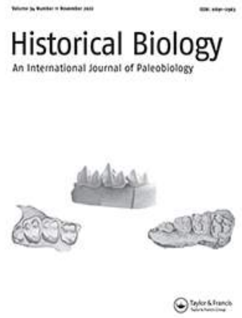

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A new Late Miocene hystricognath rodent assemblage (Caviidae, Dinomyidae, and Neoepiblemidae) from northern Brazil and its biostratigraphic relevance

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ABSTRACT

The Neogene strata of the Solimões Formation (northern Brazil) have revealed an astonishing diversity of extinct caviomorph rodents. The main exposures of this formation are found along the Juruá, Acre, and Purus rivers, and some road cuts in the State of Acre. In this paper, we reported a new locality containing a rodent assemblage. The outcrop (Coqueiro locality) is located in the Envira River, central region of State of Acre, Brazil. During fieldwork in 2010 and 2019, several isolated cheek teeth and bones of mammals were recovered in conglomeratic levels from this locality. Here, we described specimens assigned to *Cardiatherium* sp. (Caviidae: Hydrochoerinae), *Potamarchus* sp. and cf. *Pseudopotamarchus* (Dinomyidae: Potamarchinae), and *Neoepiblema* sp. (Neoepiblemidae). The locality is not yet dated by radiometric methods but based on the biostratigraphic information of the taxa here reported, we suggest that the fossil-bearing levels of this locality were deposited during the Late Miocene.

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Solimões Formation; Caviomorpha; biodiversity; fossil record; Neogene; South America

Introduction

Rodentia is one of the most expressive taxonomic and phenotypic mammalian clades, showing aproximately 41% of the diversity of living mammals (Hautier and Cox 2015 and references therein), with wide variation in shape, size (5 g, in some mice, up to 70 kg, in capybaras; D'Elía et al. 2019), and ecological habits (Fabre et al. 2015; Kerber 2017). This group emerged between the late Palaeocene and early Eocene (~58 – 48 Ma) in the northern hemisphere. However, some studies propose an older origin for this group, although fossils have not been found (see Wu et al. 2012; O'Leary et al. 2013). Today, native rodents inhabit terrestrial ecosystems on all continents, even archipelagos (Fabre et al. 2015), except for Antarctica, New Zealand, and some islands (D'Elía et al. 2019). The rapid radiation and the great success of diversification in different habitats resulted in several cases of convergent and parallel evolution (Hautier and Cox 2015).

The less inclusive group Caviomorpha includes the Neotropical hystricognath rodents – endemic to South America and the Caribbean islands (Upham and Patterson 2015). This group, in turn, has four less inclusive clades: Cavioidea (capybaras, rock cavy, guinea pigs, maras, agoutis, pacas; families Caviidae, Dasyproctidae, and Cuniculidae); Erethizontoidea (South American porcupines; family Erethizontidae); Chinchilloidea (chinchillas, pacaranas, vizcachas; families Chinchilidae, Dinomyidae, and the extinct lineages), and Octodontoidea (tuco-tucos, spiny rats, hutias; families Abrocomidae, Echimyidae, Octodontidae, Ctenomyidae, and other extinct lineages) (Patton et al. 2015; Upham and Patterson 2015; Kerber 2017; D'Elía et al. 2019).

Caviomorphs arrived in South America during the Palaeogene in one or several waves of incoming African hystricognaths (Arnal et al. 2022). Studies suggest that they originated during the middle/late Eocene (~48 – 33 Ma), and most of the less inclusive clades (i.e. families) appeared in the fossil record between the early Oligocene and Early Miocene (~28 – 15 Ma; Antoine et al. 2012; Upham and Patterson 2015; Arnal et al. 2022). The evolution and diversification of the South American hystricognath groups were probably influenced by the geological and climatic events that occurred in these time intervals and the long period of geographic isolation (Ortiz Jaureguizar and Cladera 2006; Upham and Patterson 2015; Vucetich et al. 2015a).

In Brazil, the Solimões Formation (Neogene) has revealed an astonishing diversity of extinct caviomorphs (e.g. Negri and Ferigolo 1999; Kerber et al. 2016; 2017a, 2017b, 2018, 2019a, 2019b, 2022). Here, we report a new rodent association (caviids, dinomyids, and neoepiblemids) from Envira River, located in the central region of the State of Acre, and discuss their biostratigraphic implications. This association represents the first record of fossil rodents in that region.

Geological settings

The rodent specimens were collected during field trips in 2010 and 2019, at the Coqueiro locality – PRE 06 ('Ponto Rio Envira 06'; 08° 18′12.6" S and 70°26′39.9" W), located in Envira River, Feijó city, State of Acre, Brazil (Figure 1). The locality is within the stratigraphic context of the Solimões Formation, Acre Basin (see Hsiou et al. 2022, for a review). The specimens were collected from a conglomeratic level at the base of the outcrop (Figure 2). Coqueiro locality has not yet been dated using radiometric methods. However, other outcrops of this formation have been recently dated, revealing ages within the Tortonian (Late Miocene, ~10 –

