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Late Miocene potamarchine rodents from southwestern Amazonia, Brazil—with description of new taxa

LEONARDO KERBER, FRANCISCO RICARDO NEGRI, ANA MARIA RIBEIRO, MARIA GUIOMAR VUCETICH, and JONAS PEREIRA DE SOUZA-FILHO



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The fossil rodents from the southwestern Amazonia of Brazil have been studied since the first half of the 20th century. Several caviomorph rodents were reported for the Neogene of this region, mainly neoepiblemids and dinomyids. Until recently, the record of dinomyids in the Solimões Formation (Late Miocene) was predominantly based on a few isolated teeth, which made it difficult to make more accurate taxonomic identifications due to the scarcity of diagnostic characters. Here, new remains, more complete than those previously reported, of potamarchine dinomyids from the Neogene of Brazil are described. A new species of *Potamarchus* and a new genus and species of a Potamarchinae are erected. In addition, new material of *Potamarchus murinus* and *Potamarchus* sp. is identified. These data suggest a higher diversity of dinomyids in in the western Amazonia than previously supposed.

Key words: Mammalia, Rodentia, Caviomorpha, lower latitudes, Neogene, Solimões Formation, South America, Brazil, Acre.

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Introduction

During the Late Miocene–Pliocene, the family Dinomyidae (Rodentia: Caviomorpha), which today is monospecific, was very diversified (Kraglievich 1926; Fields 1957; Mones 1981; Candela and Nasif 2006; Rinderknecht and Blanco 2008; Nasif 2009; Rinderknecht et al. 2011; Nasif et al. 2013 and references therein), diminishing to only two taxa recorded during Quaternary times: *Tetrastylus walteri* Paula Couto, 1951 from the Quaternary of Brazil and *Dinomys branickii* Peters, 1873 (without fossil record), the only survivor of this lineage. Despite the record of *T. walteri* lacks a detailed stratigraphic context, the encompassed fauna of the caves from Lagoa Santa, Brazil is exclusively from the Quaternary (Cartelle 1994). Numerical ages (^{14}C and U/Th) are in accordance with this interpretation (see Hubbe et al. 2013). Nevertheless, a taxonomic review of this taxon is required. Dinomyids had a high diversity in size, ranging from relatively small forms up to the largest rodent *Josephoartigasia monesi* Rinderknecht and Blanco, 2008.

Unquestionable dinomyids appear in the fossil record during the Middle Miocene (Vucetich et al. 1999). Notwithstanding, molecular data suggested that the origin of this group is older, originating, at the least, during the Early Miocene, between 21 and 17 myr ago (Huchon and Douzery 2001). If we consider that *Branisamys* Hoffstetter and Lavocat, 1970 is included in Dinomyidae, as argued by some authors (Fields 1957; Patterson and Wood 1982), the stratigraphic range of the family extends from the Oligocene to the Recent. However, the cladistic analysis of Kramarz et al. (2013) does not support this interpretation. It

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is also worth noting that tracks of a possible dinomyid from the late Oligocene were recently discovered in Argentina (Krapovickas and Nasif 2011).

Molecular data suggest that dinomyids are closely related to chinchillids (Huchon and Douzery 2001), while some morphological data indicate a sister group relationship to the erethizontids (e.g., Fields 1957; Grand and Eisenberg 1982; Nasif 2010). In addition, an analysis of postcranial characters combined with molecular data by Horovitz et al. (2006) grouped *Dinomys* Peters, 1873 with the neoepiblemid *Phoberomys* Kraglievich, 1926. Mones (1981) recognized the presence of the subfamilies Potamarchinae, Gyriabrinae, Phoberomyinae (today Neoepiblemidae) and Dinomyinae, the latter including two tribes: Dinomyini and Eumegamyini. However, a phylogenetic analysis carried out by Nasif (2009) recovered only Potamarchinae and Eumegamyinae as monophyletic groups. Potamarchinae are primitive dinomyids, with protohypsodont cheek teeth (Kraglievich 1926; Mones 1981). In classic taxonomic arrangements, the taxa *Scleromys* Ameghino, 1887, *Drytomomys* Anthony, 1922, *Simplimus* Ameghino, 1904, *Eusigmomys* Ameghino, 1905, and *Potamarchus* Burmeister, 1885 were included in in this subfamily, with constant changes occurring to its composition (Table 1). In the only cladistic analysis by Nasif (2009), Potamarchinae includes *Potamarchus* plus *Paranamys* Kraglievich, 1934. The genus *Potamarchus* comprises two species: *Potamarchus murinus* Burmeister, 1885 and *Potamarchus sigmodon* Ameghino, 1891, both described on the basis of material from the Miocene of Entre Ríos Province, Argentina.

The fossil rodents from the southwestern Amazonia of Brazil have been studied since the first half of the 20th century, including several caviomorphs, mainly neoepiblemids and dinomyids (Patterson 1942; Paula Couto 1978, 1983; Bocquentin-Villanueva et al. 1990; Bocquentin-Villanueva and Negri 1993; Sant'Anna-Filho 1994, 1997; Negri and Ferigolo 1999; Kerber et al. 2012). Neogene dinomyids are almost exclusively based on isolated teeth. Paula Couto (1983) described a single tooth of cf. *Gyriabrus* Ameghino, 1891. Frailey (1986) identified isolated teeth and a dentary with m1–m3 of *Potamarchus murinus*, a p4 of *Tetrastylus* Ameghino, 1886 and a fragmented skull, which he assigned a new species of *Telicomys* Kraglievich, 1926. The material described by Sant'Anna-Filho (1994) included isolated teeth of *P. murinus* and *P. sigmodon*; isolated teeth of *Simplimus* sp.; a P4 of Gyriabrinae indet.; an M2 of *Scleromys* with a high similarity to *S. colombianus* Fields, 1957; and an M1 or M2 of *Eumegamys paranensis* Kraglievich, 1926.

In this contribution, new specimens of potamarchines collected from the Solimões Formation, State of Acre, Brazil, are reported, including material assigned to a new species of *Potamarchus* and a new genus and species.

Institutional abbreviations.—MACN-Pv/A, palaeontological collection (Colección Nacional de Paleovertebrados/ Colección Nacional Ameghino) of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; UFAC(-CS), palaeontological collection of the Universidade Federal do Acre, Campus Rio Branco, Rio Branco (Campus Floresta, Cruzeiro do Sul), Acre, Brazil.

Other abbreviations.—SALMA, South American Land Mammal Age.

Material and methods

The rodents here reported were collected along the Juruá, Purus, and Acre rivers (see below). The material is housed in the palaeovertebrate collections UFAC. Comparative specimens are listed in the Appendix 1. We explored the use of micro-CT for analysis of the specimens UFAC-CS 11 and UFAC 4762. The images were obtained at the Laboratório de Análise de Minerais e Rochas of the Universidade Federal do Paraná, Brazil using a micro-CT scanner Skyscan 1172. The Skyscan software for 3D analysis DataViewer and CTVox were employed to review 3D graphics of the specimens. The measurements were taken with a digital caliper accurate to 0.01 mm and are expressed in millimeters. Additional archives of images and videos are included in the Supplementary Online Material (SOM, available at http://app.pan.pl/SOM/app61-Kerber_etal_SOM.pdf).

