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## A new Late Miocene stem Octodontoid (Rodentia: Caviomorpha: Octochinchilloi) from the Solimões Formation (Brazil): paleobiogeographic implications

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ABSTRACT— Caviomorphs are the neotropical hystricognathous rodents (Ctenohystrica: Hystricognathi: Caviomorpha). Octodontoidea are today the richest and most speciose clade of caviomorphs. Their fossil record also reveals a wide array of extinct species, including *Acarechimys*, a taxon with a widespread South American distribution and extensive temporal range. This genus comprises at least five species documented in deposits ranging from the late Oligocene to the Middle Miocene. Here, we report the discovery of a new species of *Acarechimys* from Upper Miocene deposits of the Envira River (PRE06 outcrop), situated in the Acre State, western Brazilian Amazonia. The new species differs from the other species of the genus in having lower molars with a strong posterior arm of the metaconid, the presence of a mesostylid (usually prominent) and a neomesolophid forwardly directed and connected to the metalophulid I on m1 but not on m2–3, and the absence of posterior arm of the protoconid. This taxon represents the youngest known species of the *Acarechimys* lineage to date. Its occurrence in Western Amazonia strengthens support for the hypothesis that South American rodent lineages survived longer during the Neogene at low latitudes than in the southern regions of the continent.

## INTRODUCTION

Hystricognathous rodents of the Neotropics, i.e., Caviomorpha, are a fascinating mammal group because of their astonishing taxonomic and ecological diversity, which reflects a complex evolutionary history (e.g., Huchon & Douzery, 2001; Meredith et al., 2011; Opazo, 2005; Poux et al., 2006; Upham & Patterson, 2015). These rodents appear suddenly in the South American fossil record at the end of the Eocene epoch, at least from what we know from the available record, especially that of Peruvian Amazonia (e.g., Antoine et al., 2012; Boivin et al., 2019; Frailey & Campbell, 2004). By the early Oligocene, they had already diversified, with the first representatives of the crown groups (Antoine et al., 2021; Arnal et al., 2020, 2022; Assemat et al., 2019; Bertrand et al., 2012; Boivin et al., 2017a,b, 2018, 2019, 2022; Kerber, 2017; Vucetich et al., 2010a). Present-day caviomorphs comprise 266 species, structured into two major clades and four superfamilies (e.g., Boivin et al., 2019; D'Elía et al., 2019; Mammal Diversity Database, 2024; Upham & Patterson, 2015): i) Erethicavioi Boivin, 2019 (in Boivin et al., 2019) grouping Caviioidea Fischer de Waldheim, 1817 (e.g., guinea pig and related forms) and Erethizontoidea Bonaparte, 1845 (New World porcupines), and ii) Octochinchilloi Boivin, 2019 (in Boivin et al., 2019) with Chinchilloidea Bennett, 1833 (chinchilla and pacaranas) and Octodontoidea Waterhouse, 1839 (e.g., spiny rats and related forms). The superfamily Octodontoidea includes the extant families Abrocomidae, Echimyidae, Octodontidae and Ctenomyidae, plus extinct lineages (Arnal & Vucetich, 2015; Candela, 2016; Boivin et al., 2019; D'Elía et al., 2019; Verzi et al., 2016). This is the richest and most diverse clade among Caviomorpha, both taxonomically and phenotypically through time (e.g., Verzi et al., 2017; Woods & Kilpatrick, 2005).

Dental morphology has proven to be particularly important for understanding the diversity and phylogeny of caviomorph rodents. Teeth are indeed one of the most common sources of information in the fossil record, but they also provide patterns of transformation over time, which are sources of macroevolutionary and adaptive information. According to Boivin et al. (2019), among the main dental features that characterize (at least in part) Octodontoidea are the presence of hypsodont, mesodont or brachydont teeth, with slightly or strongly oblique lophids, and dP4/dp4 retention. On upper teeth, octodontoids have a large labiodistal cusp (displaced mesostyle sensu Boivin & Marivaux, 2020), tend to lose the metacone, and generally lack the metaloph (both structures may be indistinct/lost, subsumed within the posteroloph; e.g., Boivin & Marivaux, 2020). The absence of the neomesolophid and mesostylid on the dp4 and lower molars is frequent, as well as the reduction of the posterior arm of the metaconid and protoconid, and the presence of accessory cristids.

Besides the great taxonomic diversity of extant octodontoid species, the South American fossil record also reveals a wide array of extinct species. In addition to the crown Octodontoidea, several stem lineages have been described (e.g., Arnal & Vucetich, 2015). This is the case of *Acarechimys* Patterson in Kraglievich, 1965, a rodent with a widespread

geographic distribution (from southern Argentina to Colombia) and temporal range (late Oligocene–Middle Miocene) (Verzi et al., 2017; see Arnal et al., 2017 and references therein; McGrath et al., 2023). Based on our current knowledge and interpretation of the fossil record, this group likely originated in Patagonia during the late Oligocene and diversified in this region during the Early Miocene–Middle Miocene interval (Arnal et al., 2017). Following Arnal et al. (2017), the genus *Acarechimys* includes at least five species: *A. leucothaeae* Vucetich, Dozo, Arnal, Pérez, 2015 (oldest-known species, late Oligocene, Argentina), *A. minutus* (Ameghino, 1887) [Early–Middle Miocene, Argentina, Bolivia and Chile (McGrath et al. 2023)], *A. minutissimus* (Ameghino, 1887) (Early–Middle Miocene, Colombia, Argentina and Bolivia), *A. gracilis* (Ameghino, 1891) (Early Miocene, Argentina), and *A. constans* (Ameghino, 1887) [Early Miocene, Argentina and Chile (McGrath et al. 2023)]. Arnal et al. (2017) considered *Acarechimys* as stem-octodontoid, while Verzi et al. (2017), in contrast, proposed a different composition of the genus and considered that *A. leucothaeae* and *A. minutissimus* as part of Octodontidae, and *A. minutus*, *A. constans*, *A. pulchellus* (= *A. gracilis* in Arnal et al., 2017), and *A. pascuali* (= *A. constans* in Arnal et al. 2017) as part of Abrocomidae. Furthermore, Verzi et al. (2017) erected a new genus, *Ameghinomys*, in which they included the species *Am. constans*. Hence, the genus *Acarechimys* constitutes a highly complex group of species that requires further analyses.

The Miocene record of caviomorphs in South America is extensive. The fossil-bearing localities display an abundance of genera and species of rodents, mainly in medium and high latitudes (Argentina [e.g., Busker et al., 2017; Deschamps & Tomassini, 2016; Esteban et al., 2014; Kramarz, 2001; Nasif et al., 2013; Piñero et al., 2021a; Rasia & Candela, 2018; Vucetich 2010b; Vucetich & Kramarz, 2003], Bolivia [Croft et al., 2011] and Chile [e.g., Croft et al. 2021, Flynn et al., 2008; McGrath et al., 2022, 2023, Solorzano et al., 2021]). At low latitudes, the main locations are in Colombia (e.g., Urrea-Barreto et al., 2023; Walton, 1990, 1997), Peru (e.g., Boivin et al., 2021; Tejada-Lara et al., 2015), Venezuela (e.g., Carrillo-Briceño et al., 2021), and Brazil (e.g., Fontoura et al., 2022; Kerber et al., 2017a). The Solimões Formation in northern Brazil has yielded a great diversity of Late Miocene vertebrates (see Hsiou et al., 2022 for a review), among them caviomorphs are one of the most diverse groups of mammals found there. However, the octodontoid (or stem-octodontoid) record has proven to be/remain scarce, as is also the case for other small mammals (e.g., Campbell et al., 2006; Kerber, 2017; Kerber et al., 2017b). Some studies mentioned the presence of *Acarechimys* in the Solimões Formation, but no details were provided (e.g., Campbell et al., 2006; Frailey, 1986; Sant’Anna, 1994). In 2017, Arnal et al. suggested that the fossils found in the Late Miocene of Amazonia (Madre de Dios and Pebas formations) could potentially belong to an unidentified species related to *Acarechimys*.

Recently, a new rodent assemblage including neoepiblemid and dinomyid chinchillids, together with caviid cavioids, was reported from the locality PRE06 of the Envira River in Acre State of Brazilian Amazonia (Fontoura et al., 2022; Fig. 1). Several remains of small caviomorphs have been collected in this site, which are studied here. In this report, we aim i) to describe a

new fossil interpreted as a new species of the stem octodontoid *Acarechimys* from the locality PRE06, Envira River, Acre, Brazil (Upper Miocene), and ii) to discuss the biogeographic implications of this discovery.

