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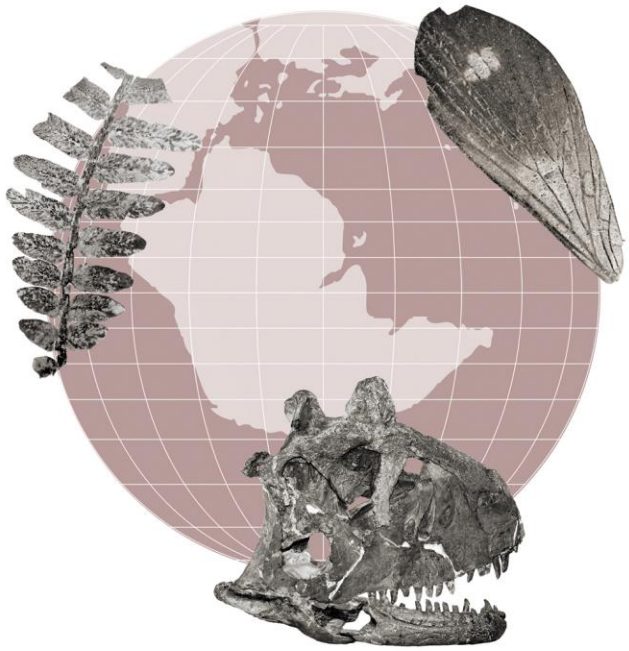

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REASSESSING THE HYPERDIVERSE DINOMYID (RODENTIA, CAVIOMORPHA) ASSEMBLAGE FROM THE LATE MIOCENE ITUZAINGÓ FORMATION (ENTRE RIOS PROVINCE, ARGENTINA)

LUCIANO LUIS RASIA[1]

[1]División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, La Plata B1900FWA, Argentina. CONICET. lucianorasia@fcnym.unlp.edu.ar

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Running header: RASIA: DINOMYIDS FROM THE ITUZAINGÓ FORMATION

Short description: The dinomyid rodent assemblage recorded in the Late Miocene Ituzaingó Formation (Argentina), the most diverse of South America, is reassessed.

Corresponding author: Luciano Luis Rasia *lucianorasia@fcnym.unlp.edu.ar*

Abstract. The Late Miocene Ituzaingó Formation (northeastern Argentina) has the most diverse caviomorph rodent assemblage of South America. The family Dinomyidae, with a single extant species (*Dinomys branickii*), also has its highest taxonomic diversity in this unit: 18 genera and 27 species, many of doubtful status. A reexamination of the holotypes of several species and other published and unpublished material leads to the following conclusions: "*Tetrastylomys castellanosi*" should be considered *Tetrastylus* sp.; the type series of "*Eumegamys contortus*" pertains to *Carlesia pendolai* and *Rusconia crassidens*; "*Pentastylomys seriei*" is a junior synonym *Gyriabrus holmbergi*; "*Protomegamys*" *coligatus* should be included in the genus *Gyriabrus*; "*Doellomys parcus*" is a junior synonym of *Gyriabrus coligatus* (new combination); "*Diaphoromys compressidens*" and "*Eumegamys dubius*" are a junior synonyms of *Diaphoromys gamayensis*; "*Briaromys trouessartianus*" is a *nomen dubium*; "*Megamys racedi*" and "*Megamys depressidens*" are *nomina vana*; and *Pseudosigmomys paranensis*, *Telodontomys compressidens*, *Diaphoromys mesopotamicus*, *Eumegamys scalabrinianus*, and *Rusconia crassidens* are valid. In addition, *Arazamys castiglionii* is recognized for the first time in Argentina. With this revision, the taxonomic diversity of Dinomyidae from the Ituzaingó Formation is reduced to 13 genera and 19 species. Nevertheless, it remains higher than other coeval units of South America, like the Urumaco Formation in Venezuela (five genera), Solimões Formation in Brazil (nine genera), Camacho Formation in Uruguay (four genera), and Cerro Azul Formation in Central Argentina (four genera).

Keywords. Neogene. South America. Mammals. Systematics.

Resumen. REEVALUANDO EL CONJUNTO HIPERDIVERSO DE DINÓMIDOS (RODENTIA, CAVIOMORPHA) DE LA FORMACION ITUZAINGÓ DEL

MIOCENO TARDÍO (PROVINCIA DE ENTRE RIOS, ARGENTINA). La Formación Ituzaingó del Mioceno Tardío (Noreste de Argentina) tiene el conjunto de roedores caviomorfos más diverso de América del Sur. La familia Dinomyidae, con una única especie viviente (*Dinomys branickii*), también tiene su máxima diversidad taxonómica en esta unidad: 18 géneros y 27 especies, muchos con un estatus dudoso. Una reexaminación de los holotipos de varias especies y otros materiales ya publicados e inéditos permitieron las siguientes conclusiones: "*Tetrastylomys castellanosi*" debería considerarse como *Tetrastylus* sp.; la serie tipo de "*Eumegamys contortus*" pertnece a *Carlesia pendolai* y *Rusconia crassidens*; "*Pentastylomys seriei*" es un sinónimo junior de *Gyriabrus holmbergi*; "*Protomegamys*" *coligatus* debería incluirse en el género *Gyriabrus*; "*Doellomys parcus*" es un sinónimo junior de *Gyriabrus coligatus* (nueva combinación); "*Diaphoromys compressidens*" y "*Eumegamys dubius*" son sinónimos junior de *Diaphoromys gamayensis*; "*Briaromys trouessartianus*" es un *nomen dubium*. "*Megamys racedi*" y "*Megamys depressidens*" son *nomina vana*; y *Pseudosigmomys paranensis*, *Telodontomys compressidens*, *Diaphoromys mesopotamicus*, *Eumegamys scalabrinianus*, y *Rusconia crassidens* son válidos. Además, *Arazamys castiglionii* es reconocida por primera vez en Argentina. Luego de esta revisión, la diversidad taxonómica de Dinomyidae de la Formación Ituzaingó se reduce a 13 géneros y 19 especies. Sin embargo, ésta permanece más alta que la de otras unidades coetáneas de América del Sur, como la Formación Urumaco en Venezuela (cinco géneros), la Formación Solimões en Brasil (nueve géneros), la Formación Camacho en Uruguay (cuatro géneros), y la Formación Cerro Azul en el Centro de Argentina (cuatro géneros).