Geological setting

The Acre basin is located in northwestern Brazil, neighboring Peru and Bolivia (between 60 S and 90 S, and 72 W and 74 W) and preserves a Paleozoic–Neogene stratigraphic sequence (Cunha 2007). The Solimões Formation (this formation has other names in neighboring countries—see Hsiou 2010 for a summary) located in the southwestern

Table 1. Classifications of Potamarchinae. * used in family level Potamarchidae; ** defined as a monophyletic group; *** see taxonomic history of *Drytomomys* in Candela and Nasif (2006), **** *Paranamys* was recently revalidated (Nasif 2009; Nasif et al. 2013), after this, the genus *Drytomomys* encompasses only taxa from the Neogene of northern South America.

Kraglievich (1926)*	Simpson (1945)	Fields (1957)	Mones (1981)	McKenna and Bell (1997)	Nasif (2009)**
Simplimus	*Simplimus*	*Scleromys*	*Simplimus*	*Scleromys*	*Paranamys*****
Potamarchus	*Potamarchus*	*Drytomomys****	*Potamarchus*	*Drytomomys****	*Potamarchus*
		Simplimus		*Simplimus*	
		Potamarchus		*Eusigmomys*	
				Potamarchus	

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Brazilian Amazonian region (states of Acre and Amazonas; Fig. 1) encompasses the Neogene section of this basin. The outcrops of this formation are exposed mainly along the Juruá, Acre, and Purus rivers, and road cuts. Latrubesse et al. (2007, 2010) recognized two main facies: a channel-dominated assemblage and a floodplain-lacustrine low energy assemblage. Tetrapods found in these beds are characterized by a high diversity of crocodiles and turtles (Riff et al. 2010; Souza-Filho et al. 2014). Among the mammals, the more common fossils are notoungulates, xenarthrans, and rodents (see Negri et al. 2010). The age of the encompassed fauna is assigned to the Huayquerian (including the "Mesopotamian") SALMA, Late Miocene (Cozzuol 2006; Latrubesse et al. 2010), although there is a discussion about the age of fossils collected near Peru, because some taxa suggest older ages (e.g., Laventan or Chasicoan; see Negri et al. 2010; Ribeiro et al. 2013 and references therein). Latrubesse et al. (2010) suggested a sedimentary environment characterized by rivers associated with megafan systems, and lakes, and marshes. The environment was predominantly composed of grasslands and gallery forests. More information about the geology and palaeontology of Amazonia can be found in Campbell et al. (2006), Latrubesse et al. (2007, 2010), Hoorn et al. (2010), Hoorn and Wesselingh (2010), and references therein (among several others).



Fig. 1. Location of the studied area (**A**) and fossiliferous localities in southwestern Amazonia, Brazil (**B**). Localities: 1, Cantagalo; 2, Talismã; 3, Lula; 4, Patos; 5, Cachoeira do Bandeira.

Systematic palaeontology

Mammalia Linnaeus, 1758

Euarchontoglires Murphy, Eizirik, O'Brien, Madsen, Scally, Douady, Teeling, Ryder, Stanhope, de Jong, and Springer, 2001

Rodentia Bowdich, 1821

Ctenohystrica Huchon, Catzeflis, and Douzery, 2000

Hystricognathi Tullberg, 1899

Caviomorpha Wood and Patterson in Wood, 1955

Dinomyidae Alston, 1876

Potamarchinae Kraglievich, 1926

Genus *Potamarchus* Burmeister, 1885

Type species: *Potamarchus murinus* Burmeister, 1885; Conglomerado Osífero (Entre Ríos Province, Argentina), Late Miocene.

Potamarchus adamiae sp. nov.

Figs. 2, 3; SOM 1: fig. S1.

Etymology: In honor of the palaeontologist Karen Adami Rodrigues, who conducted the expeditions to the Juruá River when the holotype was collected.

Type material: Holotype: palate with M1–M3 (UFAC-CS 11).

Type locality: PRJ 19 (09º05'56.0" S and 72º41'50.0" W), Locality 21 (Cantagalo) of Simpson and Paula Couto (1981), Juruá River, State of Acre, Brazil (SOM 1: fig. S2).

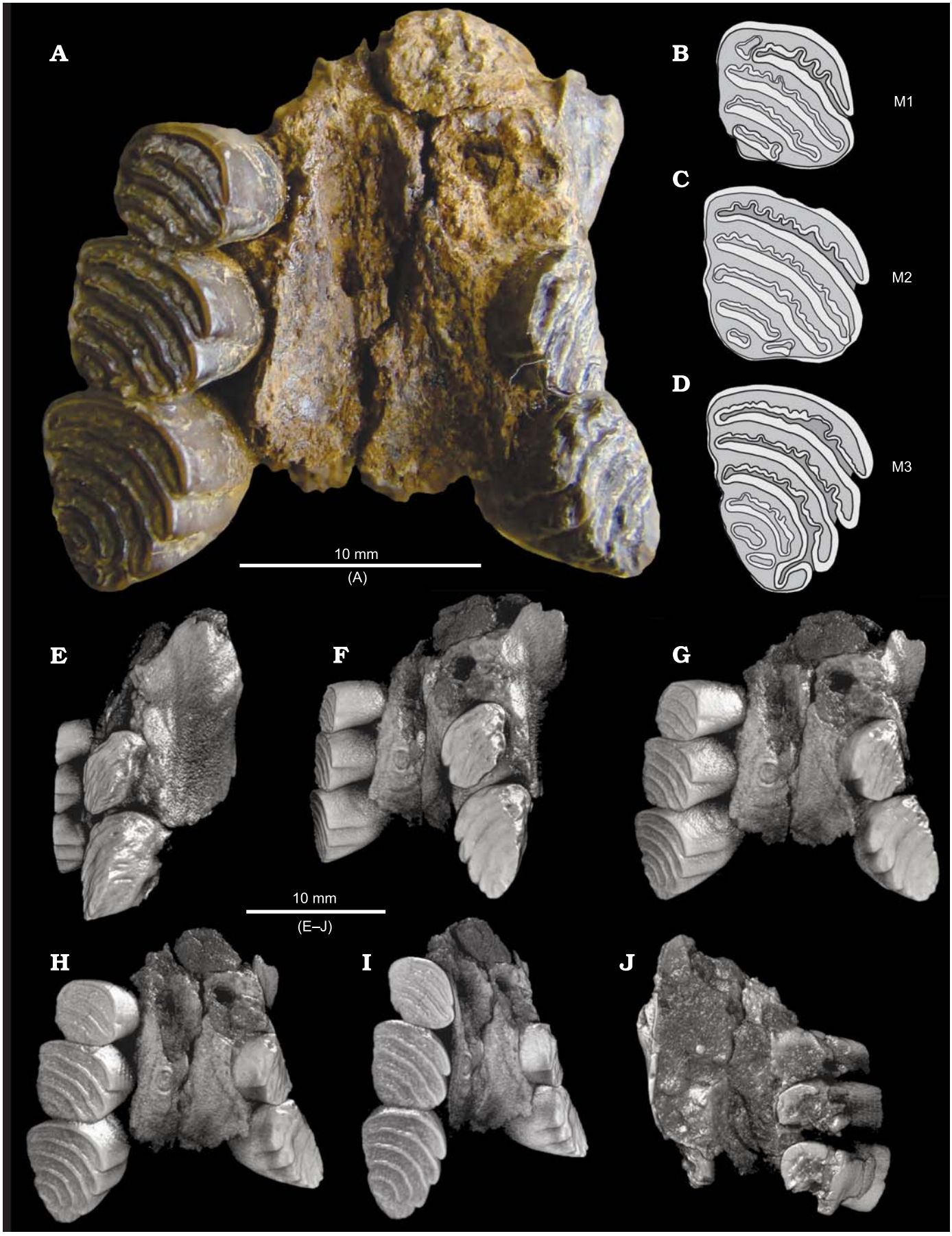
Type horizon: Solimões Formation, Late Miocene.