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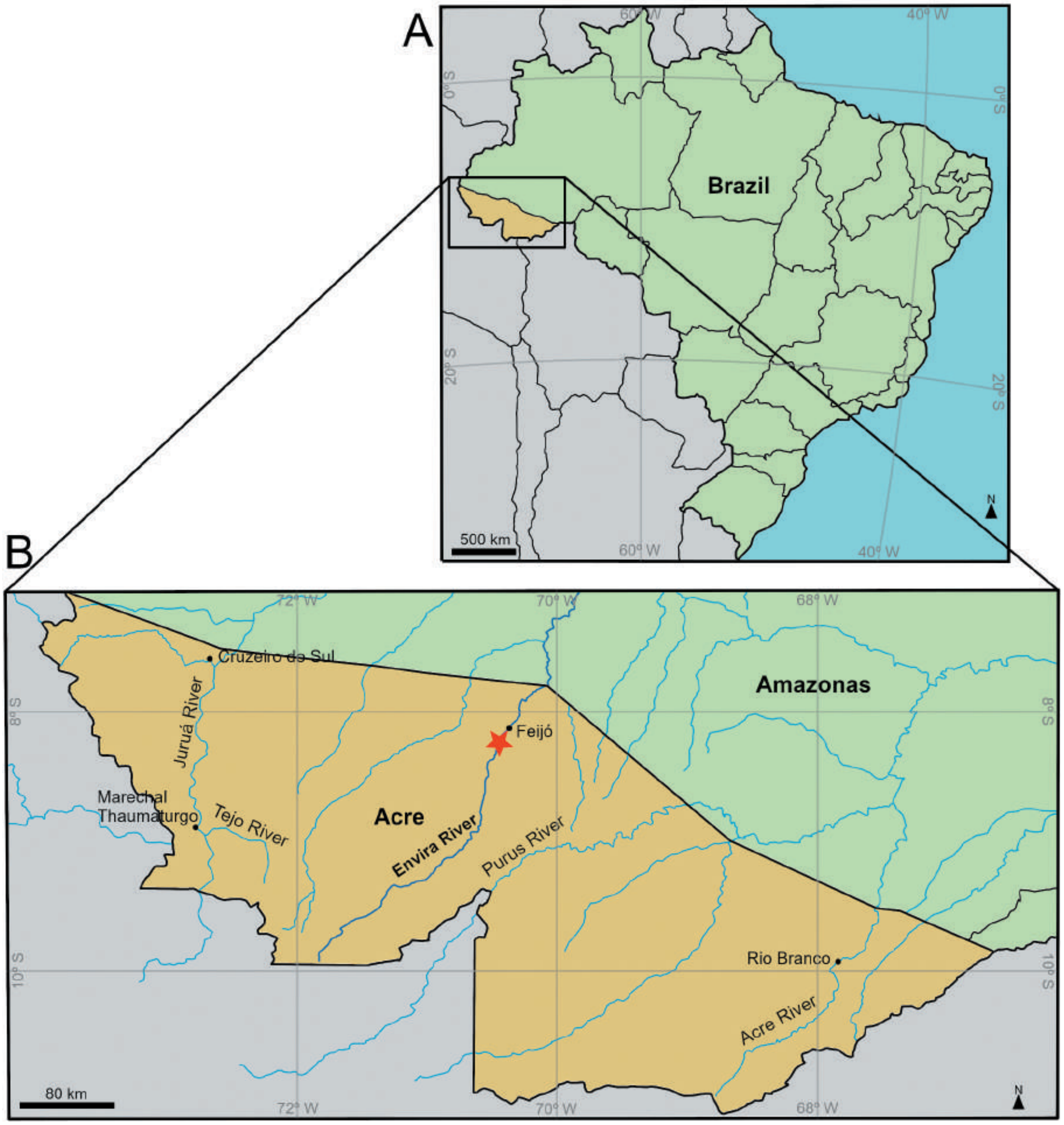

Figure 1. Location of Coqueiro locality, Envira River (red star), Feijó City, State of Acre, Brazil.

8 Ma; Bissaro-Júnior et al. 2019). Fossil vertebrates are quite abundant in this stratigraphic unit and have been found since the mid-19th century (Chandless expedition, 1866) (see Agassiz and Agassiz 1868; Cozzuol 2006; Latrubesse 2007). A great diversity of fossils of mammals (rodents, marsupials, bats, primates, cetaceans, xenarthrans, notoungulates, litopterns, and sirenians), birds, crocodiles, turtles, fishes, invertebrates, trace fossils, and plants have been documented (Cozzuol 2006; Negri et al. 2010; Rodrigues et al. 2016; Silva and Negri 2016).

Latrubesse et al. (2007, 2010) recognised two main facies in the Solimões Formation: a channel-dominated assemblage and a floodplain-lacustrine low-energy assemblage. Latrubesse et al. (2010) suggested that this formation was deposited in a sedimentary environment characterised by rivers associated with megafan systems, lakes, and marshes. The environment was predominantly composed of grasslands and gallery forests.

Material and methods

Preparation of the specimens

The sediment from the conglomeratic layer was screen washed with an aqueous hydrogen peroxide solution to find the fossils. These specimens are deposited in the vertebrate palaeontology collection of the Universidade Federal do Acre, Campus Floresta, Cruzeiro do Sul municipality, State of Acre, Brazil (UFAC-CS). Then, ultrasonic and manual cleaning were employed to prepare the specimens.