## MATERIALS AND METHODS

### Geological settings

The Solimões Formation, deposited in the Acre Basin situated in western Brazil, has yielded a great diversity of vertebrate fossils since the mid-19th century (Chandless expedition [1866], see Agassiz & Agassiz, 1868; Cozzuol, 2006; Latrubesse et al., 2007; see Hsiou et al., 2022 for a review). Fossil-bearing localities from this formation were recently dated, revealing maximum ages of deposition within the Tortonian, i.e., Upper Miocene (Niterói, ~8 Ma, and Talismã, ~10 Ma; Bissaro-Júnior et al., 2019) (but see Kerber et al. 2017a; Marivaux et al., 2023; Ribeiro et al., 2013). Mammals are among the most diverse fossils found there, including bats, cetaceans, litopterns, marsupials, notoungulates, primates, rodents, sirenians, and xenarthrans (e.g., Campbell et al., 2006; Fontoura et al., 2022; Frailey, 1986; Kerber et al., 2014, 2016, 2017a,b, 2018; Negri et al., 2010; Ribeiro et al., 2013; Sant’Anna, 1994; Stutz et al., 2023). In addition, fossil remains of birds, crocodylians, chelonians, fishes, amphibians, invertebrates, ichnofossils, and plants have also been documented (e.g., Cozzuol, 2006; Muniz et al., 2021, 2022; Rodrigues et al., 2016; Silva & Negri, 2016; Souza et al., 2021).

### Collection and analysis

The specimens studied here were collected during fields trip in 2019 and 2022 at the PRE06 outcrop (08°18’12.6”S and 70°26’39.9”W; Fig. 1), called “Coqueiros”, Envira River, Feijó city, State of Acre, Brazil. The specimens UFAC-CS 261, UFAC-CS 356, UFAC-CS 456, UFAC-CS 460, UFAC-CS 462, UFAC-CS 463 and UFAC-CS 702 were found at the level “Point B” of the outcrop (Fig. 2A, B), and the specimens UFAC-CS 250, UFAC-CS 367, UFAC-CS 373, UFAC-CS 426, and UFAC-CS 431 were found at the “Point C” (Fig 2C, D).

The Points B and C in section belong to the same stratigraphic horizon/level. The fossil-bearing locality consists of a ~50 cm-thick (Point B) and ~10 cm-thick (Point C) layer of slightly indurated conglomerate, composed of carbonate concretions and fossil fragments (currently under study; Stutz et al., 2023). We excavated and collected sediment of these levels. Gross sediments were processed by wet screening with 2 mm, 1 mm then 0.6 mm meshes, in situ with the water of the Envira River, then at the Paleontology Laboratory of the *Universidade Federal do Acre* (Cruzeiro do Sul, Acre, Brazil) and *Museu de Ciências Naturais – Seção de Paleontologia* (Porto Alegre, Rio Grande do Sul, Brazil). Ultrasonic and manual cleaning were employed to clean the specimens. The specimens are permanently housed in the collection of the Paleontology Laboratory of the *Universidade Federal do Acre*, Floresta campus, Cruzeiro

do Sul, Acre (UFAC-CS). The UFAC-CS 261, UFAC-CS 356, UFAC-CS 367, UFAC-CS 373, UFAC-CS 431 UFAC-CS 456 and UFAC-CS 702 specimens were scanned, with a resolution of 7.1  $\mu\text{m}$ , using a high-energy  $\mu\text{CT}$ -scanning station SkyScan1173 from the technical facilities of the *Instituto de Petróleo e dos Recursos Naturais, Pontifícia Universidade Católica do Rio Grande do Sul*, Brazil. The raw scan data were exported from the scanner computer in TIFF format. Segmentation and 3D surface rendering were performed using Avizo™3D software (Visualization Sciences Group, 2022).

3D Slicer software (Fedorov et al., 2012) was employed to visualize the morphological alterations in enamel and dentine resulting from occlusal tooth wear, adapting the methodology of Skandalos & van den Ostende (2023). For each tooth, cross sections of the molars were created parallel to the occlusal axis, with a spacing of seven to ten slices between each cross-cut, simulating the tooth wear of brachydont teeth (Koenigswald, 2016). The measurements (Table 1) were obtained using the Image J software (Rueden et al., 2021), including the maximum mesio-distal length (mdl) and the maximum width (mw).

## Comparisons

The specimens were described and compared firsthand with specimens of *Acarechimys* (Taxonomic determination following i) Arnal et al. [2017], and ii) Verzi et al. [2017]; Table S1) as well as bibliographic sources on extinct and extant octodontoids (e.g., Antoine et al., 2007; Arnal et al., 2014, 2017; Boivin et al., 2021; Croft et al., 2011; Kramarz & Bellosi, 2005; Vucetich et al., 2010b, 2015; Walton, 1997). We followed Boivin & Marivaux (2020, and the literature cited therein), for dental nomenclature; and Pérez (2010, and the literature cited therein) and Cox & Jeffery (2015), for mandibular nomenclature.

**Institutional Abbreviations**— **MACN**, *Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, Argentina; **MLP**, *Museo de La Plata*, Argentina; **UFAC**, *Universidade Federal do Acre*, Brazil; **UFAC-CS**, *Universidade Federal do Acre – Campus de Cruzeiro do Sul*, Brazil.

## SYSTEMATIC PALEONTOLOGY

RODENTIA Bowdich, 1821

HYSTRICOGNATHI Tullberg, 1899

CAVIOMORPHA Wood & Patterson in Wood, 1955

OCTOCHINCHILLOI Boivin in Boivin, Marivaux & Antoine, 2019

*ACARECHIMYS* Patterson in Kraglievich, 1965

*ACARECHIMYS HUNIKUINI* sp. nov.

(Figs. 3, 4, 5 and 6)

**Holotype**— UFAC-CS 261, left dentary with dp4–m3 (Fig. 3).

**Etymology**— “Huni Kuin” is the name of the indigenous people that inhabit the region of the outcrop PRE06 (*Coqueiros*) on the Envira River, Western Amazonia.

**Referred Specimens/Paratypes/etc.**— UFAC-CS 460, UFAC-CS 462 (right fragmentary dp4s; Fig. 5A, B); UFAC-CS 456, UFAC-CS 367 (left m1s; Fig. 5C, D); UFAC-CS 356 (left m2; Fig. 5E); UFAC-CS 426 and UFAC-CS 250 (left m3s; Fig. 5F, G); UFAC-CS 373, and UFAC-CS 463 (left m3s?; Fig. 5I, J); UFAC-CS 431 (right m3; Fig. 5H); UFAC-CS 702 (right m3?; Fig. 5K).

**Diagnosis**—This species displays a mandible with brachydont teeth, pentalophodont dp4s and tetra- to trilophodont molars. It is larger than *A. leucotheae*, *A. minutissimus*, similar in size to *A. gracilis* and *A. minutus*, and smaller than *A. constans* (Fig. 4; Table 1). Lower molars are characterized by a strong and long posterior arm of the metaconid, followed distally by a usually well-defined mesostylid, unlike in *A. constans*, *A. leucotheae*, and *A. minutissimus*, in which these dental traits are absent. Lower molars also present a curved neomesolophid forwardly directed, being connected to metalophulid I in m1, and remaining mesially free but weak or absent in m2–3, unlike other species of *Acarechimys* (except the specimen MACN-A 237). The m3 shows variation in this character, with the neomesolophid being less distinct. The posterior arm of protoconid (= metalophulid II *sensu* Arnal et al., 2017) is always absent on lower molars, unlike in *A. constans*, *A. gracilis*, *A. leucotheae*, and *A. minutus* (in which it is present only on m1–m2). It does not have terraced molars and the flexids are more closed than in *A. leucotheae*. The dp4 has a third transverse cristid (mesolophid or mesolophid + neomesolophid) well-developed, unlike in *A. gracilis* and *A. minutus*. As well, the posterior arm of protoconid is well developed in this locus, unlike in *A. minutissimus* and *A. leucotheae* (variably developed in *A. constans* and *A. minutus*), except in UFAC-CS 460, in which is shorter. The mesial ectolophid is less oblique and less separated to the protoconid in dp4 than in *A. leucotheae*. The lower incisors are laterally compressed, unlike in *A. constans* and *A. gracilis*.

**Locality, Horizon, and Age**— PRE06 locality, “Coqueiros”, Envira River, Feijó city, Solimões Formation, Acre, Brazil (08°18′12.6” S and 70°26′39.9” W), Western Amazonia. Late Miocene (see Fontoura et al., 2022).