Diagnosis.—Small-sized potamarchine, protohypsodont, distinguished from *P. murinus* by its smaller size (~30%) and cheek teeth with more oblique and convex lophs with respect to the mesio-distal axis.

Description.—UFAC-CS 11 is a palatal portion with the right M1–M3 series preserved while the left is damaged. The teeth are protohypsodont (sensu Mones 1968, 1982), lophodont (laminar design), with an increase in size and loph number from M1 to M3. The cheek teeth have a lingual root and two labial smaller ones (Fig. 2). The first loph of each tooth has a curved mesial enamel layer and a crenulated distal one, as described for *Potamarchus murinus* by Burmeister (1885).

The M1 is pentalophodont and it is smaller than the M2. In comparative specimens of *P. murinus* the difference in size between the M1 and M2 is not so significant. Both teeth have almost the same width. The first loph of UFAC-CS 11 has a slightly convex mesial enamel layer and the distal one is crenulated and thinner. Only the first lingual flexus is open while the others form fossets. This flexus is oblique and extends almost the entire width of the tooth. At the labial side of this flexus there is a small fosset. The other three fossets decrease their width in the distal direction. The enamel outline of these fossets is crenulated mesially and thicker and smooth distally (this occurs because the mesial enamel layer correspond to the distal layer of the loph).

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Table 2. Measurements (in mm) of the upper cheek teeth of potamarchines from the Solimões Formation and comparative specimens. LLW linguolabial width; MDL, mesiodistal length.

Taxon/Specimen	MDL of P4	LLW of P4	MDL of M1	LLW of M1	MDL of M2	LLW of M2	MDL of M3	LLW of M3	length of M1–M3 series
Potamarchus adamiae UFAC-CS 11	–	–	4.90	4.87	5.76	5.70	7.29	5.30	17.82
Pseudopotamarchus villanuevai UFAC 4762	7.88	7.60	–	6.05	–	–	–	–	–
Potamarchus sp. UFAC 2785	6.99	6.87	–	–	–	–	–	–	–
Potamarchus sp. UFAC 5426	–	–	–	–	6.16	4.89	–	–	–
Potamarchus sp. UFAC 3365	–	–	–	–	–	–	7.47	5.04	–
Potamarchus murinus MACN-Pv 5870	8.91	9.09	7.20	7.63	8.89	7.04	11.88	6.65	27.93
Potamarchus murinus MACN-Pv 3500	8.81	8.05	7.42	6.31	8.50	6.91	9.60	6.10	25.94

The M2 has a rectangular outline and has six lophs. The only open flexus is the first lingual one. This tooth shows the second lingual flex closed (fosset) while in adult specimens of *P. murinus* (MACN-Pv 3500 and MACN-Pv 5870) it is still open. The M3 is the longest tooth and has seven lophs, which are oblique and convex with respect to the mesio-distal axis. There is a reduction in the width of the lophs, from the first to the last. In *P. murinus*, the width of the lophs is more uniform. In MACN-Pv 3500, the M3 has a rectangular outline and its third loph is slightly wider than the first two. MACN-Pv 5870 also has a reduction in the width of the lophs, but not so evident as in UFAC-CS 11). The lophs of the M3 are also more convex than *P. murinus* (Fig. 3).

A comparison with the upper cheek teeth of *P. murinus* (MACN-Pv 3500; MACN-Pv 5870) (Fig. 3 and Table 2) shows that the specimen from Acre also differs from *P. murinus* in its smaller size (>30% less; length of the M1–M3 series: MACN-Pv 3500, 25.94 mm; MACN-Pv 5870, 27.93 mm; UFAC-CS 11, 17.82 mm).

Stratigraphic and geographic range.—Late Miocene of southwestern Amazonia, Brazil.

Potamarchus murinus Burmeister, 1885

Fig. 4, Table 3.

Material.—UFAC 1820, incomplete right dentary with m1–m3 series from Patos locality (= Acre 6 and LACM locality 4611; see Bocquentin and Melo 2006; Cozzuol 2006; Cozzuol et al. 2006; Kay and Cozzuol 2006 for details), Acre River, State of Acre, Brazil, Solimões Formation, Late Miocene.

Description.—The coronoid process is fragmented and its origin is located at the level of the posterior portion of the m3, as described in *P. murinus* by Burmeister (1885). On the lateral aspect of the dentary, at the level of the p4, the masseteric notch for the tendon of the medial masseter muscle is shallow. *Paranamys typicus* (Scalabrini in Ameghino, 1889) shows this notch at the level of the m1, and in *Drytomomys aequatorialis* and *Dinomys branickii* it is at the level of the p4–m1

← Fig. 2. Palatal portion in the potamarchine rodent *Potamarchus adamiae* sp. nov. (UFAC-CS 11) from Solimões Formation, Late Miocene, Brazil, in palatal view (**A**) and detail of the M1–M3 series (**B**–**D**, not to scale). Sequence of tridimentional reconstructions of the palatal portion of UFAC-CS 11 (**E**–**J**).



Fig. 3. Comparison of the occlusal surface in potamarchine rodents *Potamarchus murinus* Burmeister, 1885 (**A**, **B**) from Ituzaingó Formation, Late Miocene, Argentina and *Potamarchus adamiae* sp. nov. (**C**) from Solimões Formation, Late Miocene, Brazil. **A**. MACN-Pv 3500, P4–M3 series. **B**. MACN-Pv 5870, P4–M3 series. **C**. UFAC-CS 11, M1–M3 series.