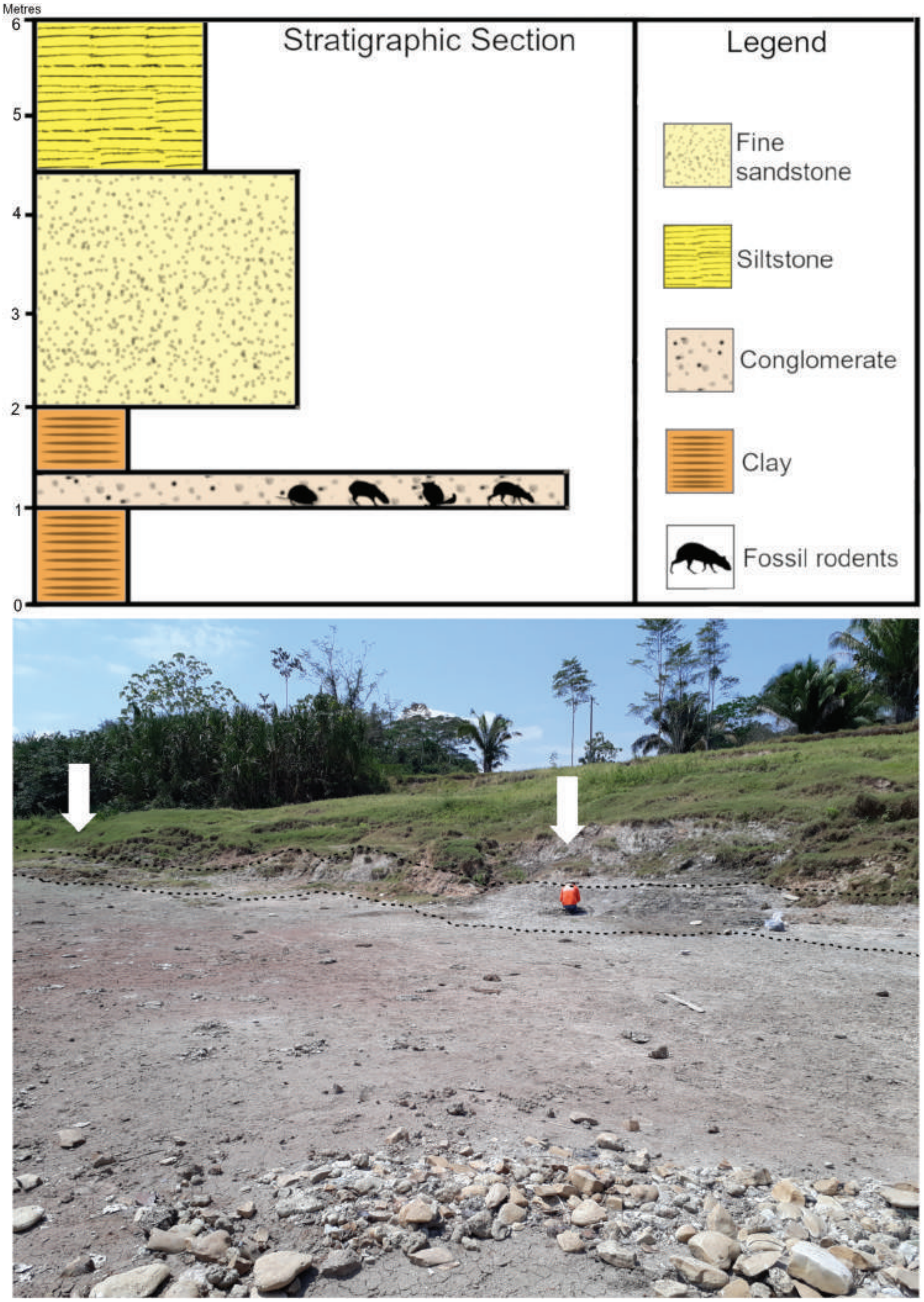

Figure 2. Stratigraphic profile at Coqueiro locality (Solimões Formation), Envira River, State of Acre, Brazil. Modified from Rodrigues et al. (2016). White arrows indicate collection sites.

The measurements of the specimens (linguo-labial width – LLW and mesio-distal length – MDL) were taken using a digital caliper.

Nomenclature and comparison

The dental nomenclature follows Mones (1991), translated from Spanish by Vucetich et al. (2005) and Cerdeño et al. (2019) for Caviidae (Hydrochoerinae). Kerber et al. (2017a) and Kerber et al. (2019a), respectively, were employed for Dinomyidae (Potamarchinae) and Neoepiblemidae. We used ‘M’ to refer to upper molars and ‘m’ to lower molars.

The specimens were compared with descriptions in literature – Caviidae (Hydrochoerinae): Vucetich et al. (2010, 2011); Vucetich & Pérez, (2012); Vucetich et al. (2014); Kerber et al. (2017a), Cerdeño et al. (2019); Dinomyidae (Potamarchinae): Kerber et al. (2016, 2017a, 2017b, 2018); Neoepiblemidae: Kerber et al. (2017a, 2017b, 2019a, 2019b).

Institutional abbreviations

UFAC-CS, Universidade Federal do Acre, Campus Floresta, Cruzeiro do Sul municipality, State of Acre, Brazil.

Systematic Palaeontology

Order RODENTIA Bowdich 1821

Suborder HYSTRICOGNATHI Tullberg 1899
Infraorder CAVIOMORPHA Wood 1955

Superfamily CAVIOIDEA (Fischer de Waldheim 1817) sensu Kraglievich 1930

Family CAVIIDAE (Fischer 1817) sensu Waterhouse 1839

Subfamily HYDROCHOERINAE (Gray 1825) Gill 1872

Genus *Cardiatherium* Ameghino 1883

Cardiatherium sp.
(Figure 3, Table 1)

Referred specimens: UFAC-CS 299, isolated left M1 or M2 (Figure 3A); UFAC-CS 354, isolated left M3 (Figure 3B).

Provenance: Coqueiro locality – PRE 06 (‘Ponto Rio Envira 06’; 08° 18′12.6”S and 70°26′39.9” W).

Description: UFAC-CS 299 (Figure 3A), left euhypsodont (sensu Mones 1986) M1 or M2, has a lanceolate shape, with Prisms I and II labially connected by a short isthmus. Both prisms are lingually projected. The H.P.E. (first external flexus), located on the labial face of the Prism I, forms a linguo-distally invagination without reaching the medial line of the tooth. The H.S.E. (second external flexus) located on the labial face of the Prism II is shallower than the H.P.E. The H.F.I. (fundamental internal fissure, hypoflexus) penetrates between both prisms transversally. UFAC-CS 354 (Figure 3B) is a M3 that preserves only its distal portion (Prisms, IV, V, and VI). The prisms have a lanceolate shape. They are parallel to each other, labio-lingually oriented. The prisms are decreasing in width distally.