## DESCRIPTION AND COMPARISONS

### Dentary

**General Comments**— The left dentary is partially preserved, lacking the anterior (mesial to the dp4) and posterior (distal to the coronoid process) portions (Fig. 3). In lateral view, the notch for the insertion of the tendon of the muscle zygomaticomandibularis, pars infraorbitalis is at the level of the dp4–m1. It is shallower than the masseteric fossa (Fig. 3D, F). Posteriorly, the masseteric crest is oriented posteroventrally. Posteriorly to this crest, the masseteric fossa is deeper than in other species of *Acarechimys*. It is located slightly more anteriorly in the dentary, unlike *A. constans* and resembling the condition displayed by *Acarechimys gracilis* (= *Acarechimys pascuali* Verzi, Olivares & Morgan, 2017, partim., pp. 414–415; 417; 42; see Arnal et al., 2017). The straight lateral crest is located anteroventrally to the basis of the coronoid process, which is located laterally to the m3, like in *Acaremys murinus*, *Prospaniomys priscus* and MACN-A 1896 (see Verzi et al., 2017:fig. 6).

Lower teeth are brachydont, pentalophodont (dp4) and tetra- trilophodont (m1–3), with straight toothrow, a tooth arrangement distinct from the convex pattern characterizing some other octodontoids, such as *Protacaremys prior* and *Echimys chrysurus* (Arnal et al., 2014, 2017). As expected, the dp4 is the most worn tooth, followed by m1, m2 and then m3, and as such corroborates the hypothesis of dp4 retention (Fig. 3A, B). The m2 is the largest tooth in the row, as in all species of *Acarechimys* (Arnal et al., 2017). All teeth present four main cuspids: entoconid, metaconid, protoconid and hypoconid (Fig. 3A–C). The posterior arm of the metaconid is present in all loci, being more developed in dp4 than in m1, m2 and m3, progressively, unlike in *Acarechimys constans*, *A. leucothaeae*, and *A. minutissimus*, in which this structure is absent (Arnal et al., 2017). A neomesolophid stemming from the mesostylid is present in the molars (variably present in m2–3). It is arched and forwardly directed, connected to the metalophulid I in the m1, whereas it is more reduced and remains mesiolabially free in m2 and m3. This structure in m1–3 is absent in other species of *Acarechimys* (except the specimen MACN-A 237 [type of *A. minutus*], which has neomesolophid in m1–3 associated with others characters [e.g., presence of posterior arm of protoconid]; Table 2).

**dp4**— The dp4 has an oval outline and is longer mesiodistally than wide (Fig. 3A–C). It has five lophids: metalophulid I, second transverse cristid (posterior arm of the protoconid + neomesolophid), third transverse cristid (mesolophid or mesolophid + neomesolophid), hypolophid and posterolophid (Figs. 3A–C, 5A, B). The metalophulid I is curved and connects labially to the protoconid and lingually to the metaconid, which shows a cristid (i.e., metaconid cristid) as wear progresses (UFAC-CS 261 and 460; Figs. 3A, B, 5A). On the lingual margin of the crown, the metaconid has an elongated and slightly curved posterior arm joining to the anterior arm of the mesostylid, which can be long as in UFAC-CS 462 (Fig. 5B). The third transverse cristid (mesolophid or mesolophid + neomesolophid) connects distolabially to the ectolophids and mesiolingually to the mesostylid. In UFAC-CS 462 (Fig. 5B), the third cristid is

composed lingually of a long neomesolophid stemming from the mesostylid and labially of a tiny and thin mesolophid. The UFAC-CS 462 and 460 (right dp4s) preserve only this mesial region.

The ectolophid is composed of two parts: the distal ectolophid, a short branch that connects distolingually to the hypolophid, and the mesial ectolophid, a long and curved branch that connects mesially to the protoconid. The hypolophid is straight or slightly curved, transverse, and connected to the entoconid. Lingually, the entoconid has an anterior arm, which in the recorded stages of occlusal wear, connects to the third transverse cristid and mesostylid (UFAC-CS 261, Fig. 3A, B; UFAC-CS 460, Fig. 5A). The entoconid also displays a subtle posterior arm, almost reaching the posterolophid distally. In the mesiolabial border of the crown, the posterior arm of the protoconid, distolingually oriented, can be short (UFAC-CS 460; Fig. 5A) or long (UFAC-CS 261 and 462; Figs. 3A, B, 5B) and is slightly or strongly connected to the third transverse cristid, respectively. In UFAC-CS 460, the mesial ectolophid and protoconid are fused (Fig. 5A). In the most distal region is the posterolophid, long and curved, which connects to the hypoconid labially and reaches the lingual side of the tooth. The hypoconid also displays an anterior arm, connected to the distal ectolophid and hypolophid.

Based on the three collected dp4s documenting different stages of wear (Figs. 3A, B, 5A, B), it can be inferred that the dp4 of *A. hunikuini* sp. nov. has probably three flexids (open) and three fossettids (i.e., flexids closed) at an early stage of wear. Distally, there would be the i) metaflexid, deeper and oval, between the posterolophid, anterior arm of the hypoconid and the hypolophid, followed by the ii) hypoflexid, in the labial side, between the hypoconid and the ectolophid (it seems to close as tooth wear progresses; Fig. 6); the iii) distal mesoflexid, between the hypolophid and the third transverse cristid (which closes at more advanced stages of wear, as seen in UFAC-CS 261 and 460 (Figs. 3A, B, 5A); the iv) mesial mesofossettid, shallower, between the third transverse cristid, mesial ectolophid and the posterior arm of the protoconid; and the v) anterofossettid, mesially, between the posterior arm of the protoconid and the metalophulid I, as seen in UFAC-CS 462 (Fig. 5B). As tooth wear progresses (at the beginning of wear, as in UFAC-CS 460, or in more advanced stages of wear, as in UFAC-CS 261), this fossettid splits into two small fossettids (Fig. 3A, B; Fig. 5A; Fig. 6), followed by the closure of the lingual fossettid, as seen in UFAC-CS 460 (Figs. 5A and 6A).

**Lower molars**— They have similar occlusal patterns but show polymorphism for some characters, as well as variations in wear (as mentioned above for UFAC-CS 261). Mesially, in occlusal view, the protoconid and metaconid are linked by a complete metalophulid I, which is straight and often thin in its labial part, near the lingual aspect of the protoconid. Lingually, the metaconid displays a short, high and strong posterior arm, connected to a mesostylid, which is usually prominent (e.g., UFAC-CS 456, 373 and 702; Fig. 5C, I, K), but which can be more crestiform (e.g., UFAC-CS 431; Fig. 5H) until it is no longer distinct, probably fused with the posterior arm of the metaconid (e.g., UFAC-CS 426; Fig. 5F). This cuspid strongly connects to the anterior arm of the entoconid in advanced tooth wear, as seen in UFAC-CS 367, 356 and 373 (Fig. 6B, E, J). The most significant difference between the lower molars is the configuration

of the structure we interpret as a neomesolophid. The latter is a short, forwardly arched branch, that projects mesiolabially from the mesostylid toward the metalophulid I (Figs. 3A–C and 5C–K). In m1, it is curved and connects to the metalophulid I, as seen in UFAC-CS 261 (Fig. 3A, B), 456 (Fig. 5C) and 367 (Fig. 5D). It is complete in UFAC-CS 261 and 456, while it is not connected to the mesostylid in UFAC-CS 367. On m2, it is shorter, appearing as a small, arched cristid, forwardly directed, and that does not reach the metalophulid I (Fig. 3A, B, 5E). This structure is visible depending on tooth stages of wear (Fig. 6E, F). On m3, the neomesolophid can be present, reduced to a tiny lophid depending on the stage of wear (UFAC-CS 261; Figs. 3A, B, 6G), or absent (UFAC-CS 373, 426, 431 and 702 Figs. 5F, H–K, 6H–J). Within each species of *Acarechimys* the mesostylid also is present or absent (personal observation), except in *A. leucothaeae*, in which it is absent. However, the latter species is documented by one specimen (Vucetich et al. 2015), which does not permit to evaluate its intraspecific variation.

From the protoconid to the middle point of the labial margin of the molars extends the ectolophid, a long and curved cristid on which the anterior arm of the hypoconid is connected (Figs. 3A, B, 5C–K) in early stage of wear. When the teeth are pristine, there is no strong anterior arm of hypoconid and the teeth seem taeniodont. On m3, the connection between the ectolophid and the hypoconid occurs later, observed at advanced stages of wear, as seen in Figures 3, 5 and 6. The posterolophid is long and curved, connects to the hypoconid labially. Lingually, on the m1, it reaches the posterior arm of the entoconid (Figs. 3A, B, 5C, D). In the m2–3, the posterolophid tends to reach the entoconid only in advanced tooth wear (Figs. 3A, B, 5E–K, 6E–J).