(Candela and Nasif 2006). The preserved cheek teeth include the m1–m3 series. The m1 has four lophids and all flexids are closed. The m2 has five lophids and the last labial flexid is almost closed. The m3 has five lophids, with the last labial flexid open. The distal enamel layer of the last lophid is more convex in m1 and m2 than in m3, which is more oblique. The mesial enamel layer of each lophid is crenulated, as described

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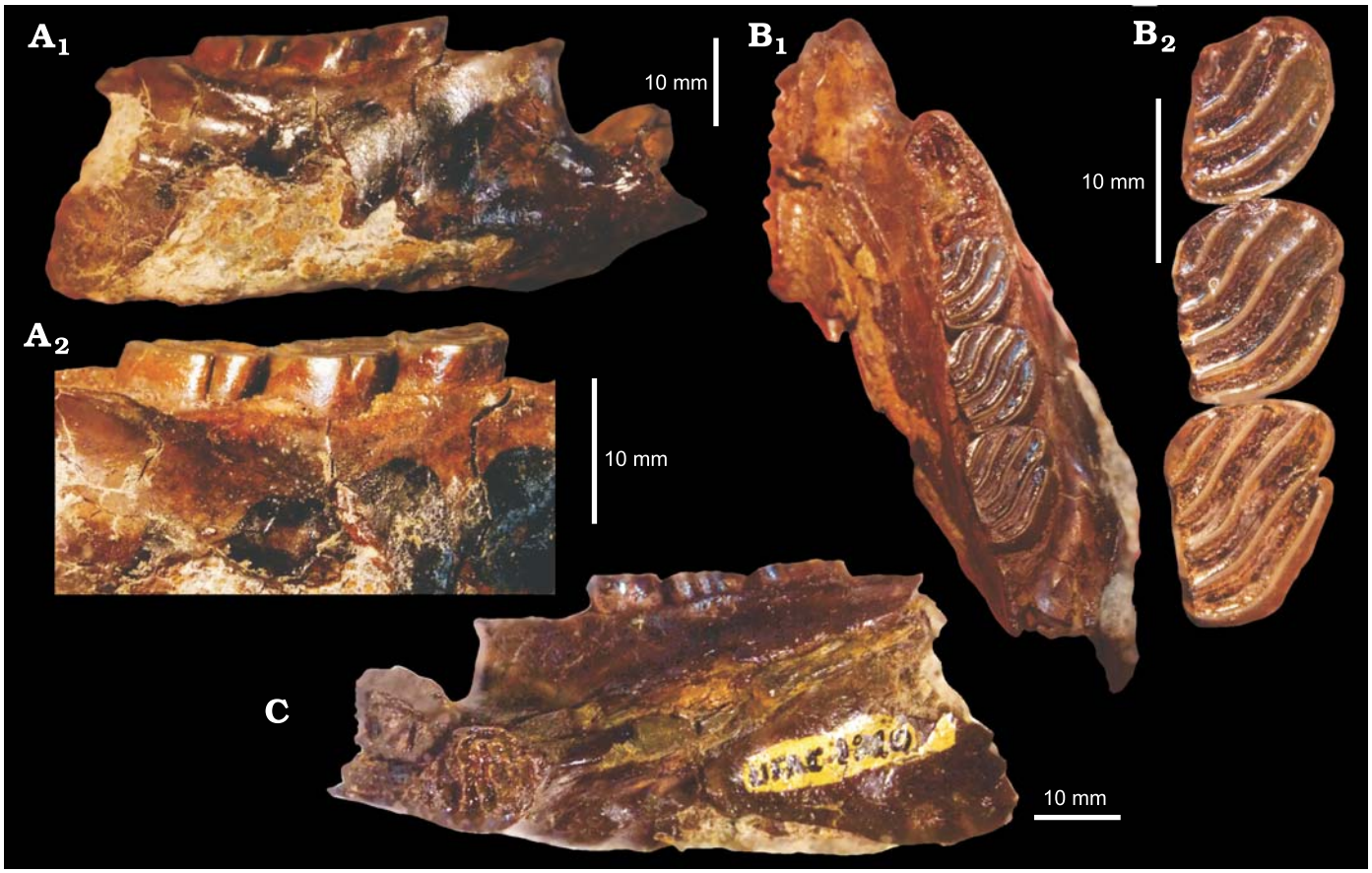


Fig. 4. Right dentary and m1–m3 series of potamarchine rodent *Potamarchus murinus* Burmeister, 1885 (UFAC 1820) from Solimões Formation, Late Miocene, Brazil; in lateral view (**A**), showing detail of the labial view of the cheek teeth (A_2); occlusal view (**B**), showing detail of the occlusal view of the cheek teeth (B_2); and medial view (**C**).

by Burmeister (1885) in *P. murinus* and by Candela and Nasif (2006) in *Paranamys* cf. *typicus*. The size is also compatible with specimens of *P. murinus* from Argentina (Table 3), differing from *Potamarchus adamiae* sp. nov.

Stratigraphic and geographic range.—Late Miocene of Argentina and Brazil (see Discussion).

Potamarchus sp.

SOM 1: fig. S3.

Material.—UFAC 2785, left P4, Talismã, Purus River; UFAC 5426, right M2, Juruá River; UFAC 3365, left M3, Talismã, Purus River (see Latrubesse et al. 2010 for details); UFAC 3249, right p4, Lula, near Sena Madureira; UFAC 4508, right m3, Patos (= Acre 6 and LACM locality 4611; see Bocquentin and Melo 2006; Cozzuol 2006; Cozzuol et al. 2006; Kay and Cozzuol 2006 for details), Acre River, State of Acre, Brazil, Solimões Formation, Late Miocene (Tables 2 and 3; SOM 1: fig. S3).

Table 3. Measurements (in mm) of the lower cheek teeth of potamarchines from the Solimões Formation and comparative specimens. Abbreviations: LLW, linguolabial width; MDL, mesiodistal length.

Taxon/Specimen	MDL of p4	LLW of p4	MDL of m1	LLW of m1	MDL of m2	LLW of m2	MDL of m3	LLW of m3
Potamarchus murinus UFAC 1820	–	–	8.96	7.84	9.71	8.32	10.63	8.56
Potamarchus sp. UFAC 3249	6.66	4.32	–	–	–	–	–	–
Potamarchus sp. UFAC 4508	–	–	–	–	–	–	8.40	5.80
Potamarchus murinus MACN-Pv 4577*	10.19	7.06	8.42	7.39	9.60	7.58	10.65	7.69
Potamarchus murinus MACN-A 5871	–	–	–	–	8.80	7.79	8.42	6.85
Potamarchus murinus MACN-Pv 3992	7.92	5.67	8.06	6.51	8.37	6.24	–	–
Potamarchus murinus MACN-Pv 3516	–	–	7.52	6.57	9.32	7.87	10.52	8.49
Potamarchus sigmodon MACN-Pv 13467*	–	–	–	–	–	–	8.74	7.28
Potamarchus sigmodon MACN-Pv 9037	–	–	–	–	8.70	7.61	9.64	7.40
Potamarchus sigmodon MACN-Pv 3502	–	–	7.82	6.65	8.69	7.38	9.28	7.19