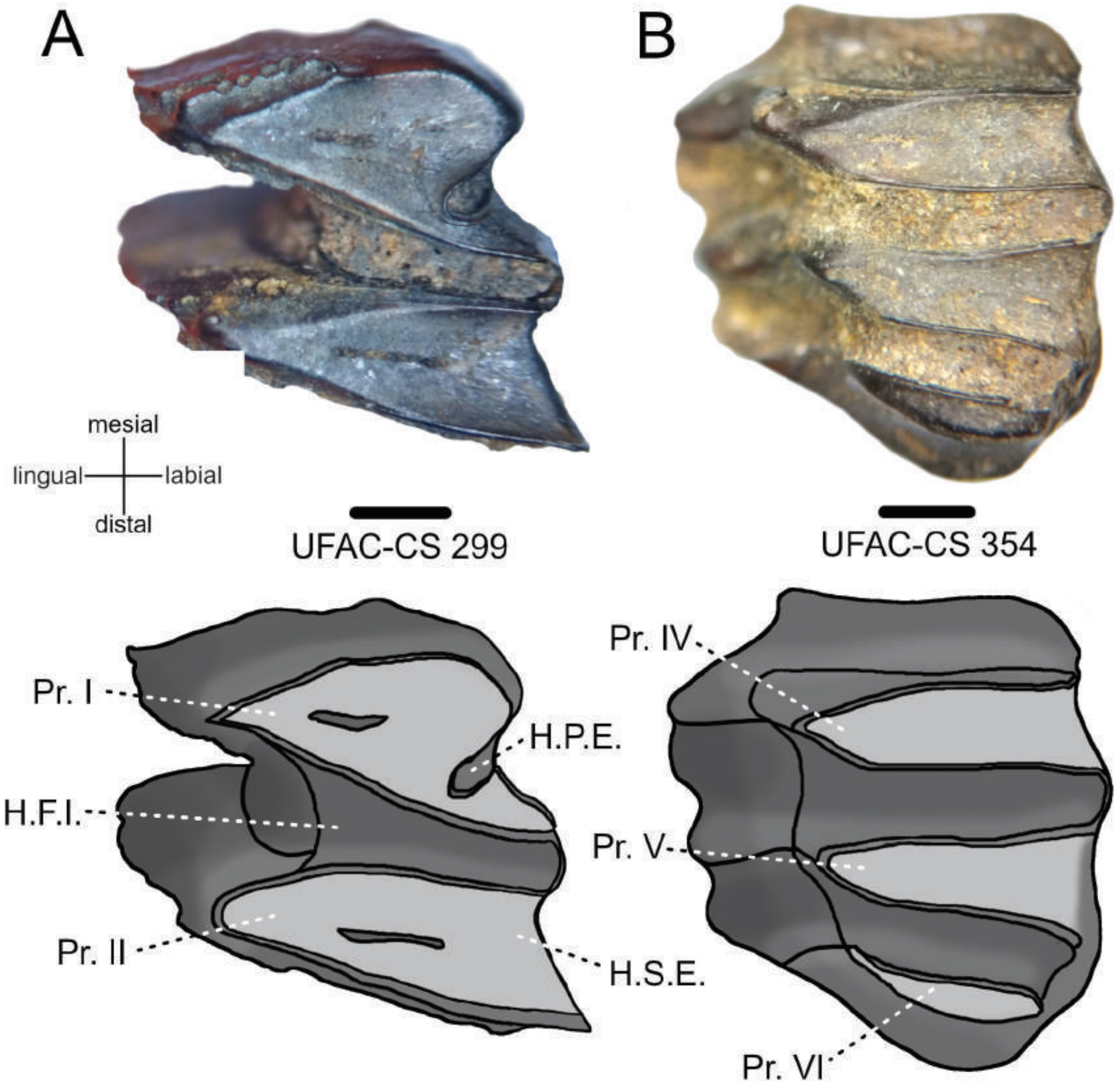

Figure 3. Occlusal view of the cheek teeth of *Cardiatherium* sp. from Envira River, State of Acre, Brazil. **A**. UFAC-CS 299, left M1 or M2; **B**. UFAC-CS 354, left M3. Scale bars = 1 mm. **Abbreviations: H.P.E.**, first external flexus; **H.S.E.**, second external flexus; **H.F.I.**, fundamental internal fissure (hypoflexus); **Pr. (I, II, IV, V, and VI)**, prism.

