyidae Alston, 1876
Potamarchinae Kraglievich, 1926
- *Potamarchus* Burmeister, 1885 [late Miocene-Pliocene]
- *Potamarchus murinus* Burmeister, 1885
- *Potamarchus sigmodon* Ameghino, 1891*
- *Potamarchus adamiae* Kerber et al., 2016
- *Drytomomys* Anthony, 1922 [middle Miocene]
- *Drytomomys* sp.
- *Simplimus* Ameghino, 1904 [middle Miocene]
- *Simplimus* sp.*
- *Pseudopotamarchus* Kerber et al., 2016
- *Pseudopotamarchus villanuevai* Kerber et al., 2016

Eumegamyinae Kraglievich, 1926
- *Eumegamys* Kraglievich, 1926 [late Miocene]
- *Eumegamys paranensis* Kraglievich, 1926*
- *Telicomys* Kraglievich, 1926 [late Miocene-Pliocene]
- *Telicomys amazonensis* Frailey, 1986
- *Tetrastylus* Ameghino, 1886 [late Miocene-?Pleistocene]
- *Tetrastylus* sp.
- cf. *Gyriabrus* Ameghino, 1883* [late Miocene]

Neoepiblemidae Kraglievich, 1926
- *Neoepiblema* Ameghino, 1889 [late Miocene-Pliocene]
- *Neoepiblema horridula* (Ameghino, 1886)
- *Neoepiblema ambrosettianus* (Ameghino, 1889)
- *Phoberomys* Kraglievich, 1926
- *Phoberomys* sp. [late Miocene]
- “*Phoberomys bordasi*” Patterson, 1942

Table 1 (continued)

Caviomorpha *incertae sedis*
"*Scleromys*"** Ameghino, 1887 [middle Miocene]
"*Scleromys*" cf. *colombianus* Fields, 1957

South America. However, several questions are still without answer, mainly concerning the age of this fauna. The data obtained in the Brazilian Amazonia correspond to the uppermost levels of the Solimões Formation, which was deposited during the Miocene, although absolute ages have so far not been provided (Cozzuol 2006; Latrubesse et al. 2010). In this context, the land mammal assemblages (SALMA) are particularly critical and useful for proposing correlations between faunas and making inferences about their relative ages (Latrubesse et al. 2010). Needless to say, the improvement of the taxonomic resolution of the fauna of the AC is very important. As pointed out before, some fossils reported (most of them collected without stratigraphic context), mainly from the Juruá River, indicate an older age than late Miocene (Paula Couto 1976, 1982; Negri et al. 2010; Ribeiro et al. 2013). In the Peruvian Amazonia, the recent increase in absolute ages (e.g., Antoine et al. 2012, 2013, 2014, 2016) has suggested a scenario with ages from the Paleogene to the late Miocene.

As we stated before, the rodents *Eoincamys* and cf. *Eobranisamys* found in the upper Juruá River could indicate the presence of Paleogene levels (Table 1). Unfortunately, the remains here reported have no exact stratigraphic provenance. However, with the discovery of these specimens a new discussion is opened about the age of the encompassed fauna. Their occurrence shows important new indications to prospect Paleogene levels in the Brazilian territory of the westernmost portion of Amazonia. Due to the geographic proximity of the points where these specimens were found to the Santa Rosa locality (late Eocene–early Oligocene), Peru, we consider the possibility that some specimens may come from similar levels. However, except for these cases, the other records of rodents from the AC are in accordance with a Miocene age (Table 1).

Most of the material documenting rodents that was collected directly from the uppermost levels of the Solimões Formation (sensu Latrubesse et al. 2010) indicates a late Miocene age (in correlation with other faunas, e.g., Urumaco, Venezuela and Mesopotamian, Argentina). Patterson (1942) correlated the AC deposits with the Mesopotamian beds from Argentina for the first time using the rodent *Phoberomys*: "Probably late Miocene; horizon approximately equivalent in age to the Paraná of Entre Rios, Argentina…" (Patterson 1942: 1). The hydrochoerids *Cardiatherium* and *Caviodon* have their fossil record predominantly associated with late Miocene deposits (Vucetich et al. 2010; Deschamps et al. 2013). But Vucetich et al. (2010) reported remains of these taxa from the San Gregorio Formation, constrained with palynological data to the late Pliocene, although Vucetich et al. (2016) recently suggested the material previously assigned to *Cardiatherium* could be a juvenile of a more derived taxon. *Neoepiblema* is often considered indicative of a late Miocene age because it is found in the deposits of Entre Rios, the AC, and Urumaco. Notwithstanding, recently the LAD of *Neoepiblema* was constrained to the Pliocene (Vucetich et al. 2010) and its FAD to the middle Miocene (Tejada-Lara et al. 2015).