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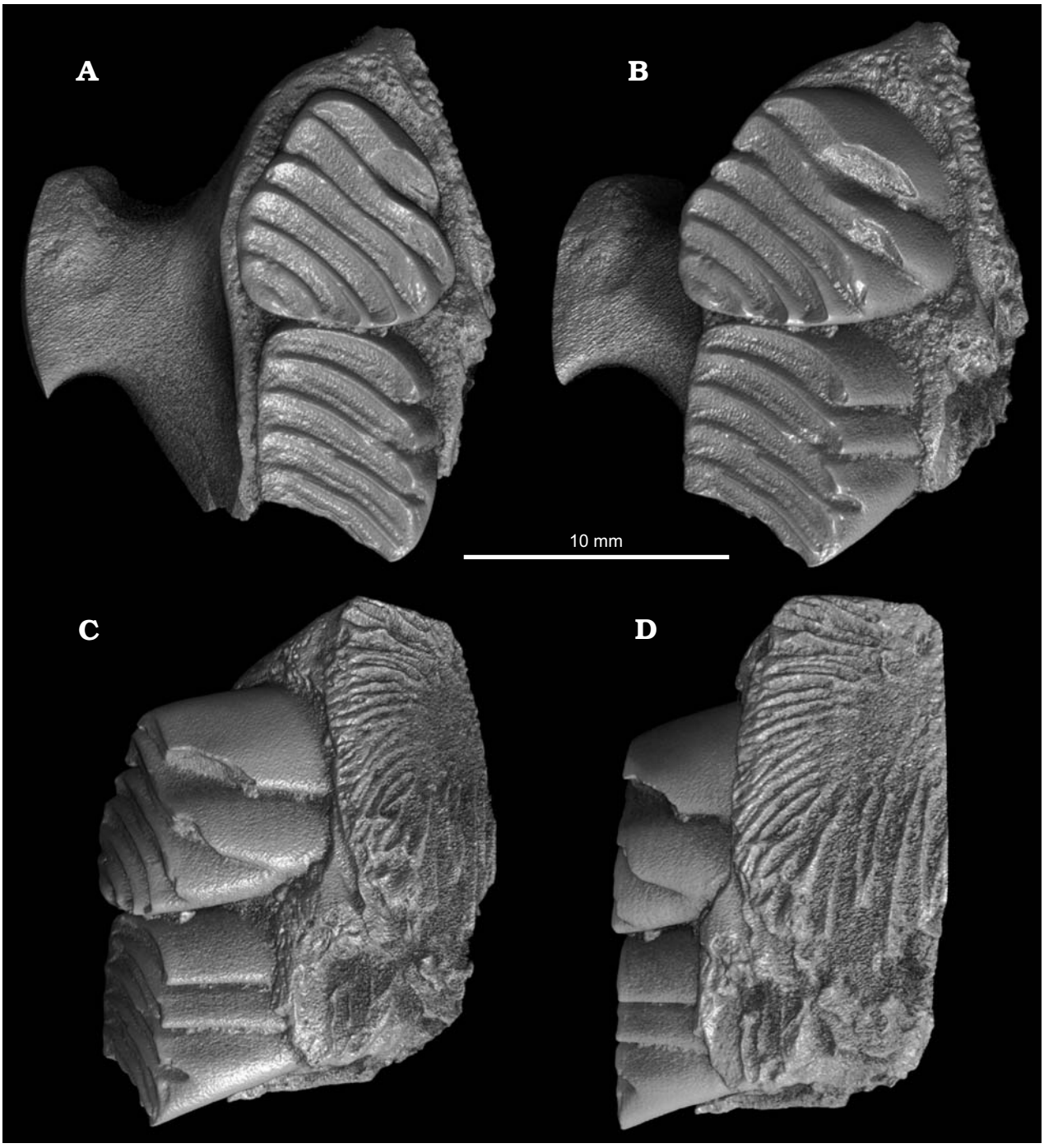


Fig. 5. Sequence of tridimentional reconstructions of the maxilla of potamarchine rodent *Pseudopotamarchus villanuevai* gen. et sp. nov. (UFAC 4762) from Solimões Formation, Late Miocene, Brazil; from occlusal to medial view (**A**–**D**).

Description.—The specimens included here are isolated teeth of uncertain specific attribution. UFAC 2785 is a left P4 with six lophs without crenulation and with little wear (SOM 1: fig. S3A). UFAC 5426 is a right M2 with six lophs showing crenulation in the distal enamel layer of each loph (SOM 1: fig. S3B). UFAC 3365 is a left M3, with six lophs. Its lophs are not as curved as seen in *P. adamiae* sp. nov (SOM 1: fig. S3C). UFAC 3249 is a right p4 with five lophids (SOM 1: fig. S3D). The first lingual flexid is closed, forming a fossetid with a crenulated outline. UFAC 4508 is a right m3 with six lophids (SOM 1: fig. S3E). All the lingual flexids are open and there is no crenulation. The lophids are oblique and are more compressed and less curved than the pattern seen in older specimens of *P. murinus* (e.g., UFAC 1820).

Genus *Pseudopotamarchus* nov.

Etymology: Meaning false *Potamarchus*, regarding to the similarity to the latter genus.

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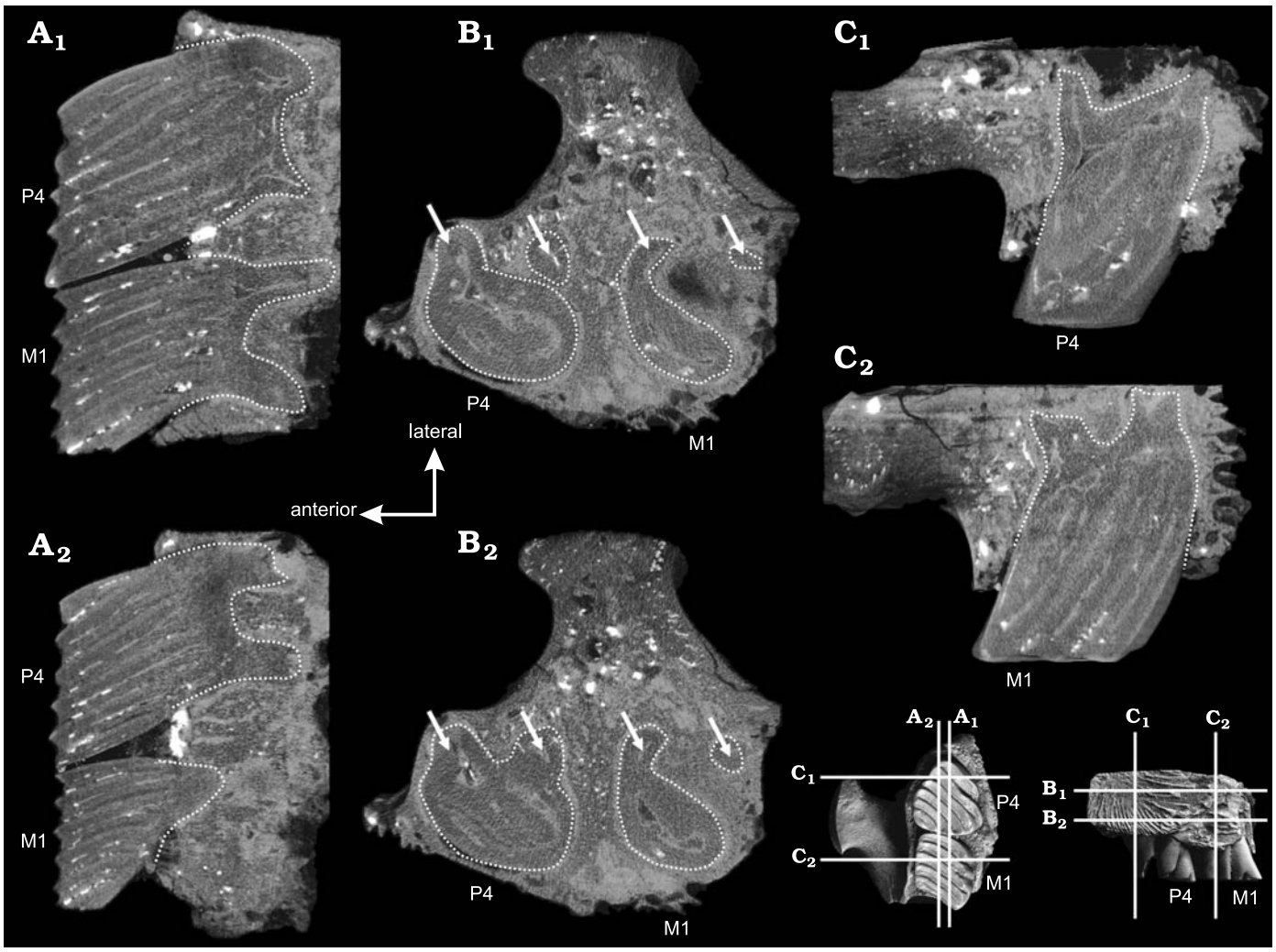