Palabras clave. Neógeno. América del Sur. Mamíferos. Sistemática.

THE CAVIOMORPH RODENT ASSEMBLAGE of the "*Conglomerado Osífero*", at the base of the Ituzaingó Formation (Chasicoan-Huayquerian stages/ages, Late Miocene; *e.g.*, Brandoni, 2013; Fig. 1), is the most diverse of South America (*e.g.*, Cione *et al*., 2000; Candela, 2005; Nasif *et al*., 2013). This assemblage has been summarized recently (*e.g.*, Cione *et al*., 2000; Candela, 2005; Nasif *et al*., 2013; Brandoni *et al*., 2019), with detailed studies on members of the families Caviidae, Chinchillidae, Echimyidae, and Neoepiblemidae that have reduced caviomorph diversity of this unit due to synonymy of several taxa (Candela & Noriega, 2004; Nasif *et al*., 2013; Vucetich *et al*., 2014; Rasia & Candela, 2018; Kerber *et al*., 2019).

The family Dinomyidae, with the pacarana (*Dinomys branickii* Peters, 1873) as the only extant species (White & Alberico, 1992), has a fossil record that extends back to the Early Miocene (Kramarz, 2006; Rasia *et al*., 2021), and was notably diverse during the Late Miocene (*e.g.*, Nasif *et al*., 2013). The taxonomy of Dinomyidae has mainly been based on cheek tooth morphology, given that most of the extinct genera and species are known by isolated cheek teeth, with some cases of well-preserved mandibles and/or cranium (*e.g.*, Fernández de Álvarez, 1958; Rinderknecht & Blanco, 2008; Rinderknecht *et al.*, 2011, 2018). Several subfamilies have been traditionally recognized (Potamarchinae, Gyriabrinae, Eumegamyinae, Dinomyinae, Tetrastylinae; *e.g.*, Kraglievich, 1932; Mones, 1981), but the lack of a comprehensive phylogenetic study that includes members of all these putative groups has prevented a consensus on their validity (*e.g.*, Kerber *et al.*, 2017; Rinderknecht *et al.*, 2019; Rasia *et al*., 2025b). It has been established that the cheek teeth show ontogenetic variation due to wear in protohypsodont dinomyids (traditionally considered as potamarchines; *e.g.*, Fields, 1957), and there is also variability in cheek tooth morphology in euhypsodont dinomyids (gyriabrines, eumegamyines, dinomyines and tetrastylines); some taxa, like

100 *Dinomys branickii* and *Gyriabrus holmbergi*, show ontogenetic occlusal variation (*e.g.*,
101 Nasif & Abdala, 2015; Rasia, 2023), whereas others, like *Isostylomys laurillardi*,
102 acquire the definitive occlusal pattern early in the development (Rinderknecht *et al.*,
103 2018).

104 The taxonomic diversity of Dinomyidae is greatest in the Ituzaingó Formation,
105 with 19 nominal genera and 34 nominal species (see Candela, 2005). The studies of
106 Ameghino (1891), Nasif *et al*. (2013), Rinderknecht *et al*. (2018), and Rasia (2023)
107 have reduced the confirmed taxa to nine genera and 12 species, with another nine
108 genera and 15 species of doubtful status (a total of 18 genera and 27 species; see Tab.
109 1).

110 FIGURE 1

111 The dinomyid diversity of other coeval units of South America is notably lower
112 than that of the Ituzaingó Formation. From the Urumaco Formation in Venezuela (Fig.
113 1), there are records of cf. *Potamarchus*, *Olenopsis*, *Tetrastylus*, *Telicomys* and
114 *Eumegamys*, but they need to be revised (*e.g.*, Horovitz *et al*., 2010). The Solimões
115 Formation of Brazil (Late Miocene, Huayquerian Stage/Age; *e.g.*, Bissaro-Júnior *et al.*,
116 2019; Fig. 1) includes records of *Potamarchus*, *Pseudopotamarchus*, *Ferigolomys*,
117 *Drytomomys*, *Eumegamys*, *Tetrastylus*, "*Telicomys*" and cf. *Gyriabrus* (*e.g.*, Kerber *et*
118 *al*., 2016, 2017, 2018; *Telicomys* is in quotation marks following Rasia *et al*., 2025a).
119 From the Camacho Formation in Uruguay (Late Miocene, Chasicoan-Huayquerian
120 stages/ages; Perea *et al*., 2013; Fig. 1) *Tetrastylus*, *Isostylomys*, *Arazamys*, and
121 *Gyriabrus* have been recorded (*e.g.*, Rinderknecht *et al*., 2011, 2018, 2019; Rasia,
122 2023). From the Cerro Azul Formation in Central Argentina (Late Miocene-Early
123 Pliocene; *e.g.*, Montalvo *et al*., 2023; Fig. 1) there are records of *Tetrastylus*,
124 *Bondesiomys*, *Diaphoromys*, and *Gyriabrus* (Sostillo *et al*., 2022; Rasia *et al*., 2025b).

TABLE 1

In this work, the dinomyids from the Ituzaingó Formation not revised in other recent works (Nasif *et al*., 2013; Rinderknecht *et al*., 2018; Rasia, 2023; see Tab. 1), are restudied in order to analyze their validity and reassess the taxonomic diversity of dinomyids in this unit.