In lower molars of *A. hunikuini* sp. nov., the flexids (open) and fossettids (closed) vary according to the tooth wear. Mesially, there is the mesoflexid + anteroflexid. On m1, this flexid can be split into a small fossettoid, delimited by the metalophulid I and neomesolophid (which disappears with the wear), and a larger flexid (which closes with wear progress; Figs. 3A, B, 5C, 6C, D). In the m2, this division can appear as tooth wear progresses (Fig. 6E), while in m3 there is no division of the mesoflexid + anteroflexid (Fig. 6G–J). Labially, the hypoflexid remains open regardless of the advanced tooth wear. The metaflexid is the distal flexid, remaining open lingually late into the stages of wear in the m3 (only closed in advanced tooth wear) and gradually tending to be closed earlier in m2 and m1 (Fig. 6B–J).

In occlusal view, the m1–2 has a quadrangular shape (Figs. 3A, B, 5C–E). The m3 has a slightly smaller metaflexid than the mesoflexid + anteroflexid, forming a triangular shape in occlusal view (Figs. 3A, B, 5F–H, K). This characteristic is absent in the specimens UFAC-CS 373 (Fig. 5I), 463 (Fig. 5J) and 702 (Fig. 5K), which have a more quadrangular shape. However, these specimens have other features usually assigned to m3 (e.g., presence of mesial/absence of distal vertical contact facets). Therefore, we assigned them to m3 with ambiguities (i.e., m3?).

The specimens UFAC-CS 373 (Fig. 5I), 463 (Fig. 5J), and 702 (Fig. 5K) are small individuals in comparison with the holotype (UFAC-CS 261; Fig. 3A, B).

## DISCUSSION

### Morphology and taxonomic remarks

In this paper, we described new dental remains of a caviomorph rodent from Upper Miocene deposits of the Solimões Formation, Envira River, Brazil (Western Amazonia). The use of computed tomography (CT) was employed to improve the visualization of structures and thus to enhance taxonomic identification, particularly in small materials. The analysis of virtual reconstructions also permitted the estimation of occlusal tooth wear. This enabled the comparison of specimens exhibiting disparate stages of wear, rendering them at the same stage digitally (Skandalos & van den Hoek Ostende, 2023). The application of these techniques is of particular significance in the context of fossil materials, where the presence of all ontogenetic stages is not a common occurrence.

These fossils document a new species of the octodontoid genus *Acarechimys*. The material is assigned to *Acarechimys* based on the combination of several features, such as (Arnal et al., 2017): i) brachydont cheek teeth; clearly evident cuspids and thin cristids separated by wide flexids; ii) retention of dp4 throughout life; iii) lower dp4 with variably developed posterior arm of protoconid, and third transverse cristid united near the metaconid; iv) long lower incisor, with its distal end located posterior to m3; and v) well-developed masseteric crest of the mandible and masseteric fossa moderately to very deep anteriorly.

The traits that differentiate the new material from other related taxa are: small size (unlike *Paralonchothrix*, *Paulacoutomys*, and *Plesiacarechimys*); presence of brachydont teeth (unlike e.g., *Acaremys murinus*, *Eumysops*, *Protacaremys prior*, and *Prospaniomys priscus*); straight tooth row (unlike e.g., *Echimys chrysurus* and *Protacaremys prior*); retention of deciduous premolar (unlike e.g., *Acaremys murinus* and *Paulacoutomys paulista*); m2 larger than m3 (unlike e.g., *Acaremys murinus*); thinner crests/cristids than the flexi/ids (unlike e.g., *Adelphomys candidus* and *Spaniomys* spp.); presence of the posterior arm of metaconid on lower molars (unlike e.g., *Dudumus*, *Caviocricetus*, *Deseadomys*, and *Metacaremys*); presence of a complete posterior arm of protoconid in dp4 (unlike e.g., *Acaremys murinus*, *Metacaremys*, *Pampamys*, and *Ullumys*) (Arnal et al., 2014, 2017; Boivin et al., 2021; Olivares et al., 2017; Olivares et al., 2012; Piñero et al., 2021a,b; Vucetich & Verzi, 1996; Vucetich et al., 1993; Wood & Patterson, 1959).

In addition to the diagnostic characters of the genus *Acarechimys* found on this new fossil material (see above), which allow it to be assigned to this genus, a combination of other dental characters in lower molars is unique to *A. hunikuini* sp. nov. (autapomorphic). This is particularly demonstrated by i) the presence of a strong posterior arm of the metaconid, ii) the development of a mesostylid and a neomesolophid (connected to the metalophid I in m1

and disconnected in m2–3), and iii) by the absence of posterior arm of protoconid (= metalophulid II in Arnal et al., 2017).

As mentioned in the Introduction, *Acarechimys* represents a complex group of species that necessitates a phylogenetic review. Assuming the inclusion of this new species in *Acarechimys* would imply a lineage duration of over 15 million years, spanning from the late Oligocene to the Late Miocene. Accordingly, a comprehensive phylogenetic analysis of the clade should provide a better understanding of the diversification and temporal variation of the broader group encompassing the species currently assigned to the genus.

### Paleobiogeographic relevance

Based on the current understanding of the South American fossil record, the *Acarechimys* clade seems to have originated in Patagonia during the late Paleogene, as the oldest species known thus far is the late Oligocene *Acarechimys leucothecae* from Cabeza Blanca, Chubut Province, Argentina (Vucetich et al., 2015). Several other species of the genus are known in Lower Miocene deposits of Argentina, with the peak of diversity of *Acarechimys* suggested by Arnal et al. (2017) at the end of the Early Miocene, with the occurrence of *A. constans* (Santa Cruz Province, Santa Cruz Formation, Argentina, and Pampa Castillo, unnamed formation, Chile [see Arnal et al., 2017 and references therein; McGrath et al., 2023]); *A. gracilis* (Chubut, Sarmiento Formation [Vucetich et al., 2010b] and Santa Cruz provinces, Santa Cruz Formation, Argentina [see Arnal et al., 2017 and references therein]); *A. minutissimus* (Santa Cruz Province, Santa Cruz and Pinturas Formation, Argentina [Kramarz & Bellosi, 2005] and Pampa Castillo, unnamed formation, Chile [see Arnal et al., (2017) and references therein; McGrath et al., 2023]); and *A. minutus* (Santa Cruz Province, Santa Cruz Formation, Argentina, and Pampa Castillo, unnamed formation, Chile [see Arnal et al., 2017 and references therein; McGrath et al., 2023]) (Fig. 7). These records seem to be restricted to Patagonia. There are some previous records of *Acarechimys* sp. from Chile (unnamed formation, Pampa Castillo, Flynn et al., 2002; McGrath et al., 2023; and Chucal Formation, northern Chile, Croft et al., 2007), however, there is no further information available on them.

In the Middle Miocene, the occurrence of the genus is restricted to species of *A. minutissimus* (Neuquén Province, Collon Curá Formation, Argentina and La Venta, Villavieja Formation, Colombia [Walton, 1997] [see Arnal et al., 2017 and references therein; Croft et al., 2011]); and *A. minutus* (Neuquén Province, Collón Curá Formation, Argentina and Quebrada Honda, unnamed formation, Bolivia [see Arnal et al., 2017 and references therein; McGrath et al., 2023]). Some previous records of *Acarechimys* sp. have been reported from the Middle Miocene in Chile (Curá Mallín Formation, Flynn et al., 2008), Colombia (La Venta, Walton, 1997), Bolivia (Quebrada Honda, Croft et al., 2011), and Peru (unnamed formation, Fitzcarrald Arch, Tejada-Lara et al., 2015). In addition to the Patagonian records of *Acarechimys*, there is also an expansion of the genus to extra-Patagonian regions.

There are also previous mentions from Late Miocene in Peru (Antoine et al., 2016; Campbell et al., 2006) and Argentina (Catamarca Province, northwestern Argentina; Esteban et al., 2014). However, because these specimens are very few isolated remains (most with significant occlusal wear), an accurate taxonomic identification is not possible. We do not exclude the presence of this group in these localities, but further studies should be carried out to understand these records.

In summary, the genus *Acarechimys* emerged at the end of the Oligocene and diversified in the Early Miocene, with its occurrence almost restricted to the Patagonian region (Arnal et al., 2017). In the Middle Miocene, the lineage shows a tendency to spread towards the north of South America, reaching Colombia (see below; Fig. 7). Here, we report the presence of a new representative of the genus, *Acarechimys hunikuini* sp. nov., in Upper Miocene deposits of Western Amazonia (Acre, Brazil). This species indicates that the *Acarechimys* lineage reached the Late Miocene before disappearing, remaining only in the extra-Patagonian region. This finding further supports the hypothesis that rodent lineages survived much longer in tropical regions than in southern South America (Carrillo-Briceño et al., 2021; Kerber et al., 2017a; Vucetich et al., 2010c), a pattern that has been documented in octodontoids, hydrochoerines, and neopiblemids (Vucetich et al., 2010c). This resilience is likely attributed to the presence of more stable conditions (persistence of fluvial environments under warm conditions) than in the austral region of the continent, which could corroborate the hypothesis of ‘*cradle and museums*’ (Carrillo-Briceño et al., 2021; Vucetich et al., 2010c). Nevertheless, it is important to consider that the absence of *Acarechimys* for the late Oligocene–Middle Miocene in northern South America (changing the origin and dispersion of the group) or in Late Miocene in southern South America (changing the dispersion hypothesis) could be due to a lack of evidence resulting from sample selection bias. This possibility should be considered when examining the origin and dispersal of the group.