Fig. 6. CT-scan slices of the maxilla of potamarchine rodent *Pseudopotamarchus villanuevai* gen. et sp. nov. (UFAC 4762) from Solimões Formation, Late Miocene, Brazil; in longitudinal (**A**), horizontal (**B**), and transverse (**C**) planes, showing the labial roots of the cheek teeth (arrows).

Type species: *Pseudopotamarchus villanuevai* sp. nov., monotypic; see below.

Diagnosis.—Small-sized potamarchine, protohypsodont, with check teeth composed of lophs, distinguished from *Potamarchus* by the presence of a notch on the anterior surface of the ventral zygomatic root.

Pseudopotamarchus villanuevai sp. nov.

Figs. 5–7; Tables 2 and 3; SOM 1: fig. S4, SOM 3.

Etymology: In honor of the palaeontologist Jean Bocquentin-Villanueva who has studied the fossil vertebrates from Amazonia.

Holotype: UFAC 4762, incomplete right maxilla with P4–M1.

Type locality: Cachoeira do Bandeira locality (see Bocquentin and Melo 2006 for details), Acre River, Solimões Formation (Late Miocene), State of Acre, Brazil.

Type horizon: Solimões Formation, Late Miocene.

Diagnosis.—As for the genus; monotypic.

Description.—The cheek teeth are protohypsodont and show little wear (Fig. 5). The P4 and M1 have two labial roots (Fig. 6). The crown of the P4 is higher than the M1 (SOM 1: fig. S4), and its last loph shows little wear. The P4 has six lophs and it preserves (although almost closed) two labial and three lingual flexi. The lophs are quite oblique in comparison with the M1. The mesial face of the first loph is not as convex as in *Potamarchus murinus*. The first loph is shorter liguo-labially than the second, which is the largest one. Distally to the second one, the lophs decrease in size towards the last one, which is almost rudimentary. The M1 is rectangular and has six lophs (the last loph is fragmented). Labially, there is no open flexus, while lingually the first and second are open and the third is almost closed. The lophs have almost the same width. The lophs of both teeth are compressed, and the rectangular outline of the M1 is distinct from older specimens of *P. murinus*, in which the M1 is subquadrangular (but see Discussion). The lingual area of the lophs of the P4 and M1 are not bent as in *Potamarchus*. The ventral root of the zygomatic process of the maxilla is posteriorly oriented and its anterior area shows a notch not present in *P. murinus* (Fig. 7). This notch is prolonged posteriorly up to the fourth loph of the P4.

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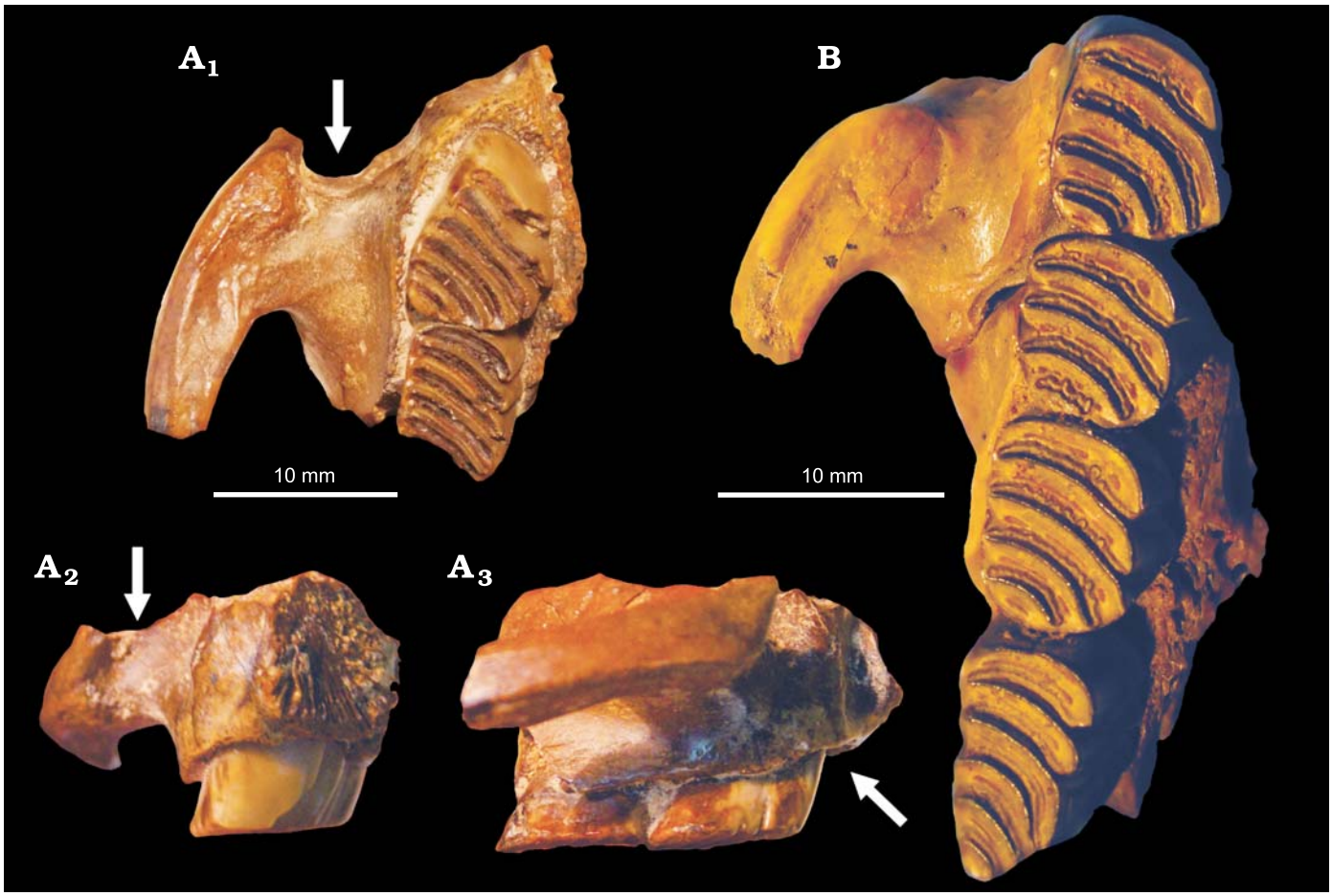


Fig. 7. Maxilla of potamarchine rodent *Pseudopotamarchus villanuevai* gen. et sp. nov. (**A**, UFAC 4762) from Solimões Formation, Late Miocene, Brazil; in occlusal (A_1), anterior (A_2), and lateral (A_3) views, in comparison with *Potamarchus murinus* (**B**, MACN-Pv 3500, inverted) from Ituzaingó Formation, Late Miocene, Argentina; showing the notch (arrows) on the anterior face of the ventral root of the zygomatic process of the maxilla.