Institutional abbreviations. MACN-A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ameghino Collection, Ciudad Autónoma de Buenos Aires, Argentina; **MACN-PV,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Vertebrate Paleontology Collection, Ciudad Autónoma de Buenos Aires, Argentina; **MAS,** Museo "Antonio Serrano", Paraná, Argentina; **MLP-PV,** Museo de La Plata, Vertebrate Paleontology Collection, La Plata, Argentina; **MNHN,** Museo Nacional de Historia Natural, Montevideo, Uruguay.

Anatomical abbreviations. LLW, labio-lingual width; **M1, M2, M3,** first, second and third upper molar; **m1, m2, m3,** first, second and third lower molar; **MDW,** mesio-distal width; **P4,** fourth upper premolar; **p4,** fourth lower premolar.

MATERIAL AND METHODS

The studied material is deposited in the MACN-A, MACN-PV and MLP-PV. All the material included in this analysis was recovered from the Ituzaingó Formation (Late Miocene; *e.g*., Cione *et al*., 2000; Brandoni, 2013). This material pertains to old collections and lacks precise stratigraphic provenance within the Ituzaingó Formation; in most cases, specimens also lack precise geographic location and are only labeled as having been collected near Paraná (Entre Ríos Province, Argentina).

Cheek tooth nomenclature (Fig. 2) follows homology proposals of Nasif (2009), Rasia & Candela (2019), Rasia *et al*. (2021), and Rasia (2023). The locus and

upper/lower position of isolated cheek teeth was determined via comparisons with maxillae and dentaries with teeth *in situ*. Although Nasif *et al*. (2013) suggested that isolated teeth of euhypsodont dinomyids cannot be taxonomically identified due to ontogenetic variation, comparing isolated cheek teeth with more complete material allows at least some specimens to be identified based on unique features.

Some taxa are considered *nomina dubia* or *nomina vana* following definitions of Mones (1989).

FIGURE 2

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Infraorder CAVIOMORPHA Wood & Patterson in Wood, 1955

Superfamily CHINCHILLOIDEA Kraglievich, 1940

Family DINOMYIDAE Peters, 1873

Genus ***Potamarchus*** Burmeister, 1885

1885. *Potamarchus* Burmeister: 154.

1891. *Theridomys* Burmeister, 1885: 154. Ameghino: 244–245.

1891. *Discolomys* Ameghino, 1889: 148. Ameghino: 244–245.

Type species. *Potamarchus murinus* Burmeister, 1885.

Included species. The type species, *Potamarchus sigmodon* Ameghino, 1891 and *P. adamiae* Kerber *et al*., 2016.

Distribution. Middle Miocene of Peru (Tejada-Lara *et al*., 2015) and Late Miocene of Argentina (*e.g.*, Tauber, 2005; Nasif *et al*., 2013), Brazil (*e.g.*, Kerber *et al*., 2017), and Venezuela (*e.g.*, Horovitz *et al*., 2010).

Remarks. Three species are traditionally recognized within this genus: *Potamarchus murinus*, *P. sigmodon* and *P. adamiae*. The differences between these species are mainly the presence of crenulations in the enamel bands of *P. murinus* and *P. adamiae* and their absence in *P. sigmodon*. However, Kerber *et al*. (2017) attributed these variations to ontogeny. A more comprehensive study of this genus is needed that includes species from Argentina and Brazil and comparisons with other protohypsodont dinomyids, given that other authors (*e.g.*, Candela & Nasif, 2006; Nasif *et al.*, 2013) consider *P. murinus* and *P. sigmodon* as valid species.

Potamarchus murinus Burmeister, 1885

Figure 3.A–3.D

1885. *Potamarchus murinus* Burmeister: 154–155, lam. 2, fig. 4.

1891. *Theridomys americanus* Burmeister, 1885: 109–110. Ameghino: 244–245.

1891. *Discolomys cuneus* Ameghino, 1889: 148–149, lam.5, figs. 17, 23, lam. 24, fig. 8. Ameghino: 244–245.

Type material. MACN-PV 4577, right dentary with p4–m3.

Referred material. MACN-A 5870, right portion of palate with P4–M3 (Fig. 3.A); MACN-A 1498 (holotype of "*Discolomys cuneus*"), isolated upper cheek tooth (Fig. 3.B–3.D).

Geographic occurrence. Entre Ríos Province (Argentina; Nasif *et al.*, 2013), Acre region (Brazil; Kerber *et al.*, 2017), and Fitzcarrald Arch (Peru; Tejada-Lara *et al*., 2015).

Stratigraphic occurrence. Ipururo Formation (Middle Miocene; Tejada-Lara *et al*., 2015), Ituzaingó Formation (Late Miocene; Nasif *et al*., 2013), and Solimões Formation (Late Miocene; *e.g.*, Kerber *et al.*, 2017).

Description. The isolated upper cheek tooth, holotype of "*Discolomys cuneus*" (MACN-A 1498), is pentalophodont (Fig. 3.B–3.C) and protohypsodont, with evident

roots (Fig. 3.D). It is badly preserved and not possible to assign to locus but is similar to the P4 and M2 of MACN-A 5870 (Fig. 3.A).

Comments. Ameghino (1889) erected the genus and species "*Discolomys cuneus*" based on an isolated upper cheek tooth. Later, Ameghino (1891) considered "*D. cuneus*" and "*Theridomys americanus*" (genus and species created by Burmeister, 1885) to be junior synonyms of *Potamarchus murinus*. Moreover, MACN-A 1498 cannot be referred to other protohypsodont dinomyids like *Potamarchus sigmodon* or *Paranamys typicus* given the lack of crenulations in the enamel in these species (but see above). It further differs from *Potamarchus adamiae* in its smaller size and more convex lophs.