The northward dispersion also corroborates the presence of an ecological corridor between southern and northern South America. According to Kerber et al. (2017), Negri et al. (2010) and Walton (1997), the ecological corridor may have occurred during the Late Miocene. However, the evolutionary history of *Acarechimys* dispersal to northern South America possibly began in the end of the Early Miocene. This paleobiogeographic connection was a continuous with similar paleoenvironments (Kerber et al., 2017a; Novillo & Ojeda, 2014; Walton, 1997), which allowed the dispersion and inter-migration. However, it is worth noting that evidence of rodent dispersion, according to Walton et al. (1997), is mostly based on high-crowned and large species, such as some dinomyids (*Eumegamys* and *Gyriabrus*), *Phoberomys* and Hydrochoeridae (see Walton, 1997 and references therein; Negri et al., 2010).

The evolution of the Neogene rodents (and faunal in general) in the Neotropics is closely linked to the dynamics of the Pebas megawetland complex. This ecologically permeable biogeographical system in tropical South America created favorable conditions for the adaptive radiation of endemic taxa (Cozzuol, 2006; Hoorn et al., 2022; Hoorn & Wesselingh, 2010; Tejada-Lara et al., 2015; Marivaux et al., 2016). During the Middle to Late Miocene the lake

and swamp systems reached their maximum extension, hosting a rich vertebrate fauna (Hoorn et al., 2010). In the Solimões Formation, from the Late Miocene onwards, there was a transition from the “Pebas System” to the predominantly fluvial “Acre System”, which was influenced by Andean orogenesis and increased sedimentation rates (Hsiou et al., 2022). The drainage of the Pebasian Mega-Wetlands System in the Late Miocene–Pliocene intensified habitat fragmentation in this region (emerging/submerging lands), increasing speciation and diversification through time (Cozzuol, 2006; Hoorn et al., 2010a, 2022; Marivaux et al., 2016, 2020 and references therein).

## CONCLUSION

A new species, *Acarechimys hunikuini* sp. nov., is described from the Late Miocene of Envira River, Brazil. This record underscores the coexistence of several caviomorph superfamilies (octodontoids, chinchilloids and cavioids; see Fontoura et al., 2022) at the PRE06 locality, in addition to many other taxonomic groups, highlighting the existence of a rich fauna in the Brazilian Amazonia, in line with what was expected for this region (Fig. 8; Cozzuol, 2006; Hoorn & Wesselingh, 2010; MacFadden, 2006; Vucetich et al., 2010b). The recent discovery, coupled with earlier fossils unearthed at the Envira River outcrop, makes the PRE06 locality an excellent site for studying small vertebrates that inhabited Proto-Amazonia before the significant environmental changes that took place in South America following the Great American Interchange. These changes could ultimately lead to the extinction of several autochthonous lineages, including several rodents.

*Acarechimys* possibly emerged during the late Oligocene and diversified in the Patagonian region during the Lower Miocene. During the Middle Miocene, it spread to extra-Patagonian regions, towards the north of South America. During the Late Miocene, the lineage remained only in extra-Patagonian regions. This new record, which is the last appearance of the genus, supports the hypothesis of the late survival of rodent lineages in the tropics, a pattern that has been documented in octodontoids, hydrochoerines and neopiblemids (Vucetich et al., 2010c). The rapid diversification and radiation of *Acarechimys*, as well as the scarcity of data, divergence of opinions between studies dedicated to this group, and the many isolated teeth reported for the Amazonian region, make the research of this genus challenging. Further research is required to enhance our comprehension of the diversification and temporal variation of this broad lineage of Octodontoidea.

Finally, computed tomography can be used for the estimation of tooth wear, which is an important method in paleontology, especially when complete specimens from all life stages are not available. This approach using this technology can help taxonomic identification and allows comparison of specimens at similar stages of tooth wear, both in hypsodont (e.g., Skandalos & van den Hoek Ostende, 2023) and in brachydont teeth (reported here).

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## AUTHOR CONTRIBUTIONS

EF, AMR, LK designed research. EF drafted the manuscript, gathered the data, analyzed the data and wrote the paper. FRN managed field work seasons. EF, LM, P-OA, NSS, FRN, AMR participated in the field and collected the materials. All authors reviewed the manuscript and provided edits.

The data that support the findings of this study are available from the corresponding author, [EF], upon reasonable request.

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TABLE 1. *Acarechimys hunikuini* sp. nov. dental measurements. **mdl**, maximum mesio-distal length; **mw**, maximum width.

	Specimen	mdl (mm)	mw (mm)
dp4	UFAC-CS 460	-	1.21
	UFAC-CS 462	-	1.37
	UFAC-CS 261	1.63	1.11
m1	UFAC-CS 456	1.77	1.6
	UFAC-CS 367	1.69	1.48
	UFAC-CS 261	1.38	1.29
m2	UFAC-CS 356	1.87	1.77
	UFAC-CS 261	1.57	1.43
m3	UFAC-CS 426	1.96	1.73
	UFAC-CS 250	1.74	1.52
	UFAC-CS 431	1.65	1.49
	UFAC-CS 373	1.55	1.3
	UFAC-CS 463	1.38	1.2
	UFAC-CS 702	1.43	1.1
	UFAC-CS 261	1.67	1.4

TABLE 2. Main dental characters of *Acarechimys hunikuini* sp. nov. in comparison with other species of this genera (based on Arnal et al., 2017). ‘\*’ Information from the Table 3 from Arnal et al., 2017 (Table 3); ‘\*\*’ based only on photos from Arnal et al. (2017) and Vucetich et al. (2015).

	<i>A. hunikuini</i> sp. nov.	<i>A. constans</i>	<i>A. gracilis</i>	<i>A. leucotheae</i>	<i>A. minutissimus</i>	<i>A. minutus</i>
Incisors	Laterally compressed	Not laterally compressed*	Not laterally compressed*	-	Laterally compressed*	Laterally compressed*
Size (Fig. 3)	Larger than <i>A. minutissimus</i> and <i>A. leucotheae</i> . Smaller than <i>A. constans</i> . Similar to <i>A. gracilis</i> and <i>A. minutus</i> .	Larger than <i>A. minutissimus</i> , <i>A. leucotheae</i> , <i>A. minutus</i> , <i>A. gracilis</i> and <i>A. hunikuini</i> sp. nov.	Larger than <i>A. minutissimus</i> , <i>A. leucotheae</i> , and <i>A. minutus</i> . Similar to <i>A. hunikuini</i> sp. nov.	Smaller than <i>A. constans</i> , <i>A. gracilis</i> and <i>A. hunikuini</i> sp. nov.** Similar to <i>A. minutissimus</i> **	Smaller than <i>A. constans</i> , <i>A. gracilis</i> and <i>A. leucotheae</i>	Smaller than <i>A. constans</i> and <i>A. gracilis</i> . Larger than <i>A. minutissimus</i> and <i>A. leucotheae</i> . Similar to <i>A. hunikuini</i> sp. nov.
dp4						
Posterior arm of protoconid (= Metalophid II in Arnal et al., 2017)	Well-developed	Variably-developed (conspicuous or reduced)*	Well-developed*	Reduced*	Reduced to a spur	Variably-developed (usually reduced)*
Third transversal cristid (= Mesolophid in Arnal et al., 2017)	Well-developed	Well-developed*	Reduced*	Well-developed*	Well-developed*	Usually reduced*
Mesial ectolophid	More perpendicular, joined to the protoconid	More perpendicular, joined to the protoconid	More perpendicular, joined to the protoconid	More oblique, more separated from protoconid**	More perpendicular, joined to the protoconid	More perpendicular, joined to the protoconid
m1						
Posterior arm of protoconid (=	Absent	Variably developed	Variably developed*	Present, but reduced*	Reduced to a spur or absent*	Present, but reduced*