Two of the most important fossiliferous localities from the AC are Niterói (Acre River) and Talismã (Purus River). Santos et al. (1993) and Negri (2004 and references therein) discussed the ages of these deposits based on their fossil content (mainly xenarthrans), suggesting that the fauna from Talismã is possibly older than that from Niterói, possibly Laventan or Santacrucian. According to Negri (2004), the first locality records *Neoepiblema ambrosetianus*, while in the second, remains of *N. horridula* are found. This interpretation about the taxonomic differences in *Neoepiblema* specimens between the two localities is here expanded (see above). Like the xenarthrans mentioned by Negri (2004), the rodent *Drytomomys* also formerly occurred in the? middle Miocene of Ecuador (Anthony 1922) (see discussion in Patterson and Wood 1982: 447 about the age of this deposit), middle Miocene of La Venta, Colombia (Fields 1957; Candela and Nasif 2006), and in the middle Miocene of the Fitzcarrald Local Fauna (Tejada-Lara et al. 2015). Caviomorphs recorded from Juruá River are more problematic, because most of them have scarce stratigraphic information. As stated by Sant'Anna-Filho (1994), the fauna from the Juruá River, in terms of biochronology, ranges from the middle to late Miocene. In addition, some fossils found there without context are from the Quaternary (Ranzi 2008). The rodents *Simplimus*, erethizontids with an affinity to *Microsteiromys* (Campbell et al. 2006), and "*Scleromys*" are more related to the Laventan SALMA (middle Miocene). However, it is important to note that these records are problematic as they are based on very fragmentary remains and the taxa are poorly defined. Besides, with few exceptions, such as *Potamarchus adamiae*, which was collected within the sedimentary levels from the Cantagalo locality (Kerber et al. 2016) and "*Scleromys*" cf. *colombianus* (UFAC-CS 070), most of the data documenting rodents derive from material stemming from reworked concentrations, such as "cachoeiras" and "corredeiras" (Sant'Anna-Filho 1994; several specimens reported here – UFAC-CS 048, UFAC-CS 044, UFAC-CS 049, UFAC-CS 059, UFAC-CS 062) (see definitions in Simpson and Paula Couto 1981). Sant'Anna-Filho (1994) considered the possibility that some reworked fossils from Juruá came from older levels or were brought from other areas where there is exposure of other geologic formations. In addition to these rodents, other taxa such as astrapotheres and notoungulates could also indicate older ages, as discussed by Ribeiro et al. (2013). Astrapotheres have their

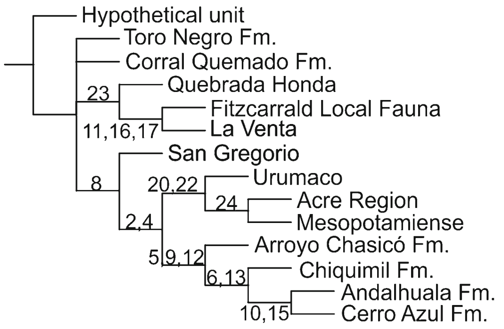

Fig. 3 Most parsimonious tree of the PAE analysis (47 steps, CI: 0.511; RI: 0.635). The numbers indicate the presence of shared taxa (see ESM 3)

youngest records associated with absolute ages in the middle Miocene (Kay et al. 1997).

Latrubesse et al. (2007, 2010) and Cozzuol (2006) considered the presence of diachronism between the localities of the AC, but still within the late Miocene. Cozzuol (2006) compared the case of the AC with the Mesopotamian assemblage that was considered previously as a mixed fauna with Chasicoan, Huayquerian, and Montehermosan ages, but that was constrained to the Huayquerian (late Miocene – 9.0–6.8 Ma) by Cione et al. (2000). Recently Tejada-Lara et al. (2015) described a mammal fauna from the Fitzcarrald Arch area, Peru, for which a middle Miocene age was proposed on biochronological grounds. As in the Neogene of the AC, that fauna from the Fitzcarrald Arch shows an apparent multitemporal character, because the biochronological information from the referred taxa shows affinities with the faunas from the early, middle, and late Miocene. The authors explained this situation as being due to tropical faunistic features, such as high diversity, stable and long-lasting environmental conditions, and long survival of lineages, which have a wide distribution. In fact, the tropics has this characteristic of conserving lineages for more time than other portions of the continent (Jablonski et al. 2006), a pattern observed in rodents. The late survival of *Cardiatherium*?, *Caviodon*, and *Neoepiblema* in the Pliocene of Venezuela was interpreted as evidence of the tropics being museums of biodiversity (Vucetich et al. 2010). Hence, two hypotheses are suggested to explain the pattern of the biochronological range of the Neogene rodent fauna(s) observed in the AC: 1, there are middle Miocene levels yielding vertebrates; or 2, the fauna is constrained to the late Miocene, as argued by Cozzuol (2006) and Latrubesse et al. (2007, 2010), and conserves some old lineages such as *Drytomomys*, in the context of tropical faunistic characteristics evidenced by several authors (e.g., Hirschfeld 1985; Jablonski et al. 2006; Vucetich et al. 2010; Tejada-Lara et al. 2015). In this latter case, the records of *Simplimus*, “*Scleromys*,” and *Drytomomys* could indicate the last occurrence of these taxa during the late Miocene. These questions remain open until new fossils with a better stratigraphic context are found, associated with other methods to better constrain the ages of these faunal assemblages.