FIGURE 3

Genus ***Tetrastylus*** Ameghino, 1886

1886. *Tetrastylus* Ameghino: 46.

Tetrastylomys Kraglievich, 1926: 128, fig. 3; new synonymy.

Type species: *Tetrastylus laevigatus* (Ameghino, 1885).

Included species: The type species, *Tetrastylus diffisus* Ameghino, 1886, *T. araucanus* Ameghino, 1904, *T. intermedius* Rovereto, 1914, *T. montanus* Ameghino, 1891, *T. walteri* Paula Couto, 1951, and *T. (Protelicomys) atavus* Kraglievich, 1931.

Distribution: Late Miocene of Argentina, Brazil, Uruguay, and Venezuela (*e.g.*, Horovitz *et al*., 2010; Nasif *et al*., 2013; Kerber *et al*., 2017; Rinderknecht *et al*., 2019); Pliocene-Pleistocene of Brazil (Kerber *et al*., 2020).

Tetrastylus sp.

Figure 3.E–3.F, 3.H–I

Tetrastylomys castellanosi Kraglievich, 1926: 128, fig. 3; new synonymy.

Referred material: MACN-PV 3332 (holotype of "*Tetrastylomys castellanosi*"), isolated left p4; MACN-PV 2596, isolated right P4.

Description: The holotype of "*Tetrastylomys castellanosi*" (MACN-PV 3332) is a euhypsodont and tetralophodont left p4 with all four lophids separated from each other (Fig. 3.E–3.F).

MACN-PV 2596 is a right P4 that is euhypsodont and tetralophodont. The first and second lophs are separated, and the last two are joined lingually (Fig. 3.H–3.I).

Comments: The holotype of "*Tetrastylomys castellanosi*" (MACN-PV 3332) is similar in morphology to the p4 of a juvenile *Tetrastylus laevigatus* from the Ituzaingó Formation (MACN-PV 2610; see also Rinderkencht *et al.*, 2019) in which the first and second lophids not joined labially (Fig. 3.G), indicating a little worn tooth (see Rinderknecht *et al.*, 2019). MACN-PV 3332 is larger than all *Tetrastylus* specimens recorded in the Ituzaingó Formation and equivalent to *T. laevigatus* from the Cerro Azul Formation (La Pampa Province; Sostillo *et al.*, 2022); it is smaller than *Tetrastylus montanus* from the Late Miocene of northwestern Argentina (Rovereto, 1914), the largest species of the genus. Given the presence of a tetralophodont p4, the type material of "*Tetrastylomys castellanosi*" is here identified as a juvenile specimen of *Tetrastylus*, probably representing a large species of the genus. The only euhypsodont dinomyids with a tetralophodont p4 are *Tetrastylus*, *Telicomys*, which is more than 30% larger than *Tetrastylus* (see Rasia *et al.*, 2025a), and *Gyriabrus*, which has a pentalophodont p4 that become tetralophodont with wear (Rasia, 2023).

MACN-PV 2596 is labeled as the holotype of "*Tetrastylopsis entrerrianus*", but this name was not published, so the species is not valid. This occurred with several other material deposited in the MACN; Lucas Kraglievich labeled these specimens as new taxa but never published them. Fernández de Álvarez (1947) published several of these labeled new genera and species, giving them validity, but that was not the case for "*Tetrastylopsis entrerrianus*". The specimen is assigned to *Tetrastylus* sp. because it

resembles the P4 of *Tetrastylus intermedius* (MACN-PV 8323), but upper cheek teeth are unknown for most *Tetrastylus* species.

Genus ***Carlesia*** Kraglievich, 1926

1926. *Carlesia* Kraglievich: 126.

1926. *Megamys*, Burmeister, 1891: 380-381. Kraglievich: 126.

2013. *Tetrastylus*, Kraglievich, 1931 (in part). Nasif *et al.*: 156–157.

Neoepiblema, Ameghino, 1889: 906 (in part).

Dabbenea, Kraglievich, 1926: 127–128 (in part).

Eumegamys, Kraglievich, 1940: 750 (in part).

Type and only species. *Carlesia pendolai* Kraglievich, 1926.

Distribution. Late Miocene of Entre Ríos Province and Late Pliocene of Buenos Aires Province, Argentina (Nasif *et al*., 2013). A specimen referred to this taxon from the Late Miocene Cerro Azul Formation at Buenos Aires Province (Bondesio, 1979; Bondesio *et al*., 1980) was recently recognized as a distinct species, *Bondesiomys chasiquensis* (see Rasia *et al*., 2025b).

Carlesia pendolai Kraglievich, 1926

Figure 4.A–4.E

1926. *Carlesia pendolai* Kraglievich: 126, lam. 4, figs 1 and 2.

1926. *Megamys patagoniensis*, Burmeister, 1891: 380–381 (in part). Kraglievich: 126.

Neoepiblema? *contorta* Ameghino, 1889: 906, lam. 80, fig. 1 (in part); new synonymy.

Dabbenea contorta (Ameghino, 1889). Kraglievich, 1926: 127–128 (in part); new synonymy.

Eumegamys contortus (Ameghino, 1889). Kraglievich, 1940: 750 (in part); new synonymy.

Type material. MACN-PV 3986, portion of right mandible with incisor and m2–m3.

Referred material. MACN-PV 4576 (sintype of *Neoepiblema contorta*), isolated right lower molar; MACN-PV 4067 (cotype of *Eumegamys contortus*), isolated right lower molar.

Geographic occurrence. Entre Ríos Province, Argentina (Nasif *et al*., 2013).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al*., 2013).

Description and comparisons. MACN-PV 4576 is an anterior portion of a right lower molar with the first two lophids joined labially and the third lophid separated. It is missing the fourth lophid (Fig. 4.A–4.B).