Metalophulid II in Arnal et al., 2017)		(usually conspicuous)*				
Mesostylid	Present/absent	Absent?	Present/absent	? (fractured)**	Present/absent	Present/absent
Posterior arm of metaconid	Present/absent	Absent*	Present*	Absent*	Absent*	Present*
Neomesolophid m2	Present	Absent?	Present/Absent	Absent**	Present/Absent	Present/Absent
Posterior arm of protoconid (= Metalophulid II in Arnal et al., 2017)	Absent	Present, but reduced*	Present, but reduced*	Present, but reduced*	Absent*	Present, but reduced*
Mesostylid	Present/absent	Absent (present? only in MLP 15-391a)	Present/absent	Absent**	Present/absent	Present/absent
Posterior arm of metaconid	Present/absent	Absent*	Present*	Absent* **	Absent*	Present*
Neomesolophid m3	Present	Absent (present? only in MLP 15-391a)	Present/Absent	Absent**	Absent?	Present/Absent
Posterior arm of protoconid (= Metalophulid II in Arnal et al., 2017)	Absent	Present, but reduced*	Reduced/absent*	Present, but reduced*	Absent*	Absent*
Mesostylid	Present/absent	Present?/absent	Present/absent	Absent**	Absent	Absent (present only on MACN-A 237)
Posterior arm of metaconid*	Present/absent	Absent	Present	Absent*	Absent	Present
Neomesolophid	Present	Absent (present? only in MLP 15-391a)	Absent	Absent**	Absent	Absent (present only on MACN-A 237)



FIGURE 1. **A**, map of Brazil showing the location of the State of Acre; **B**, map of the State of Acre showing the geographic location of the PRE06 “Coqueiros” fossil-bearing locality on the right bank of the Envira River (red star) (modified from Fontoura et al., 2022).

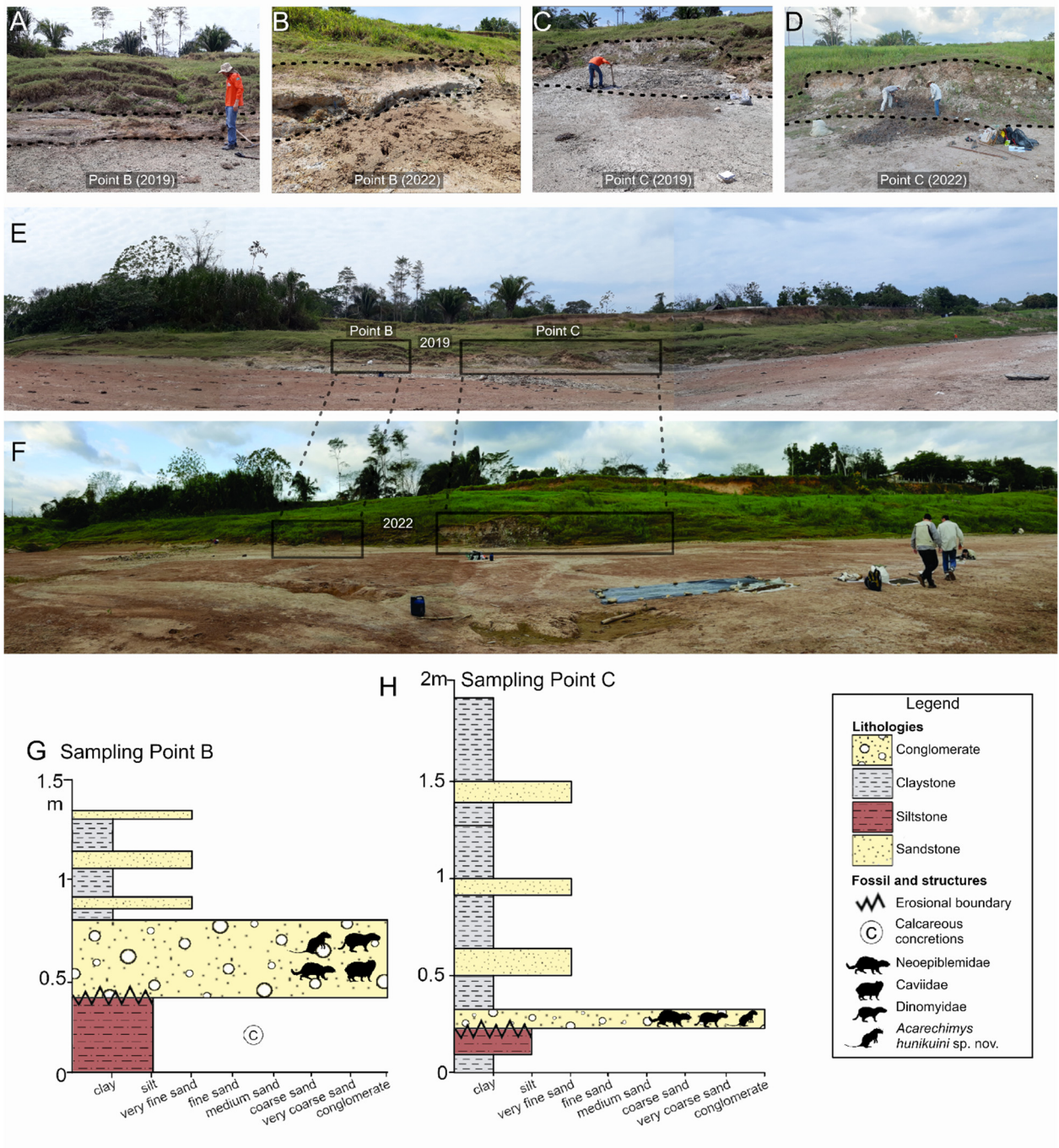


FIGURE 2. Outcrop PRE06 "Coqueiros" (Envira River, Solimões Formation, State of Acre, Brazil). A, B, C, D, E, F, photographs of the outcrop on the right bank of the river showing the changes through time; Point B in 2019 (A) and 2022 (B); Point C in 2019 (C) and 2022 (D); general view of the outcrop in 2019 (E) and 2022 (F); G, H, stratigraphic section of Point B (G) and Point C (H). The specimens were attributed to the conglomerate layer based on Fontoura et al. (2022), modified from Stutz et al. (2023).