Diversity, Environments, and Paleobiogeographic Comparisons with Other Neogene South American Faunas

A test of Parsimony Analysis of Endemicity (PAE) modified in order to include only Neogene rodents and localities from low and middle latitudes of South America (ESMs 1, 3) was employed to test the biogeographic relationships of the AC rodents. In this analysis, a single most parsimonious tree (47 steps, CI: 0.511; RI: 0.635) was recovered (Fig. 3). As previous interpretations suggested (e.g., Cozzuol 2006; Tejada-Lara et al. 2015; Carrillo et al. 2015), the AC Neogene rodent fauna shows closer taxonomic similarities with the “Conglomerado Osífero,” Ituzaingó Formation, Argentine Mesopotamia (Cozzuol 2006) and Urumaco, than with other well-known Neogene faunas. This cluster is supported by the shared presence of *Eumegamys* and *Phoberomys*. A cluster including the Mesopotamian and AC faunas is supported by the presence of *Caviodon*. In the analysis

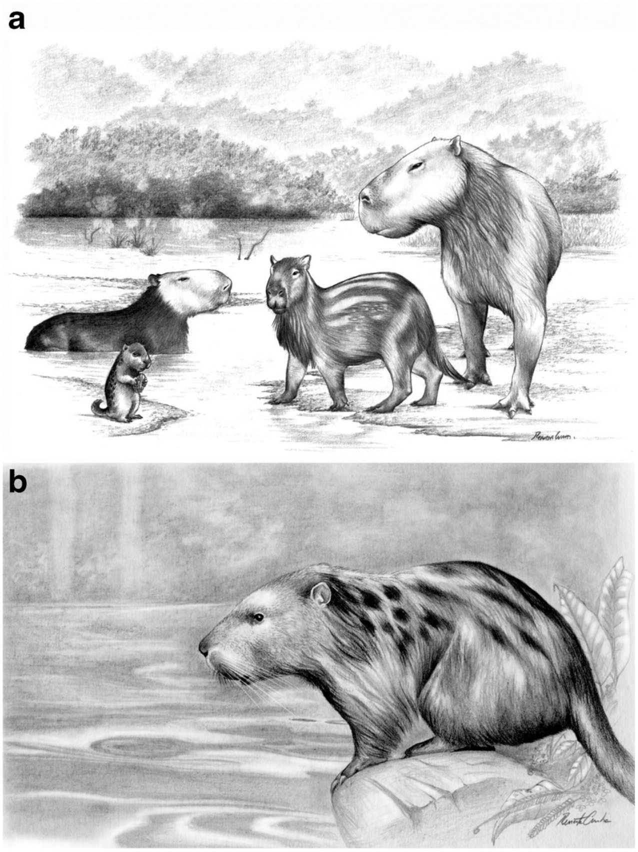

Fig. 4 Reconstruction of the hypothetical late Miocene environment from the southwestern Amazonia and caviomorph rodents. **a** *Telicomys amazonensis* (left and behind) and *Potamarchus* (left) (Dinomyidae), *Neoepiblema* and *Phoberomys* (right, respectively) (Neoepiblemidae). **b** *Potamarchus adamiae*. Drawings by Renata Cunha

of Brandoni (2013), who considered the mammalian assemblage and localities only from Argentina, the Mesopotamian fauna was close to that from the Arroyo Chasicó Formation. Here, *Potamarchus* and *Tetrastylus* (taxa with a wide geographic range) support a cluster composed of the AC, Urumaco, and the Mesopotamian fauna, plus a cluster of the Arroyo Chasicó, Chiquimil, Andalhuala, and Cerro Azul faunas, which is supported by the presence of lagostomines, *Cardiomys* Ameghino, 1885, and *Orthomyctera* Ameghino, 1889. The fauna recently described from Fitzcarrald shows a close affinity to the middle Miocene Laventan fauna by the shared presence of *Prodolichotis* Kraglievich, 1932, *Drytomomys*, and *Microsteiromys*, as supported by Tejada-Lara et al. (2015). La Venta and Fitzcarrald share with Quebrada Honda, the presence of *Acarechimys* Patterson, 1965.