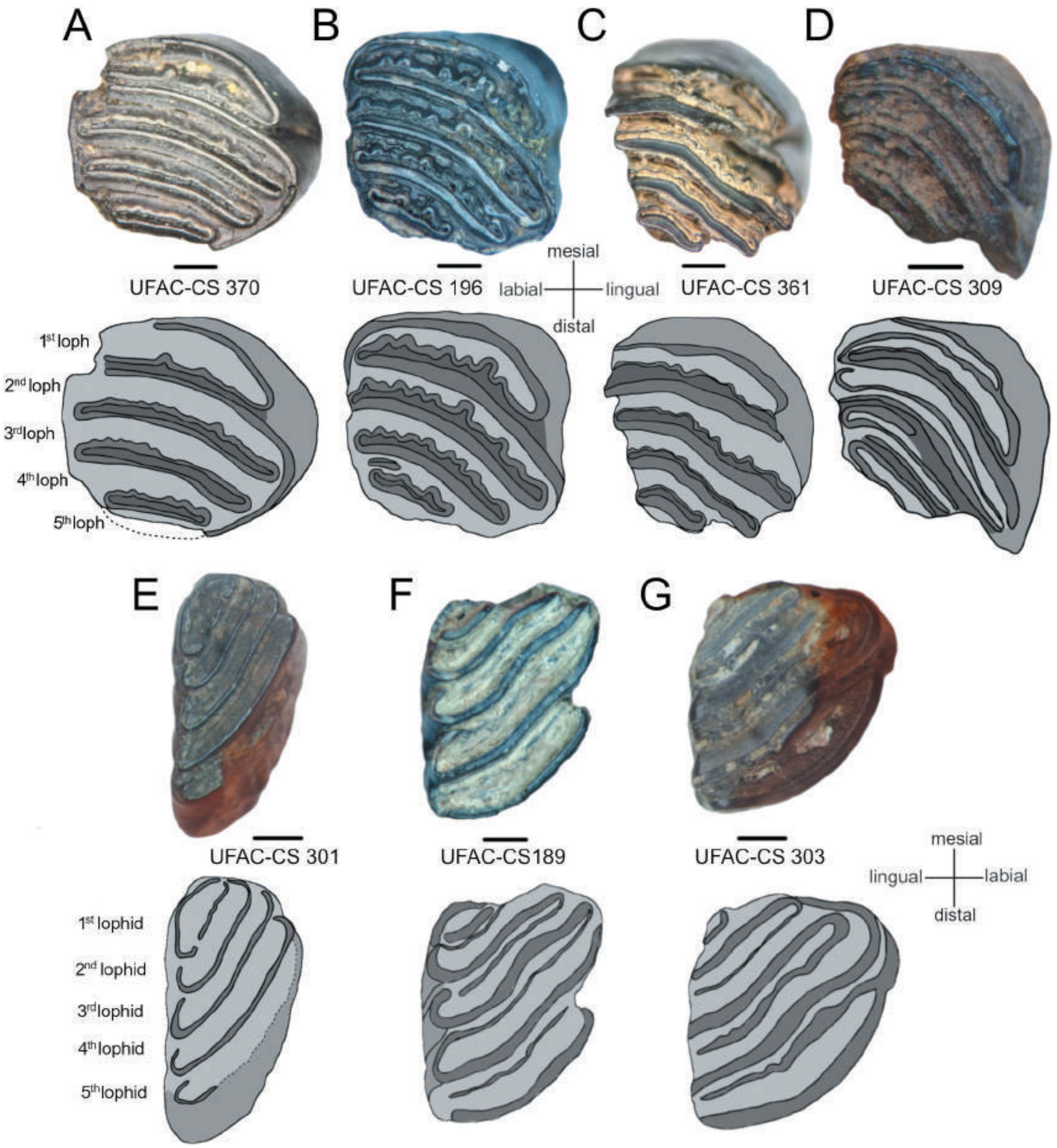

Figure 4. Occlusal view of the cheek teeth of *Potamarchus* sp. from Envira River, State of Acre, Brazil. **A**. UFAC-CS 370, left premolar (P4) (inverted). **B**. UFAC-CS 196, upper right molar (M1 or M2). **C**. UFAC-CS 361, upper right molar (M1 or M2). **D**. UFAC-CS 309, upper right molar (M3). **E**. UFAC-CS 301, lower right premolar. **F**. UFAC-CS 189, lower left molar (m3) (inverted). **G**. UFAC-CS 303, left lower molar (m3?) (inverted). Scale bars = 1 mm.

Superfamily CHINCHILLOIDEA Bennet 1833

Family DINOMYIDAE Alston 1876

Subfamily POTAMARCHINAE Kraglievich 1926

Genus *Potamarchus* Burmeister 1885

Potamarchus sp.

(Figure 4, Table 1)

Referred specimens: UFAC-CS 370, isolated left P4 (Figure 4A); UFAC-CS 196, isolated right M1 or M2 (Figure 4B); UFAC-CS 361, isolated right M1 or M2 (Figure 4C); UFAC-CS 309, right molar M3 (Figure 4D); UFAC-CS 301, isolated right premolar (Figure 4E); UFAC-CS 189, left molar m3 (Figure 4F); UFAC-CS 303, left lower molar (Figure 4G).

Provenance: Coqueiro locality – PRE 06 ('Ponto Rio Envira 06'; 08° 18′12.6”S and 70°26′39.9“W” W).

Description: The material assigned to *Potamarchus* is composed of several isolated protohypsodont (*sensu* Mones 1986) cheek teeth (Figure 4).

UFAC-CS 370 (Figure 4A) is a left P4, subrounded in occlusal view. It is well preserved, but the mesio-labial corner is missing, and the last loph is fragmented. It is composed of five lophs oblique and slightly curved, labially connected. In all lophs, the mesial enamel layer is thicker than distal, and the distal is crenulated. The first loph is shorter than the second one, different from the M1-M2. It is not lingually connected to the other lophs, and it is separated by an oblique flex that almost crosses the occlusal surface. From the second to the fifth loph, they are lingually connected, which means that the flexa are closed, forming fossettes. The second loph

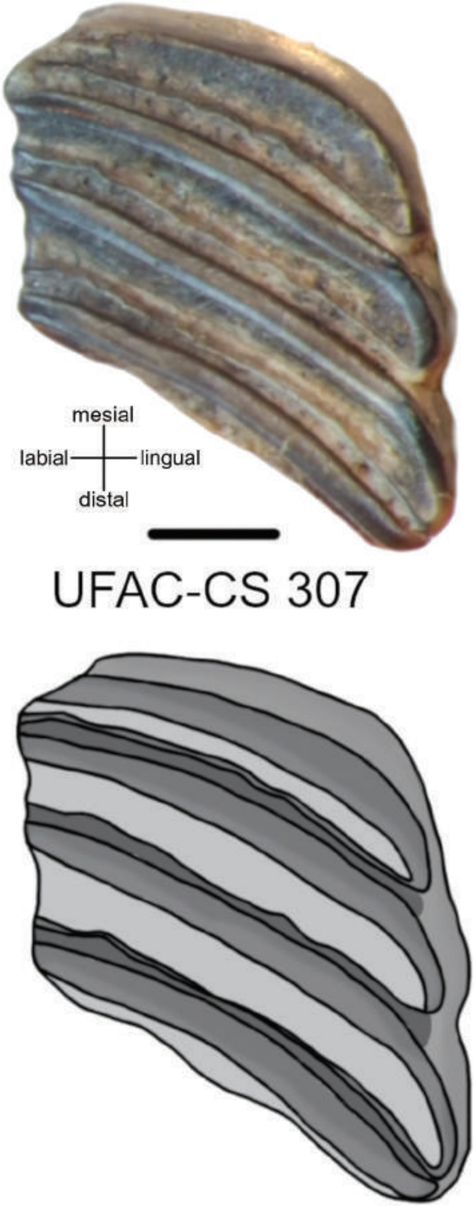

Figure 5. Occlusal view of the upper molar (UFAC-CS 307) of cf. *Pseudopotamarchus* from Envira River, State of Acre, Brazil. Scale bar = 1 mm.

is the widest, and the remaining lophs reduce progressively in width distally.

UFAC-CS 196 and UFAC-CS 361 are isolated right M1 or M2 (Figures 4B-C). They are similar to each other, but UFAC-CS 361 is quite damaged. Both teeth are pentalophodont. The first loph is not lingually connected to the others, while the others are lingually connected. They show a similar structure to the P4 described above. The first loph is shorter than the others, but this difference is not so evident as in the P4. For this reason, the M1-M2 are subrectangular in outline.

UFAC-CS 309 (Figure 4D) is a fragmented M3 with the occlusal surface damaged. It preserves the first two lophs and portions of the third and fourth. The lophs are oblique and slightly curved. It is not possible to observe the presence of crenulation in the distal enamel layer.