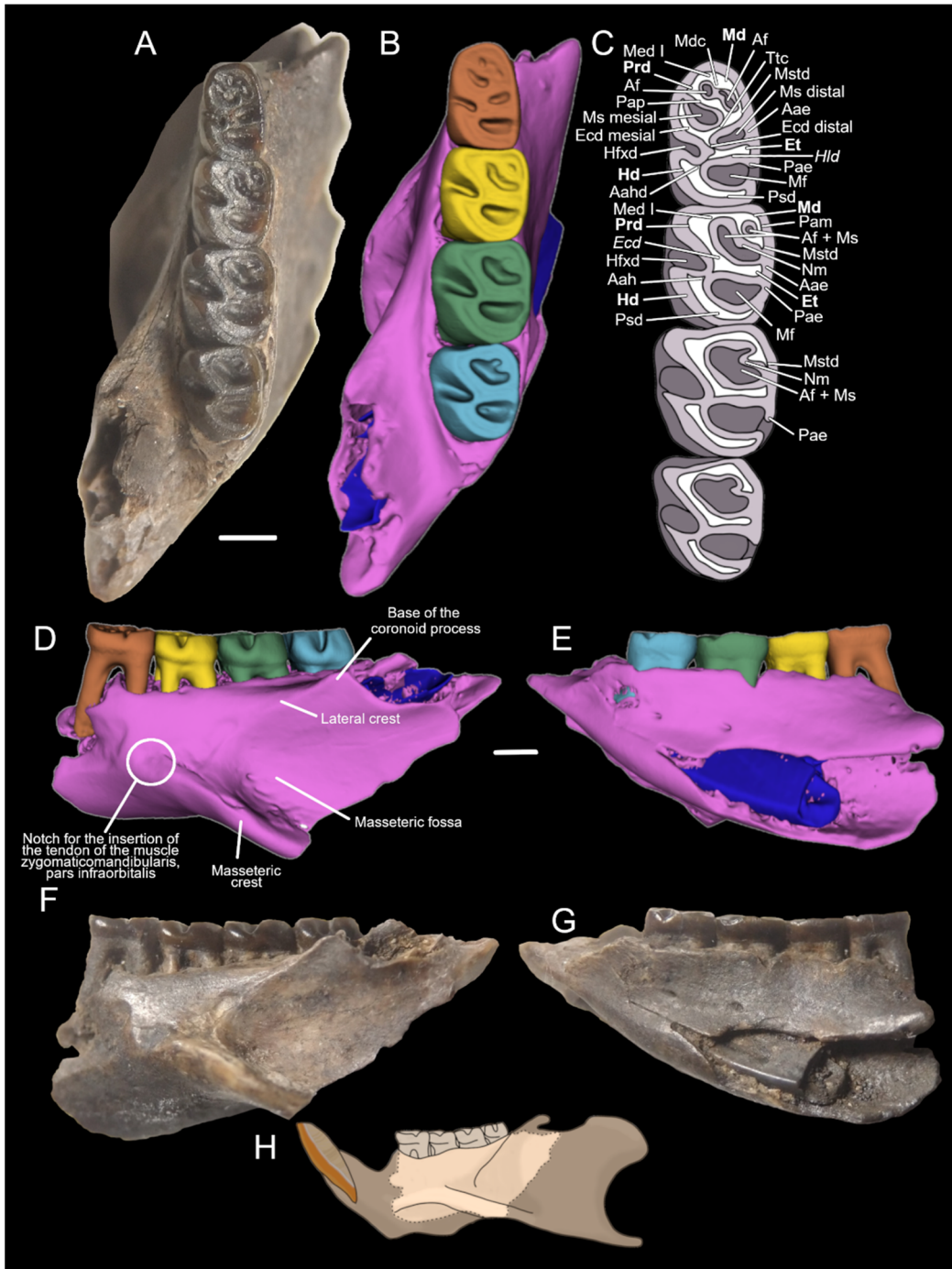


FIGURE 3. Left dentary and cheek teeth (dp4-m3) (UFAC-CS 261) of *Acarechimys hunikuini* sp. nov. **A**, photo of the specimen in occlusal view; **B**, three-dimensional surface reconstruction of the specimen, in occlusal view; **C**, schematic drawing and nomenclature, in occlusal view; **D-G**, three-dimensional surface reconstructions (**D-E**) and photos (**F-G**) of the specimen, in lateral (**D** and **F**) and mesial (**E** and **G**) views; **H**, reconstruction of the dentary, highlighting the preserved area of the dentary, in lateral view. **Abbreviations:** **Aae**, anterior arm of the entoconid; **Aahd**, anterior arm of the hypoconid; **Af**, anterofossettoid/flexid; **Ecd**, ectolophid; **Et**, entoconid; **Hd**, hypoconid; **Hfxd**, hypoflexid; **Hld**, hypolophid; **Md**, metaconid; **Mdc**, metaconid cristid; **Med I**, metalophulid I; **Mf**, metaflexid; **Ms**, mesofossettoid/flexid; **Mstd**, mesostylid; **Nm**, neomesolophid; **Pae**, posterior arm of the entoconid; **Pam**, posterior arm of metaconid; **Pap**, posterior arm of the protoconid; **Prd**, protoconid; **Psd**, posterolophid; **Ttc**, third transverse cristid. Scale bars equal 1 mm.

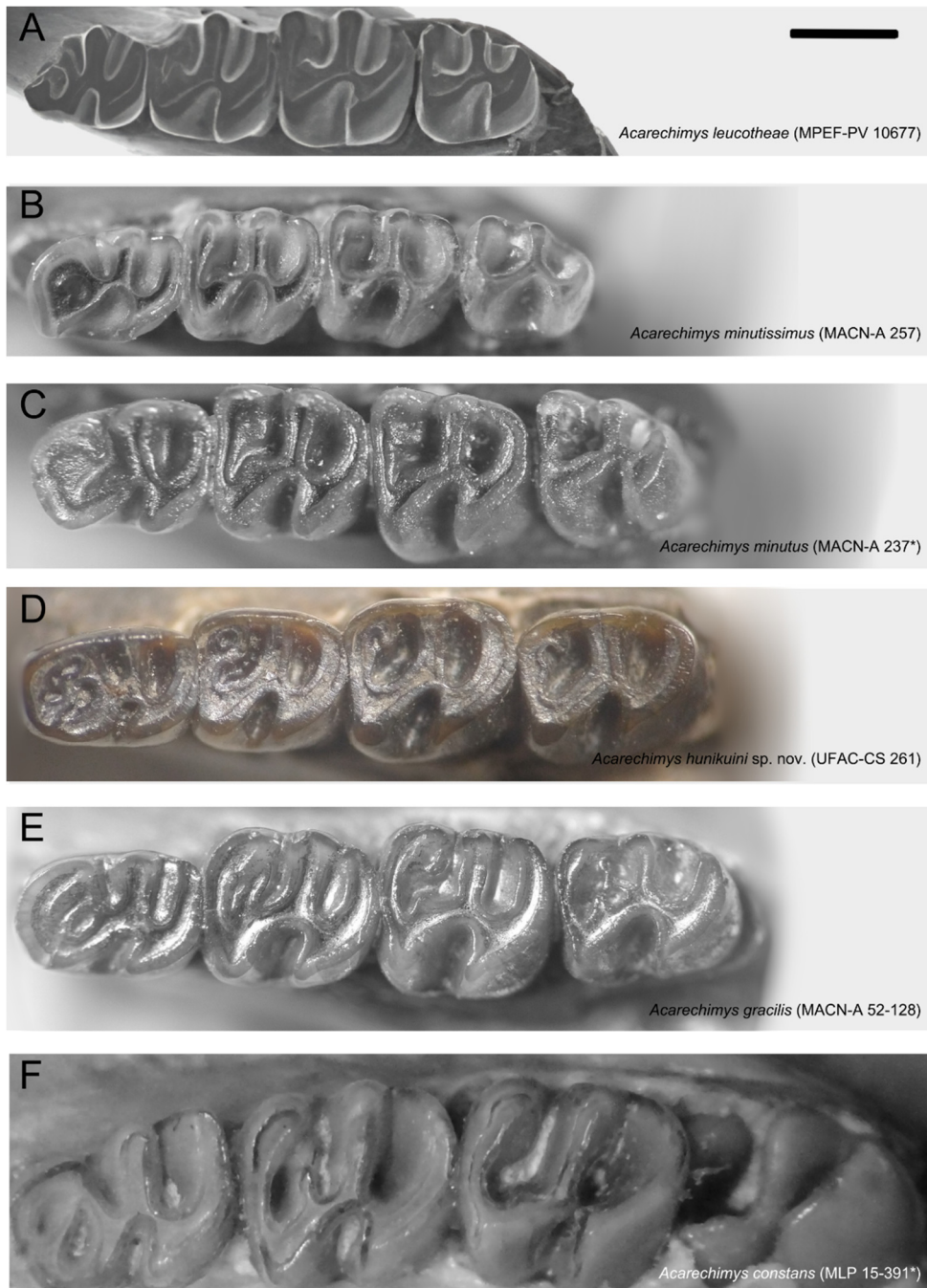


FIGURE 4. *Acarechimys* mandibles (with dp4-m3) in proportion to size. ‘\*’ for inverted photos. **A**, *Acarechimys leucotheae*; **B**, *Acarechimys minutissimus*; **C**, *Acarechimys minutus*; **D**, *Acarechimys hunikuini* sp. nov.; **E**, *Acarechimys gracilis*; **F**, *Acarechimys constans*. Scale bar equals 1 mm.