MACN-PV 4067 is a poorly preserved right lower molar, tetralophodont, with the first two lophids joined labially and the last two lophids separated. The fourth and last lophid are broken posteriorly (Fig. 4.C–4.D).

These two lower molars are identical in morphology and similar in size to the m2–m3 of *Carlesia pendolai* (Fig. 4.E). They also resemble the m1 of *Eumegamys paranensis* Kraglievich, 1926 and the m1–m2 of *E. scalabrinianus* Kraglievich, 1926 but are larger and have less convex and more sinuous lophids.

Comments. *Neoepiblema*? *contorta* was erected by Ameghino (1889) and doubtfully included in the neoepiblemid genus *Neoepiblema*. It was based on two isolated and fragmentary cheek teeth (MACN-PV 4576 and MACN-PV 4575). Later, Kraglievich (1940) included this species in the genus *Eumegamys* Kraglievich, 1926, referring to it new material (MACN-PV 4067, labeled as cotype).

Two of the specimens (MACN-PV 4576 and MACN-PV 4067; Fig. 4.A–4.D), part of the type series of *Eumegamys contortus*, are here referred to *Carlesia pendolai*. The third specimen (MACN-PV 4575) is discussed below.

FIGURE 4

Genus ***Pseudosigmomys*** Kraglievich, 1931

1931. *Pseudosigmomys* Kraglievich: 394.

Type species. *Pseudosigmomys paranensis* Kraglievich, 1931.

Included species. Only the type species.

Distribution. Late Miocene Ituzaingó Formation. Entre Ríos Province, Argentina (Kraglievich, 1931).

Pseudosigmomys paranensis Kraglievich, 1931

Figure 5.A–5.B

1931. *Pseudosigmomys paranensis* Kraglievich: 394.

Type material. MACN-PV 3453, isolated left lower molar.

Geographic occurrence. Entre Ríos Province, Argentina (Nasif *et al*., 2013).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al*., 2013).

Description. The type and only known material is a euhypsodont left lower molar with four lophids (Fig. 5.A–5.B). The first two and the last two lophids are joined lingually, and the first three lophids are joined labially (see also Kraglievich, 1931, 1932). There is a crenulation of the enamel band in all lophids. Its size is comparable to *Gyriabrus holmbergi* (Ameghino, 1891) (see Rasia, 2023), measuring: MDW 8.43 mm and LLW 8.34 mm.

Comments. The morphology of the holotype of *Pseudosigmomys paranensis* is identical to the molars of *Gyriabrus sokka*, especially m1–m2 (Rasia *et al.*, 2025b), but the latter lacks the crenulation in the enamel band. *P. paranensis* resembles lower molars of *G. holmbergi*, especially m1, which is pentalophodont and becomes tetralophodont with fusion of the first two lophids (see Rasia, 2023). However, the first two lophids of the tetralophodont pattern fuse lingually and labially in *P. paranensis* rather than labially, and the lower molars have a sigmoid pattern not present in *G. holmbergi*. This sigmoid pattern resembles the occlusal morphology of *Eusigmomys oppositus* (Ameghino, 1904) from the Middle Miocene of Patagonia (Argentina; see Kraglievich, 1931; Vucetich, 1984), based on an upper cheek tooth (see Rasia & Candela, 2018). In contrast to *P. paranensis*, *E. oppositus* is trilophodont and not euhypsodont, according to Kraglievich (1931).

FIGURE 5

Genus ***Gyriabrus*** Ameghino, 1891

1891. *Gyriabrus* Ameghino: 246–247.

1930. *Megamys*, Ameghino 1885: 31–33 (in part). Kraglievich: 221.

Pentastylomys Kraglievich, 1926: 128–129; new synonymy.

Protomegamys Kraglievich, 1932: 212; new synonymy.

Doellomys Fernández de Álvarez, 1947: 60; new synonymy.

Type species. *Gyriabrus glutinatus* Ameghino, 1891 (= "*Megamys*" *holmbergi* Ameghino, 1885).

Included species. *Gyriabrus holmbergi*, ?*G. quadratus* Rusconi, 1945, *G. latidens* Rusconi, 1945, ?*G. royoi* Stirton, 1946, *G. sokka* Rasia *et al.*, 2025b, and *G. coligatus* new combination.

Distribution. Late Miocene to Pliocene of Argentina, Uruguay, Colombia and Brazil (Rasia, 2023).

Gyriabrus holmbergi (Ameghino, 1885)

Figure 5.C–5.E

1930. *Megamys holmbergi* Ameghino, 1885: 29. Kraglievich: 221.

2023. *Gyriabrus glutinatus* Ameghino, 1891: 246–247. Rasia: 349–351.

2023. *Gyriabrus teisseirei* Kraglievich, 1930: 219–222. Rasia: 349–351.

2023. *Gyriabrus rebagliattii* Kraglievich, 1932: 223. Rasia: 349–351.

2023. *Gyriabrus indivisus* Kraglievich, 1932: 224. Rasia: 349–351.

Pentastylomys seriei Kraglievich, 1926: 128–129, lam. 2, fig. 2; new synonymy.

Type material. MACN-A 5879, isolated right lower incisor. Despite being labeled as the holotype, the original material described by Ameghino (1885) is a lower molar (see also Rasia, 2023).

Referred material. MACN-PV 3468, isolated left p4 (holotype of "*Pentastylomys seriei*").

Geographic occurrence. Entre Ríos Province, Argentina (Nasif *et al.*, 2013; Rasia, 2023) and San José Department, Uruguay (Rasia, 2023).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al.*, 2013) and Camacho Formation (Late Miocene; Rasia, 2023).

Description. MACN-PV 3468 is an isolated left p4, euhypsodont, pentalophodont, with all five lophids separated (Fig. 5.C–5.D); they correspond to metalophulid I, metalophulid II, mesolophid, hypolophid, and posterolophid.