Stratigraphic and geographic range.—Late Miocene of southwestern Amazonia, Brazil.

Discussion

Taxonomy, morphology, and ontogeny.—Here we assign new remains of potamarchines from the Late Miocene of northern South America to a new species of *Potamarchus*: *P. adamiae* sp. nov. and also describe material assigned to *P. murinus*. *P. adamiae* sp. nov. is distinct from *P. murinus* mainly in its small size and in having cheek teeth with more oblique and convex lophs with respect to the mesio-distal axis. Other specimens assigned to *Potamarchus* sp. do not have sufficient characteristics to enable a more accurate identification. Another new taxon is erected based on an incomplete maxilla: *Pseudopotamarchus villanuevai* gen. et sp. nov., which reassembles *Potamarchus* in tooth morphology, but it has a notch on the anterior face of the zygomatic ventral root not present in *Potamarchus* or other dinomyids, revealing a new taxonomic unit (Figs. 5, 7).

Scleromys, *Drytomomys*, *Simplimus*, *Eusigmomys*, *Paranamys*, and *Potamarchus* have been included in Potamarchinae (but see Introduction and Table 1). *Scleromys* shows a distinct occlusal morphology to *Potamarchus* by possessing a general s-shaped configuration; the M2 is the largest tooth in the upper series, and the ventral root of the zygomatic process of the maxilla is anterior to the P4 (among other characters) (see Fields 1957; Cerdeño and Vucetich 2007; Kramarz 2006). The cheek teeth of *Potamarchus* are distinct from *Drytomomys aequatorialis* Anthony, 1922 in the presence of more compressed flexi/ids and fossets/ids, and more oblique lophids on the lower teeth. Information about *Simplimus* is very scarce, because this taxon was described on the basis of a few isolated teeth from the "Friasian" age of Argentina (see Vucetich 1984). According to Kraglievich (1926: 56), the holotype of *Simplimus indivisus* figured in Rovereto (1914: 35, fig. 12) is similar to *Potamarchus*, but the crown of this tooth is "más larga y voluminosa" (longer and more voluminous). The tooth in this illustration is quite similar to the left M1 of *Potamarchus*. The m1 or m2 figured in Vucetich (1984) shows that the lophs are less oblique (mainly the distal one) and the flexids wider than in *Potamarchus*. The dentary of *Paranamys typicus* (Scalabrini in Ameghino, 1889) has the masseteric notch for the tendon of the medial masseter muscle at the level of

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m1; in *Drytomomys aequatorialis* it is at the level of the p4–m1 (Candela and Nasif 2006). In the specimen UFAC 1820, assigned to *P. murinus*, this fossa is at the level of the p4. The general configuration of the occlusal surface of the lower cheek teeth of *Paranamys typicus* is quite similar to *Potamarchus* (see Nasif et al. 2013: fig. 2.3). An example of this fact is that Candela and Nasif (2006) reported an m1 or m2 of *Paranamys* cf. *P. typicus* that shows no differences in comparison to *Potamarchus*. The tooth figured by Rovereto (1914) of *Eusigmomys oppositus* is euhypsodont and has three lophs in a sigmoid configuration. The taxonomic validity of this taxon was questioned by Nasif (2009).

Two species of *Potamarchus* have been recognized from the Late Miocene of Argentina: *P. murinus* and *P. sigmodon*. *P. murinus* was described by Burmeister (1885) based on a right dentary with the p4–m3 series from Entre Ríos Province; *P. sigmodon* was erected based on a right dentary with the m3 collected near to Paraná city, Entre Ríos Province (Ameghino 1891). Subsequently, Pascual et al. (1966) figured superior teeth of *P. murinus*. In the upper cheek teeth of *P. murinus*, the mesial layer of enamel is smooth and thicker than the distal, which is thinner and crenulated, while in the lower teeth, the opposite occurs (Pascual et al. 1966). This trend is also present in *P. adamiae* sp. nov. *P. sigmodon* is of a similar size to *P. murinus*, but according to Ameghino (1891), the mesial enamel layer of each loph (lower teeth) does not show the crenulation found in *P. murinus*. The lophs are curved with the exception of the last one. In addition, the holotype of *P. sigmodon* shows a tenuous masseteric fossa and a short symphysis (Nasif et al. 2013). Frailey (1986) argued that some specimens from Acre reported by him have considerable variation in the crenulation of the enamel layer. In the material here analyzed, the variation is also evidenced. In the specimen UFAC 4762, which shows little wear, the crenulation is present only on the first loph of the M1. In the specimen UFAC 1820, which shows considerable wear, the crenulation is present on all lophs. As stated by Frailey (1986), it is possible that this character (crenulation) is associated with ontogenetic variation and not suitable as a trait to distinguish two species. Similar pattern of enamel crenulation on the occlusal surface is also present in other dinomyids, such as the Eumegamyinae *Eumegamys paranensis* (see Candela et al. 2013).

Potamarchines show considerable variation during dental ontogeny, which modifies the configuration of the structures and the diameter of the cheek teeth from juveniles to senile adults (Pascual et al. 1966). According to Pascual et al. (1966), the anterior lingual flexus and the last labial flexid are deeper, persisting for longer. In this way, the fossets begin their formation disto-mesially and the fossetids in a mesio-distally direction. The wear also promotes the disappearance of the distal lophs in the upper teeth. Juveniles that have a pentalophodont pattern usually lose the last loph, becoming tetralophodont (Nasif 2009: 167). This reduction in the number of lophs tends to result in a quadrangular outline of the cheek teeth (Pascual et al. 1966).