From the southern faunas, the most similar one to the AC fauna is the assemblage recovered from the Argentine Mesopotamian (Cozzuol 2006). This fauna is characterized by abundant dinomyids, neoepiblemids, and other forms related to wet environments. Vucetich et al. (2010) and Nasif et al. (2013) pointed out that neoepiblemids are common in the Mesopotamian (Argentina), AC and Urumaco (Venezuela), localities that were likely under tropical and humid conditions, while they are absent in the Miocene of northwestern Argentina, where the environments were possibly much drier. The same pattern is repeated with the caviids, which are related to open and dry areas, and are scarce in the Mesopotamian and the AC, but common in the Neogene from northwestern Argentina. Differing from the AC, the Mesopotamian fauna shows some Patagonian influences, marked by the presence of Lagostominae, represented by *Lagostomus antiquus* Ameghino, 1883, and the abrocomyid *Protabrocoma* Kraglievich, 1927 (Vucetich et al. 2015), which likely inhabited open and dry environments. This similarity in the fossil content suggests a strong paleobiogeographic connection between northern South America and northwestern Argentina during the Neogene.

This pattern of predominance of tropical rodents contrasts with other Miocene faunas, for example Quebrada Honda, Bolivia (middle latitudes) (Croft et al. 2011). In this fauna, the diversity is associated with open and dry environments with lagostomines and caviids being the more abundant rodents (Croft et al. 2011). Tejada-Lara et al. (2015) suggested that it is possible that the Pebas system (see Hoorn et al. 2010a) could have worked like an isolating mechanism between the southern and northern regions of South America during the middle Miocene. With the end of this system, near the close of the middle Miocene, this mechanism ended, thereby promoting a connection between the south and north, an assumption that is evidenced by the similarity in the fossil record of the Mesopotamian, AC, and Urumaco.

In summary, we believe that the similarity of the Mesopotamian, AC, and Urumaco faunas is better explained by a strong climatic/environmental controlling factor in these areas than by only a temporal cause, because the southern faunas with similar times of deposition to the former ones have distinct faunistic elements.

Concluding Remarks

The AC fossiliferous deposits provide substantial information about the evolution of caviomorph rodents, and are particularly critical to further our understanding of Cenozoic tropical mammal evolution in South America. Here, we provided a review of this fauna for which the taxonomic identification of the specimens was improved (Table 1; ESM 1). However, the critical issue surrounding the age(s) of these finds is still unresolved. In this paper, we reported material of cf. *Eobranisamys* and *Eoincamys* that indicates the possibility of finding older levels in the AC. Concerning the Neogene levels, as stated by Cozzuol (2006), the fauna as a whole shows more similarities with the late Miocene Mesopotamian and Urumaco faunas. Some forms seem to indicate an affinity with those of the middle Miocene (e.g. *Simplimus*, *Drytomomys*). As stated by Negri (2004) and in this work, *Neoepiblema ambrosettianus* and *N. horridula* (also *Potamarchus murinus* and *P. adamiae*) are not found in the same deposits. However, whether these differences in fossil content are related to differences in age or are just an artifact of preservation is still an open question.

The paleoenvironmental interpretation proposed for the uppermost levels of the Solimões Formation by Latrubesse et al. (2007, 2010) indicates the presence of a giant wetland similar to the current environment found in the modern ecosystem of Pantanal, with rivers associated with megafan systems and lakes and marshes. The authors also suggest the presence of open environments and gallery forests. As discussed above, the presence of hydrochoerids and neoepiblemids, a low abundance and diversity of caviids, and the absence of chinchillids are in accordance with the hypothesis of the presence of wet and humid paleoenvironmental conditions (Fig. 4).

A large fraction of the knowledge about the fossil record of rodents from the AC derives from material without stratigraphic context. An increase in prospecting, mainly in the Juruá River, looking for rodents (among other vertebrates) with a stratigraphic context and the acquisition of absolute ages will contribute substantially to a better understanding of the evolution of the tropical South American rodents.

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