Comments. The isolated p4 MACN-PV 3468, holotype of "*Pentastylomys seriei*", is very similar to the p4 of *Tetrastylus* with little wear (see above); all lophids are separated, but there are five (as opposed to four in *Tetrastylus*). MACN-PV 3468 is here interpreted as a little-worn p4 of *Gyriabrus holmbergi*; with more wear, the first two lophids (metalophulid I and metalophulid II) would have fused labially, resulting in the adult occlusal pattern (Fig. 5.E). With advanced wear, the occlusal pattern of p4 becomes tetralophodont in *G. holmbergi* (see Rasia, 2023). MACN-PV 3468 is smaller (MDW 8.19 mm, LLW 6.54 mm) than the smallest known material for *G. holmbergi* (MDW 9.69 mm, LLW 7.09 mm; see Rasia, 2023), supporting the hypothesis that it is a juvenile specimen. Other dinomyids in which the p4 is euhypsodont and pentalophodont include *Isostylomys* Kraglievich, 1926 and *Diaphoromys* Kraglievich, 1931, but MACN-PV 3468 is 34% smaller than a juvenile specimen of *Isostylomys laurillardi* (see Rinderknecht *et al*., 2017) and 44% smaller than the smallest specimen of *Diaphoromys gamayensis* (see Rasia *et al*., 2025b).

Gyriabrus coligatus (Kraglievich, 1932) new combination

Figure 6.A–6.H, 6.K–6.M

Protomegamys coligatus Kraglievich, 1932: 212, fig. 6d; new combination.

Doellomys parcus Fernández de Álvarez, 1947: 60, fig. 2; new synonymy.

Type material. MACN-PV 4727 (holotype of "*Protomegamys*" *coligatus*), isolated left M2 (Fig. 6.A–6.C).

Referred material. MACN-PV 4071 (holotype of "*Doellomys parcus*"), right portion of palate with M1–M2 (Fig. 6.D–6.E); MLP-PV 41-XII-3-183, isolated left upper cheek tooth (Fig. 6.F–6.H).

Geographic occurrence. Entre Ríos Province, Argentina (Kraglievich, 1932).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Kraglievich, 1932).

Emended diagnosis (based on the holotype). Dinomyid with euhypsodont and pentalophodont upper molars, with the first two lophs (anteroloph and protoloph) joined labially, and the last three lophs (mesoloph/mesolophule, metaloph, and posteroloph) joined lingually. With straight lophs, differing from *Gyriabrus sokka*, and larger than all other species of *Gyriabrus*.

Description and comparisons. The holotype (MACN-PV 4727) of *Gyriabrus coligatus* new comb. is an isolated left M2. It is a pentalophodont euhypsodont tooth with the first two lophs joined labially, and the last three joined lingually (Fig. 6.A–6.B). It is identical to the M2 of MACN-A 5879 (Fig. 6.I), referred to *Gyriabrus holmbergi* (see Rasia, 2023), but at least 50% larger (Fig. 6.I, 6.M).

The holotype of "*Doellomys parcus*" (MACN-PV 4071) is a right portion of a palate, including part of the maxillary and palatine, with euhypsodont M1–M2. The M1 is tetralophodont, with the first two lophs joined labially, and the third and fourth lophs joined lingually; the M2 is pentalophodont, with the first and second lophs separated from other structures, and the last three lophs joined lingually (Fig. 6.D–6.E). This morphology is almost identical to specimen MACN-A 5879, holotype of *Gyriabrus holmbergi* (Fig. 6.I); the only difference is that the first two lophs in the M2 of MACN-A 5879 are joined labially rather than separate (Fig. 6.I, 6.K). The first two lophs of the less worn M3 of MACN-A 5879 are separated, so MACN-PV 4071 is interpreted here as an earlier wear stage but larger than *Gyriabrus holmbergi* (Fig. 6.I, 6.K).

MLP-PV 41-XII-3-183 is an isolated left upper cheek tooth, probably a P4 due to the marked crown curvature (Fig. 6.H), larger than any other known material referred to *Gyriabrus holmbergi* (Fig. 6.I–6.J). It is a tetralophodont euhypsodont tooth with the first two lophs joined labially, and the last two joined lingually; it is similar to upper molars of *G. holmbergi* with advanced wear, but the first two lophs are joined lingually (Fig. 6.J, 6.L), indicating a more advanced wear stage.

Comments. Kraglievich (1932) described the holotype of "*Protomegamys coligatus*" but provided no diagnosis or remarks about diagnostic characters of this genus or species. Due to the identical morphologies of the holotype of *"P. coligatus"* and specimens of *G. holmbergi* and the considerably larger size compared to all other species of the genus, the new combination *Gyriabrus coligatus* is here proposed.

Fernández de Álvarez (1947) stated that the morphology of "*Doellomys parcus*" is unique among dinomyids, but the holotype is almost identical to material referred to *G. holmbergi* (see above) except for its larger size, so it is here considered a junior synonym of *Gyriabrus coligatus*.

The specimen MLP-PV 41-XII-3-183 probably corresponds to a P4 given the strong curvature of the crown, with the first two lophs joined labially.

The material here referred to this species is larger than all specimens referred to *G. holmbergi* but have an identical morphology; they are also larger than all other species of the genus (*i.e.*, ?*G. quadratus*, *G. latidens*, ?*G. royoi*, *G. coligatus*, and *G. sokka*; Rasia, 2023; Rasia *et al.*, 2025b). In addition, *Gyriabrus* is here supported as a valid genus and not juvenile individuals of other taxa as was previously proposed (see Rinderknecht *et al.*, 2018).

FIGURE 6

Genus ***Telodontomys*** Kraglievich, 1931

1931. *Telodontomys* Kraglievich: 392.