As discussed above, the differences of the occlusal morphology among the generic and specific levels of the primitive dinomyids are very subtle. In part, this fact possibly occurs because several taxa have been proposed based exclusively on isolated cheek teeth, which, if not analyzed from an ontogenetic perspective, could lead to a definition of new taxonomic units based on distinct ontogenetic stages of the same taxon. In this way, the diversity of the group could be overestimated. For example, *Pentastylomys seriei* Kraglievich, 1926 and *Telodontomys compressidens* Kraglievich, 1931 are each one based on a single tooth, and their relationships were considered as incertae sedis by Mones (1981). According to Rinderknecht et al. (2010), the *Pentastylomys seriei* tooth could be an M3 of *Potamarchus*. The holotype of *T. compressidens* is a tooth with five lophs; the first two are united labially and the last two united lingually. Based on the ontogenetic trend of reduction of the number of lophs (Pascual et al. 1966; Nasif 2009), this material could be a left m3 of *Potamarchus* or *Paranamys*. Among the specimens here studied, the M3 UFAC 4508 assigned to *Potamarchus* sp. has six lophs, being probably a young specimen and the old specimens of *P. murinus* (e.g., MACN-Pv 4577; UFAC 1820) having five or four lophs. Thus, a reevaluation of the holotypes of extinct dinomyids should be carried out to analyze their taxonomic validity.

In this sense, *Potamarchus adamiae* sp. nov. is based on a specimen (UFAC-CS 11) smaller than *P. murinus*. In our view, the smaller size is a characteristic of this species because its M2 shows the second lingual flex closed (fosset) while in adult specimens of *P. murinus* (MACN-Pv 3500 and MACN-Pv 5870), which have larger size, it is still open. This fact suggests that UFAC-CS 11 shows more wear than the comparative specimens. Besides, the cheek teeth have differentiated roots. Although the formation of roots in protohypsodont teeth of extinct caviomorphs is not completely studied, the presence of these structures is associated with the growth arrest of the tooth (Mones 1968). Vucetich (1984) stated that the roots of the cheek teeth of *Simplimus* possibly are not differentiated in an early ontogenetic stage.

In the holotype of *Pseudopotamarchus villanuevai* gen. et sp. nov. (UFAC 4762) the crown of the P4 is slightly higher than the M1 (SOM 1: fig. S4), and its last loph shows little wear. This aspect suggests that this tooth has less wear and was erupted after the M1, not being a deciduous tooth. The sequence of eruption of the cheek teeth in caviomorphs is variable. In some taxa, the P4 is functional before the eruption of the M3 (e.g., *Elasmodontomys* Anthony, 1916 and *Amblyrhiza* Cope, 1868; Ray 1964), while in others the DP4 is lost after the M3 erupts (e.g., *Drytomomys aequatorialis*, *Erethizon* Cuvier, 1823, *Dinomys*, *Dasyprocta* Illiger, 1811, and *Cuniculus* Brisson, 1762 (Fields 1957; Ray 1964). Among the extinct primitive dinomyids, according to Fields (1957) the P4 erupts after the M3 in *D. aequatorialis*. If *Pseudopotamarchus villanuevai* gen. et sp. nov., had a similar pattern to this dinomyid, it could be indicating that the specimen had the definitive dentition, which sometimes is

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correlated to the beginning of adulthood. In most mammals, the acquisition of definitive dentition is associated to the sexual maturity (Rodrigues et al. 2011). However, in some rodents, the eruption of all teeth precedes the sexual maturation (Shigehara 1980). Unfortunatly, in UFAC 4762 the region posterior to the M1 is lacking by fragmentation, depending on new findings to study its dental replacement. The intermaxillary suture was not closed when the animal died, as can be seen by the surface of the medial surface of the maxilla (Fig. 5). Different from other mammal groups, such as peccaries and otariids, where an early closure of the palatal sutures occurs (Herring 1974; Brunner et al. 2004), hystricognath rodents do not close early these sutures (except for the interpalatine; see Wilson and Sanchez-Villagra 2009). Hence, although the specimen UFAC 4762 has a definitive premolar, due to the absence of more characteristics, is not possible to confirm if this specimen reached the adulthood. The absence of fossets in the cheek teeth suggests that it not an old individual. However, it is important to note the presence of a notch on the on the anterior surface of the ventral zygomatic root was not described in any ontogenetic stage of dinomyids (see Fields 1957; Nasif 2009).

Palaeobiogeographic aspects.—An Andean foot hill corridor was proposed to explain the high degree of similarity between the Miocene faunas of southern and northern South America (Walton 1997), evidenced by several vertebrate groups sharing these areas (e.g., Cione et al. 2000; Candela and Nasif 2006; Cozzuol 2006; Negri et al. 2010).

Potamarchus had a wide distribution during the Late Miocene of South America including southern and northern regions. The fossil record of *Potamarchus* includes those specimens from Entre Ríos, Argentina (Burmeister 1885; Ameghino 1891) and Acre referred to above. Specimens not identified at the specific level include a left dentary from the middle portion of the Urumaco Formation, Venezuela (Linares 2004); a maxillary fragment without stratigraphic context from Uruguay (Rinderknecht et al. 2010); and *Potamarchus* sp. mentioned by Pascual et al. (1966) from the Arroyo Chasicó Formation. In the comparative faunistic list of Cione et al. (2000), the record of *Potamarchus* in the Arroyo Chasicó Formation and Cerro Azul Formation (= Epecuén "Formation") is considered dubious. Tauber (2005) reported a maxilla fragment with P4–M2 from the Salicas Formation, Late Miocene. Horovitz et al. (2010) reported isolated teeth assigned to cf. *Potamarchus*; according to these authors, the illustration of *Potamarchus* sp. from the middle portion of the Urumaco Formation reported by Linares (2004) is not sufficiently informative to verify this identification.

The wide distribution of *Potamarchus* is in accordance with the interpretation of the palaeobiogeographic connection between both areas. However, the new collection from the Brazilian Amazon revealed a presence of two endemic dinomyids distinct from the Late Miocene taxa from southern South America, where the majority of the taxa have been described.

Conclusions

Until recently the record of dinomyids in the Solimões Formation was predominantly based on a few isolated teeth, which made more accurate taxonomic identification difficult due to the scarcity of diagnostic characters. Now, based on new material, two new taxa of potamarchines (a new species of *Potamarchus* and a new genus and species) have been erected from the Neogene of southwestern Amazonia, Brazil.

Potamarchines have a considerable variation in the occlusal surface of the cheek teeth, which is mainly an ontogenetic feature. This needs to be analyzed in a major review, including a phylogenetic analysis incorporating the taxa here described for a better understanding of these Late Miocene dinomyids.

Historically, fossil rodents from the Neogene of southwestern Amazonia have been poorly studied. Now, with the increase in data, the diversity and endemism in this region show a necessity of reevaluation.

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Appendix 1

Comparative specimens from "Conglomerado Osífero", Ituzaingó Formation, Late Miocene, Entre Rios Province, Argentina.

Potamarchus murinus: MACN-Pv 4577 (holotype), right dentary incomplete p4–m3; MACN-A 5871, incomplete dentary with m2–m3; MACN-Pv 3500, incomplete left maxilla with P4–M3; MACN-Pv 3516, incomplete dentary with p4–m3; MACN-Pv 3992, right dentary with p4–m2; MACN-Pv 5870, incomplete right maxilla with P4–M3.

Potamarchus sigmodon: MACN-Pv 13467 (holotype), incomplete right dentary with the m3; MACN-Pv 9037, incomplete right dentary with m2–m3; MACN-Pv 3502, incomplete right dentary with m1–m3.

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