UFAC-CS 301 (Figure 4E) is a lower premolar, possibly of a young individual, judging by its poorly worn surface. It is composed of five quite obliquely (linguo-mesially) oriented lophids. The first lophid is almost mesio-distally oriented. Its distal face is formed by crenulated enamel. It is separated from the other lophids by a lingual flexid mesio-distally oriented. In the other lophids, there is no crenulation. Because the tooth is poorly worn, the lophids are connected to each other, and the flexi are not visible. The last lophid is fragmented.

UFAC-CS 189 and UFAC-CS 303 (Figure 4F-G) are lower molars (m3). UFAC-CS 189 shows the occlusal surface well preserved, but UFAC-CS 303 is damaged. They are pentalophodont, composed of oblique lophids with the mesial enamel layer thinner than the distal. The first four lophids are mesio-labially connected, while the fifth one is free. UFAC-CS 189 shows crenulations in the mesial enamel layer. However, in UFAC-CS 303 it is not visible due to the preservation.

cf. *Pseudopotamarchus* Kerber et al. 2016

(Figure 5; Table 1)

Referred specimens: UFAC-CS 307, fragmented left ?M1.
Provenance: Coqueiro locality – PRE 06 ('Ponto Rio Envira 06'; 08° 18′12.6"S and 70°26′39.9"W" W).
Description: The protohypsodont tooth is fragmented and preserves four lophs of similar width, obliquely oriented, with the lingual tips distally oriented. The lophs are separated by lingual flexa. It displays subrectangular outline. The mesial enamel layer is thicker than the distal. The distal enamel layer of the lophs shows tenuous crenulation.

Family NEOEPIBLEMIDAE Kraglievich 1926

Genus *Neoepiblema* Ameghino 1889

Neoepiblema sp.

(Figure 6; Table 1)

Referred specimens: UFAC-CS 315, left maxilla, with M1-M3; UFAC-CS 308, lower left molar (m1 or m2); UFAC-CS 312, lower left molar (m1 or m2).
Provenance: Coqueiro locality – PRE 06 ('Ponto Rio Envira 06'; 08° 18′12.6"S and 70°26′39.9" W).
Description: UFAC-CS 315 (Figure 6A) is a left maxilla preserving the molar teeth. The bone surface of this specimen is quite damaged. The M1 and M2 are composed of three lophs, obliquely (linguo-mesially) oriented, separated by two flexa of similar orientation. The labial and lingual surfaces are not preserved, and it is not possible to observe the connections between lophs. The M3 is tetralophodont, composed of oblique lophs separated by three flexa showing a progressive reduction in width from the first to the fourth loph. The lower molars (UFAC-CS 308 and UFAC-CS 312; Figure 6B-C) are euhypsodont and composed of three obliquely (linguo-mesially) oriented lophids separated by two flexi. The three specimens show loss of dental tissues on the extra alveolar portion of the cheek teeth (see below).

Discussion

A high diversity of extinct rodents has been reported from the Neogene sediments of the Solimões Formation (northern Brazil). The main exposures of this geologic unit are found along the Juruá, Acre, and Purus rivers, and some road cuts (Cozzuol 2006; Latrubesse et al. 2010). Coqueiro locality is the first studied assemblage from the Envira River, located in the central region of Acre, filling a gap in the distribution of vertebrate assemblages in the Acre region. In this paper, three groups of caviomorph rodents are