Pentastylodon Fernández de Álvarez, 1947: 62–64, fig. 4 (in part).

Type and only species. *Telodontomys compressidens* Kraglievich, 1931.

Distribution. Late Miocene of Entre Ríos Province, Argentina.

Telodontomys compressidens Kraglievich, 1931

Figure 7.A–7.H

1931. *Telodontomys compressidens* Kraglievich: 392.

Pentastylodon racedi (Ameghino, 1885), Fernández de Álvarez, 1947: 62–64 (in part).

Type material. MACN-PV 4567, isolated left lower molar (Fig. 7.A–7.C).

Referred material. MACN-PV 13358, isolated left lower molar (Fig. 7.D–7.H).

Geographic occurrence. Entre Ríos Province, Argentina (Nasif *et al.*, 2013).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al.*, 2013).

Description. The type of this species (MACN-PV 4567) is a left lower molar, euhypsodont and with six lophids. The first three lophids are joined labially, the fourth is separated, and the last two (fifth and sixth) are joined lingually. All lophids are very compressed, with narrow flexids (Fig. 7.A, 7.B).

MACN-PV 13358 is a euhypsodont and hexalophodont lower molar, with the first four lophids joined labially and the last two separated (Fig. 7.G, 7.H).

Comments. There is no other known dinomyid with six lophids in the lower molars except for a single tooth (MACN-PV 13358) referred to *Pentastylomys racedi* by Fernández de Álvarez (1947) and here referred to *Telodontomys compressidens*. *Eumegamys paranensis* has six lophids in the p4, but not in the molars.

There are differences between the holotype of *Telodontomys compressidens* (MACN-PV 4567) and MACN-PV 13358 that could be attributed to changes during ontogeny, given the size difference between the two specimens.

The only euhypsodont dinomyids with labial and lingual fusion of the lophids on the lower cheek teeth (also in the lophs on upper cheek teeth) are "gyriabrines" such as *Gyriabrus*, so *Telodontomys* could be closely related to *Gyriabrus*.

FIGURE 7

Genus ***Diaphoromys*** Kraglievich, 1931

1931. *Diaphoromys* Kraglievich: 392.

Eumegamys, Kraglievich, 1932: 117–118 (in part).

Type species. *Diaphoromys gamayensis* Kraglievich, 1931.

Included species. The type species, *Diaphoromys mesopotamicus* Kraglievich, 1932, and *D. arctus* Rusconi, 1945.

Distribution. Late Miocene of La Pampa, Buenos Aires and Entre Ríos provinces, and Pliocene of Buenos Aires Province, Argentina.

Comments. The only species of the genus known from partially complete mandibles with complete cheek tooth series is *Diaphoromys gamayensis*. The other two recognized species are known from isolated teeth, and future discoveries would help assess their validity.

Diaphoromys gamayensis Kraglievich, 1931

Figures 8.A–8.L, 9.A–9.D

1931. *Diaphoromys gamayensis* Kraglievich: 392–393.

2022. *Diaphoromys fiegi* Rusconi, 1934: 104–106, fig. 25. Sostillo *et al.*: 9.

Diaphoromys mesopotamicus Kraglievich, 1932: 212 (in part).

Eumegamys dubius Kraglievich, 1932: 213–214, fig. 2; new synonymy.

Diaphoromys compressidens Fernández de Álvarez, 1947: 59–60, fig. 1; new synonymy.

Type material. MACN-PV 6742, left mandible with p4–m1, right mandible with m1–m3. Kraglievich (1931) listed the number of the holotype as 5742, and later (Kraglievich, 1932) figured it as 6742. The specimen labeled as the holotype in MACN

collections is MACN-PV 6742. The material comes from the Cerro Azul Formation in La Pampa Province (Kraglievich, 1931; Sostillo *et al*., 2022).

Referred material. MACN-PV 3969 (holotype of "*Eumegamys dubius*"), portion of a right mandible with m1–m3 (Fig. 8.A–8.B); MACN-PV 4055 (topotype of "*Eumegamys dubius*"), portion of a right mandible with m1–m3 (Fig. 8.C); MACN-PV 13357 (holotype of "*Diaphoromys compressidens*"), right m1 (Fig. 8.D–8.F); MACN-PV 4581 (topotype of "*Diaphoromys mesopotamicus*"), left m1 (Fig. 8.G–8.I); MACN-PV 4592 (topotype of "*Diaphoromys mesopotamicus*"), right m1; MACN-PV 9028, right m1 (Fig. 8.J–8.L).

Geographic occurrence. Entre Ríos, La Pampa and Buenos Aires provinces, Argentina (Nasif *et al.*, 2013; Sostillo *et al.*, 2022; Rasia *et al.*, 2025b).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al.*, 2013), Cerro Azul Formation (Late Miocene-Early Pliocene; Sostillo *et al.*, 2022; Rasia *et al.*, 2025b), "*Arenas Puelchenses*" (Pliocene?; Rusconi, 1934).

Description. The holotype of "*Eumegamys dubius*" (MACN-PV 3969) and MACN-PV 4055 (topotype of the same species) have m1 with four lophids, the first two joined labially and the last two separated. The m2 and m3 are pentalophodont, with the first three lophids joined labially and the last two separated (Fig. 8.A, 8.C, 9.D). The notch for the tendon of the *masseter medialis pars infraorbitalis* is large, anteroposteriorly long, and located at the level between the m1 and m2 (visible only in MACN-PV 3969; Fig. 8.B), as in other material assigned to *Diaphoromys gamayensis* (see Rasia *et al.*, 2024). In some dinomyids, this notch is below the m1 (*e.g.*, *Dinomys branickii*, *Tetrastylus laevigatus*) or the m2 (*e.g.*, *Carlesia pendolai*, *Rusconia crassidens*). The alveolus of the incisor extends posteriorly to the level of the m3, as in all euhypsodont dinomyids.