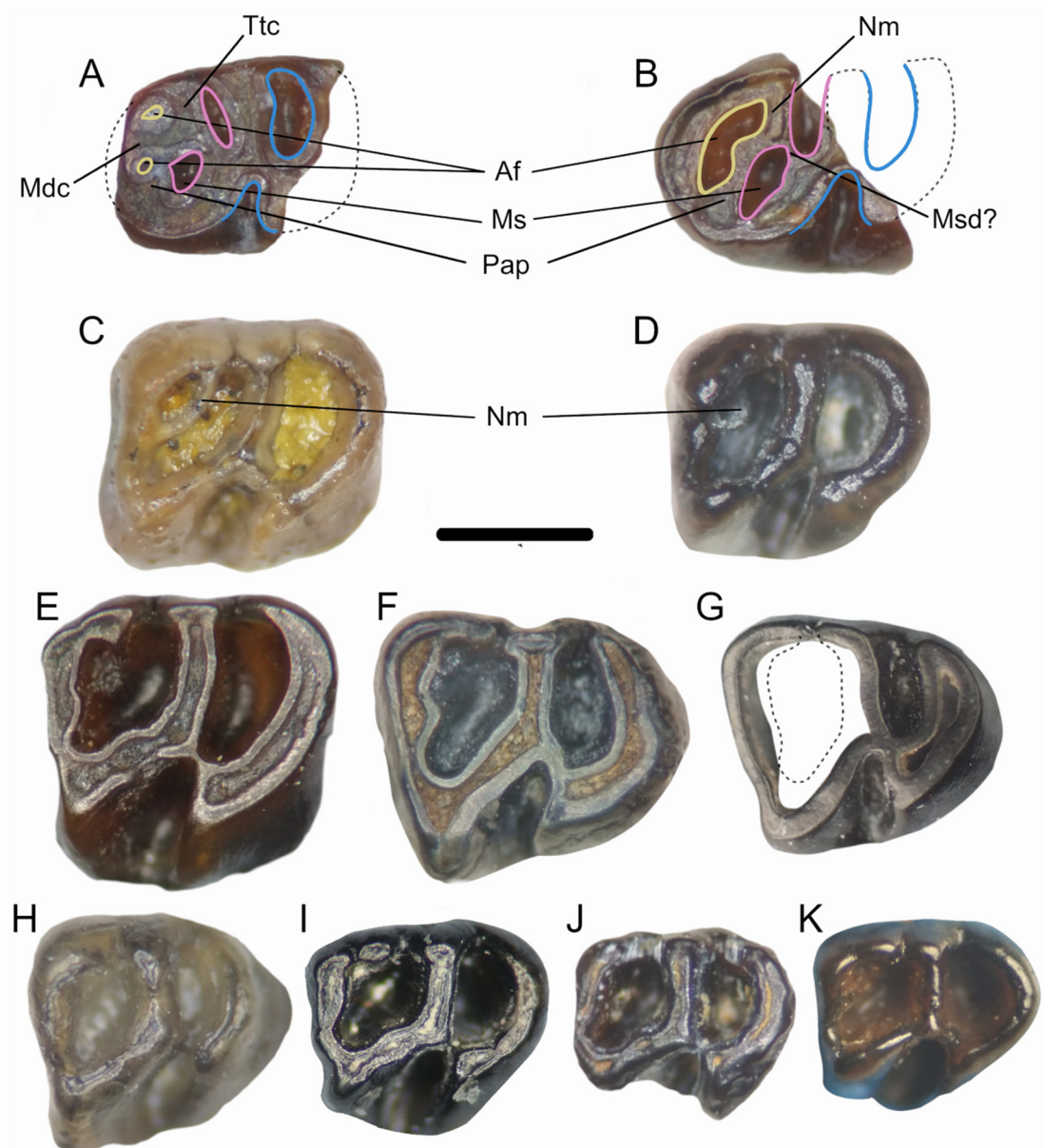


FIGURE 5. Lower molars of *Acarechimys hunikuini* sp. nov. **A**, UFAC-CS 460, right dp4 (inverted); **B**, UFAC-CS 462, right dp4 (inverted); **C**, UFAC-CS 456, left m1; **D**, UFAC-CS 367, left m1; **E**, UFAC-CS 356, left m2; **F**, UFAC-CS 426, left m3; **G**, UFAC-CS 250, left m3; **H**, UFAC-CS 431, right m3 (inverted); **I**, UFAC-CS 373, right m3? (inverted); **J**, UFAC-CS 463, left m3?; **K**, UFAC-CS 702, right m3 (inverted). **Abbreviations:** **Af**, anterofossettids; **Mdc**, metaconid cristid; **Ms**, mesofossettids; **Msd**, mesolophid; **Nm**, neomesolophid; **Pap**, posterior arm of protoconid; **Ttc**, third transverse cristid. Scale bar equals 1mm.

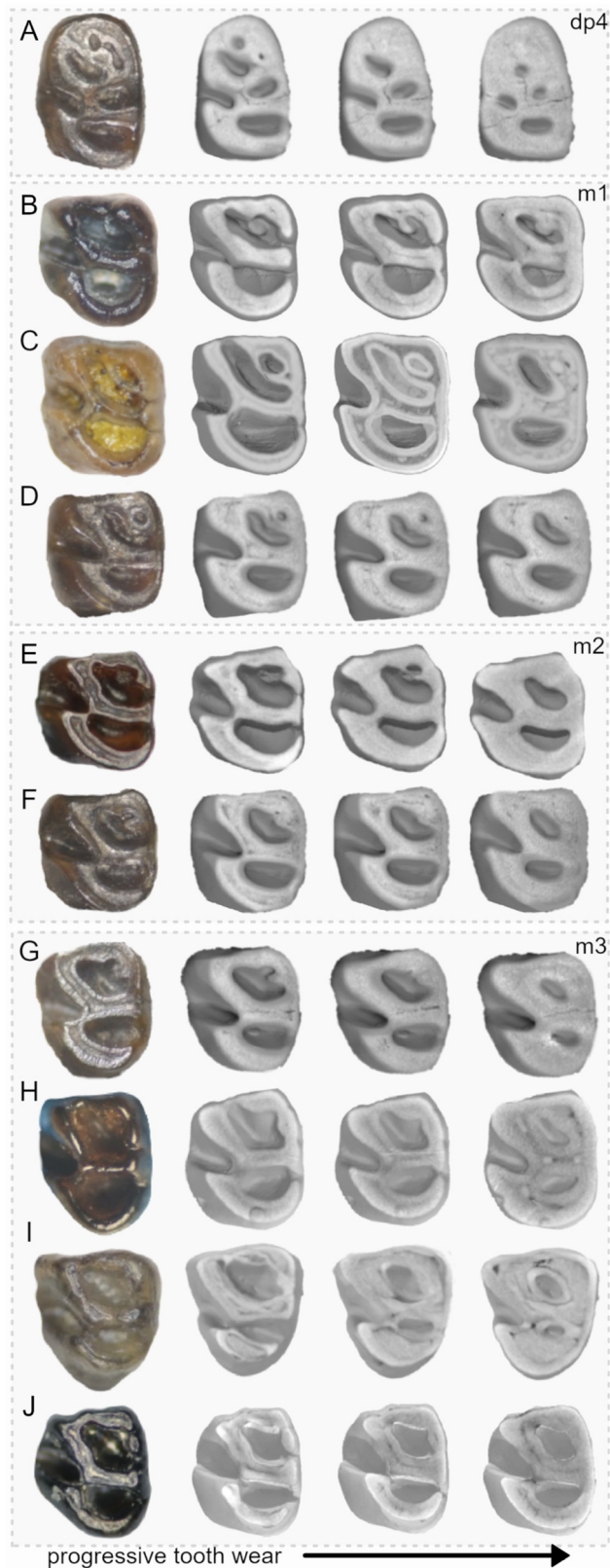


FIGURE 6. Hypothetical scenario of tooth wear based on the volume rendering of  $\mu$ CT scans of *Acarechimys hunikuini* sp. nov. Wear progresses in the reconstructions on the right: dp4 (A), m1 (B-D), m2 (E-F), m3 (G-J). A, D, F, G, UFAC-CS 261; B, UFAC-CS 367; C, UFAC-CS 456; E, UFAC-CS 356; H, UFAC-CS 702 (inverted); I, UFAC-CS 431 (inverted); J, UFAC-CS 373. Out of scale.

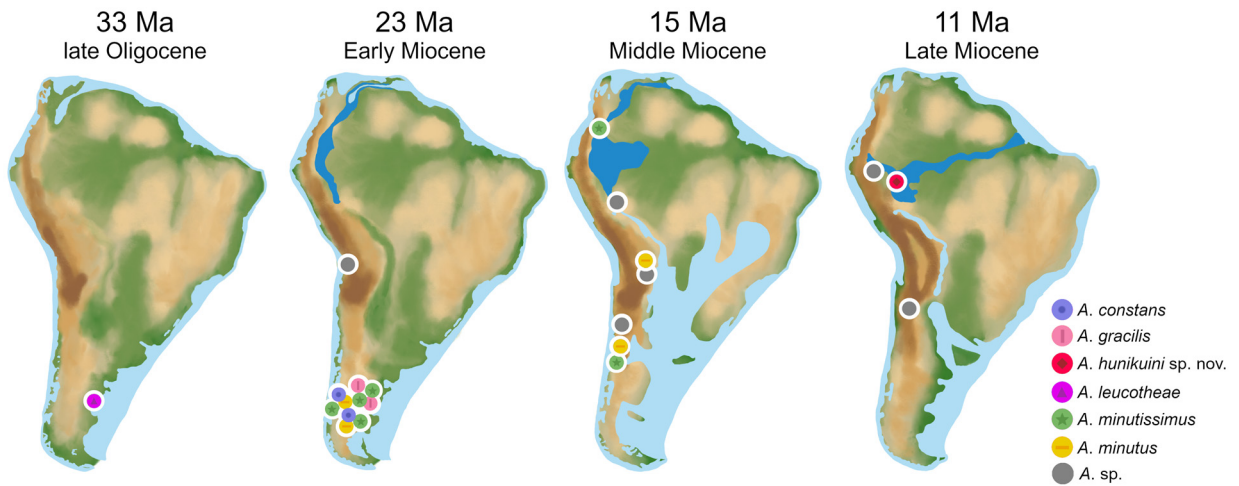


FIGURE 7. Temporal and geographic distribution of the genus *Acarechimys* in South America. Occurrence of *Acarechimys* based on Arnal et al. (2017), McGrath et al. (2023) and references therein. Paleogeographic map modified from Hoorn et al. (2022).



FIGURE 8. Hypothetical artistic reconstruction of *Acarechimys hunikuini* sp. nov. Art by Márcio Castro.