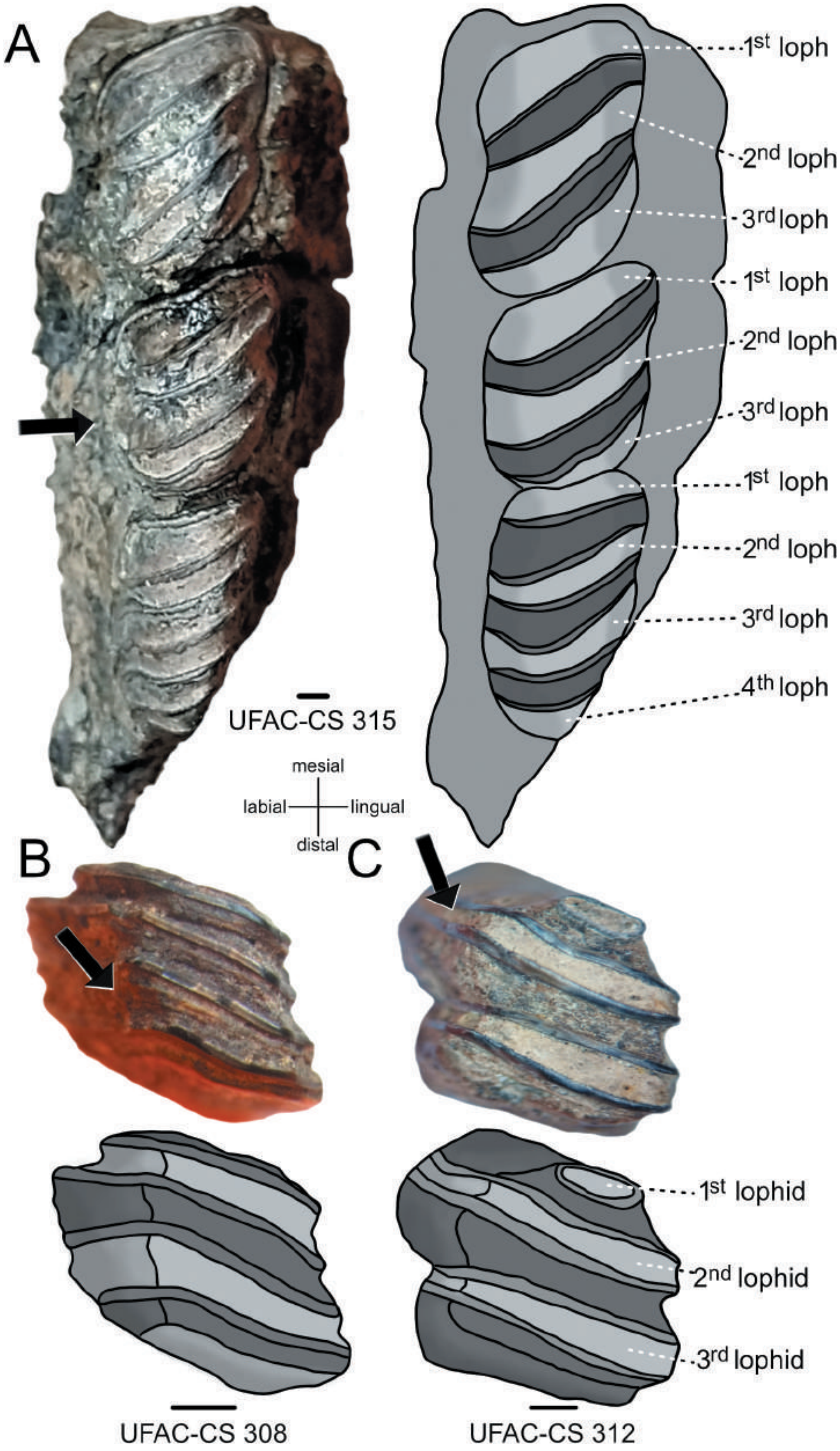

Figure 6. Occlusal view of the cheek teeth of *Neoepiblema* sp. from Envira River, State of Acre, Brazil. **A**. UFAC-CS 315, left maxilla with M1-M3. **B**. UFAC-CS 308, lower left molar (m1 or m2). **C**. UFAC-CS 312, lower left molar (m1 or m2). The arrows indicated the areas with loss of dental tissues. Scale bars = 1 mm.

Table 1. Measurements (in mm) of the analysed specimens. LLW: linguo-labial width, MDL: mesio-distal length.

Taxa/referred specimens			LLW	MDL
Cardiatherium sp.	UFAC-CS 299	Left M1 or M2	4.3	4.4
	UFAC-CS 354	Left M3	4.7	—
Potamarchus sp.	UFAC-CS 370	Left P4?	6.3	5.4
	UFAC-CS 196	Right M1 or M2	5.8	5.3
	UFAC-CS 361	Right M1 or M2	5.1	4.0
	UFAC-CS 309	Right M3	4.4	3.6
	UFAC-CS 301	Right p4	3.3	6.0
	UFAC-CS 189	Left m3	4.1	4.9
	UFAC-CS 303	Left molar	4.7	5.4
cf. *Pseudopotamarchus* sp.	UFAC-CS 307	Left ?M1	5.1	—
Neoepiblema sp.	UFAC-CS 308	Left m1 or m2	4.7	3.3
	UFAC-CS 312	Left m1 or m2	5.3	4.7
	UFAC-CS 315	Left M1	6.6	9.5
	UFAC-CS 315	Left M2	6.3	7.7
	UFAC-CS 315	Left M3	5.4	8.0

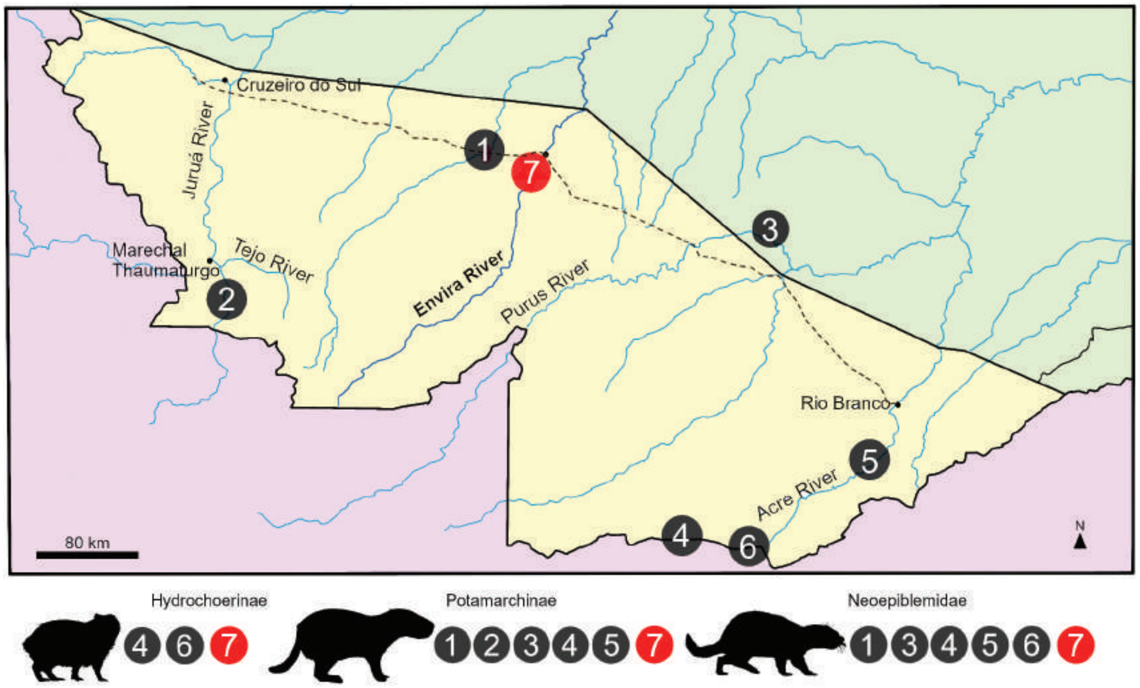

Figure 7. Main outcrops with records of hydrochoerine caviids, potamarchine dinomyids, and neoepiblemids (Frailey et al. 1986; Kerber et al. 2016, 2017a, 2018, 2019a). Localities: **1**. Morro do Careca locality, BR364; **2**. Cantagalo locality, Jurua River; **3**. Talismã locality, Purus River; **4**. Patos locality, Acre River; **5**. Niterói locality, Acre River; **6**. Cachoeira do Bandeira locality, Acre River; **7**. Coqueiro locality, Envira River.

studied: Caviidae (Hydrochoerinae), Dinomyidae (Potamarchinae), and Neoepiblemidae.

Hydrochoerines are identified as *Cardiatherium* sp. because the prisms (or lobes) of UFAC-CS 299 (especially the second one) are mesio-distally compressed and lanceolate, different from the cordiform morphology found in the coeval hydrochoerines *Caviodon* and *Cardiomys* (Vucetich et al. 2010, 2011; Vucetich and Pérez 2011). This specimen shows the prisms labially connected, different from the pattern observed in more derived taxa, such as *Phugatherium*, *Hydrochoerus*, and *Neochoerus* (Vucetich et al. 2015b). Despite the difference in size, which can be explained by ontogenetic variation, this tooth has a morphology similar to *Cardiatherium paranaense*. However, as it is an isolated tooth, it is not possible to confidently identify it at specific level. *Cardiatherium* has been previously reported in Argentina (Vucetich et al. 2005, 2012), Uruguay (Francis and Mones 1965), Venezuela (Linares 2004), and Brazil. In Brazil, previous records are restricted to localities in Juruá (Sant'Anna-Filho 1994) and Acre rivers (Frailey 1986; Kerber et al. 2017a) (Figure 7).

Dinomyidae is represented in Coqueiro locality only by potamarchines, the protohypsodont members of the group. Two taxa are recorded: *Potamarchus* and cf. *Pseudopotamarchus*. The current taxonomic framework of *Potamarchus* recognises three species: *P. murinus, P. sigmodon*, and the recently described *P. adamiae* (Burmeister 1885; Ameghino 1891; Kerber et al. 2016). The specimens studied here share the occlusal morphology pattern of *Potamarchus* – presence of protohypsodont cheek teeth, with lophs (ids) and complex patterns of crenulation. The presence/absence of crenulations has been employed to differentiate *P. sigmodon*, in which the trait is absent, from *P. murinus* and *P. adamiae* (Ameghino 1891; Kerber et al. 2016) (as well as the specimens here studied). However, Kerber et al. (2017a) described a specimen in which the m3 is erupting. The premolar, m1, and m2 have crenulations, but in the m3 (more recently erupted) they are not evident. Hence, the presence/absence of crenulations in the cheek teeth seems to be an ontogenetically variable trait instead a taxonomic character to differentiate *Potamarchus* species. The genus *Potamarchus* is recorded in Argentina (Burmeister 1885; Ameghino 1891; Nasif et al. 2013), Venezuela (Linares 2004; Carrillo-Briceño et al. 2019), Uruguay (Rinderknecht et al. 2010), and Brazil. In Solimões Formation, there are records from Acre (Frailey 1986; Kerber et al. 2016, 2017a), Juruá (Kerber et al. 2016, 2017a), and Purus rivers, and Morro do Careca locality (Kerber et al. 2017a) (Figure 7). The occlusal morphology of UFAC-CS 307 resembles the M1 of the enigmatic *Pseudopotamarchus villanuevai*, described by Kerber et al. (2016), Unlike *Potamarchus*, the tooth is longer, the lophs have similar size, and crenulations of the distal enamel layer are absent or are less complex. This taxon is endemic from the Late Miocene of western Amazonia, represented by fossils from the upper Acre and Juruá rivers (Kerber et al. 2016, 2017a).

The cheek teeth morphology and size of the neoepiblemids analysed here are compatible with the pattern found in *Neoepiblema*. However, as the specimens are quite damaged, it is not possible to identify the species confidently. The specimens assigned to neoepiblemids show loss of dental tissues. This pattern of morphological modification was described by Kerber et al. (2017b) and interpreted as evidence that they went through digestive processes before fossilisation. The modifications were observed in dozens of specimens from Solimões Formation. They consisted of loss of enamel and dentin corrosion in the extra-alveolar portion of the tooth. In most cases, the intra-alveolar portion does not present the same corrosion, indicating that the dentary bone and soft tissues protected the teeth from the acids of the digestive process. More studies are necessary to test this interpretation and, in case to confirm it, to identify the potential producer of this ichnofossil. Neoepiblemids have a scarce fossil record, restricted to Brazil, Argentina, Peru, and Venezuela (Vucetich et al. 2010; Carrillo and Sánchez-Villagra 2015; Tejada-Lara et al. 2015; Rasia and Candela 2018; Kerber et al. 2019a, 2019b). According to Kerber et al. (2019a), neoepiblemids from Solimões Formation are assigned to *N. acreensis, N. horridula*, and *Phoberomys* sp., and have been found in Purus and Acre rivers (Frailey 1986; Kerber et al. 2017a; Kerber et al. 2019a, 2019b) (Figure 7), and Morro do Careca locality (Kerber et al. 2017a).

Among the known localities of Solimões Formation, previously to our new records, the shared presence of hydrochoerine caviids, potamarchine dinomyids, and neoepiblemids in a single locality was exclusively found in the upper Acre River (Frailey 1986; Kerber et al. 2016, 2017a, 2022). The Coqueiro locality has not yet been dated by radiometric methods. Other localities with strata containing vertebrate fossils were probably deposited during the Late Miocene (Cozzuol 2006; Latrubesse et al. 2007; Negri et al. 2010). This age was initially estimated based on the fossiliferous content of the Solimões Formation (relative age), and recently corroborated by dating of detrital zircons in two localities, Niterói and Talismã, which indicated a time interval between 10.89 and 8.5 million years ago (Tortonian) (Bissaro-Junior et al. 2019). The stratigraphic range of the taxa fossils reported here in other localities of the Solimões Formation and other geological units in South America (Vucetich and Pérez 2011; Vucetich et al. 2010, 2011; Kerber et al. 2016, 2017a, 2019a,b; Pérez et al. 2017; Cerdeño et al. 2019; Carrillo-Briceño et al. 2019), suggest a similar age for this assemblage (Tortonian, Late Miocene).

Conclusion

In this work, we reported the first fossils of hystricognath rodents from the Coqueiro locality, Envira River. They were assigned to *Cardiatherium* sp. (Hydrochoerinae), *Potamarchus* sp., and cf. *Pseudopotamarchus* (Potamarchinae), and *Neoepiblema* sp. (Neoepiblemidae). Based on the temporal ranges of the taxa reported here, we suggest that the fossil-bearing levels of this locality were deposited during the Late Miocene. Finally, further fieldwork and the study of other vertebrates collected in this locality need to be carried out to increase knowledge about the fossiliferous content of the strata of the Solimões Formation that outcrops in the Envira River.

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