MACN-PV 4581 and 4592 are isolated left and right m1s, respectively, both euhypsodont and tetralophodont, with the first three lophids joined labially, and the fourth lophid separated (Fig. 8.G–8.H).

MACN-PV 13357 (holotype of *"Diaphoromys compressidens"*) is an isolated right m1, euhypsodont, tetralophodont, with the first three lophids joined labially, and the fourth lophid separated (Fig. 8.D–8.E).

MACN-PV 9028 is an isolated right m1 with four lophids, the first three joined labially and the last one separated (Fig. 8.J–8.K).

Comments. The holotype of "*Eumegamys dubius*" (MACN-PV 3969; Fig. 9.D) and MACN-PV 4055 (also referred to "*Eumegamys dubius*" in Kraglievich, 1932) were compared to *Eumegamys paranensis* by Kraglievich (1932), but these specimens lack the crenulations characteristic of *Eumegamys* (Fig. 9.E; see emended diagnosis of *Diaphoromys gamayensis* by Sostillo *et al.*, 2022); they are more similar to *D. gamayensis*, particularly the specimen reported by Sostillo *et al.* (2022), in which the first two lophids are joined labially in m1 (Fig. 9.B) rather than the first three as in the holotype (MACN-PV 6742) of *D. gamayensis* (Fig. 9.A). Therefore, the synonymy of "*Eumegamys dubius*" with *Diaphromys gamayensis* is here proposed.

MACN-PV 4581 and 4592, considered to be topotyes of *Diaphoromys mesopotamicus* by Kraglievich (1932), are here referred to *D. gamayensis* considering their size and proportions; LLW of m1 is similar to that of other specimens of *D. gamayensi* and larger than that of the holotype of *D. mesopotamicus* (see below).

MACN-PV 13357 is an isolated right m1 and was the sole material used by Fernández de Álvarez (1947) to erect the new species *Diaphoromys compressidens*. Despite being smaller and slightly more compressed anteroposteriorly (mesiodistally)

than other materials referred to *D. gamayensis*, MACN-PV 13357 is within the variation of *D. gamayensis*, so synonymy is here proposed.

MACN-PV 9028 was identified by Kraglievich (1932) as *Diaphoromys gamayensis* and represents the first record of this species for the Ituzaingó Formation.

Diaphoromys gamayensis and *Eumegamys paranensis* are closely similar in molar occlusal pattern (see Sostillo *et al.*, 2022). However, the p4 is quite different, having five lophids in *D. gamayensis* (Fig. 9.A–9.C) and six lophids in *E. paranensis* (Fig. 9.E), as mentioned by Kraglievich (1926) and Rinderknecht *et al.* (2018). Another feature that distinguishes the species is the location of the notch for the tendon of the *masseter medialis pars infraorbitalis*, which is between m1 and m2 in *D. gamayensis* (though not preserved in the holotype) and below m1 in *E. paranensis*.

FIGURE 8

Diaphoromys mesopotamicus Kraglievich, 1932

Figure 8.M–8.O

1932. *Diaphoromys mesopotamicus* Kraglievich: 212, fig. 5h.

Type material: MACN-PV 9029, isolated left m1 (Fig. 8.M–8.O).

Geographic occurrence. Entre Ríos Province, Argentina (Kraglievich, 1932).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al.*, 2013).

Description. The holotype of *Diaphoromys mesopotamicus* (MACN-PV 9029) is an isolated left m1 with four lophids, the first three joined labially and the last one separated (Fig. 8.M–8.N).

Comments. Kraglievich (1932) indicated that the m1 of *Diaphoromys mesopotamicus* is identical to that of *D. gamayensis* but narrower. This is supported by measurements; LLW is 69% of MDW in the holotype of *D. mesopotamicus*, whereas it is 74-94% in *D. gamayensis*. In the other two specimens referred to *D. mesopotamicus* (see above), it is 84–88%. Since the holotype of *D. mesopotamicus* is the only specimen referred to this

558 species, the range of variation is not known. Better preserved material would give more
559 information about this species.

560 Genus ***Eumegamys*** Kraglievich, 1926

561 1926. *Megamys*, Ameghino, 1889 (in part). Kraglievich: 122.

562 1926. *Eumegamys* Kraglievich: 122–125.

563 **Type species.** *Eumegamys paranensis.*

564 **Included species.** The type species and *Eumegamys scalabrinianus*.

565 **Distribution.** Late Miocene of Argentina (*e.g.*, Nasif *et al*., 2013), Brazil (*e.g*., Kerber
566 *et al*., 2017), and Venezuela (*e.g*., Horovitz *et al*., 2010).

567 ***Eumegamys scalabrinianus*** Kraglievich, 1926

568 Figure 9.F

569 1926. *Megamys patagoniensis*, Ameghino, 1889, lam. 21, fig. 4 (in part). Kraglievich: 122.

570 1926. *Eumegamys scalabrinianus* Kraglievich: 122–125, figs, 4, 5.

571 **Type material.** Right mandible with p4 alveolus, and m1–m2. This material could not
572 be found in the MLP, MAS or MACN, so comparisons are based on the illustration of
573 Kraglievich (1926).

574 **Geographic occurrence.** Entre Ríos Province, Argentina (Kraglievich, 1926).

575 **Stratigraphic occurrence.** Ituzaingó Formation (Kraglievich, 1926).

576 **Description.** The holotype and only known material is a partially preserved right
577 mandible with the alveolus of the p4 and complete m1–m2 (Fig. 9.F). Both molars are
578 tetralophodont, with the first two lophids joined labially, but there is a separate column
579 in m2, located lingually between the second and third lophids.

580 **Comments.** This species is clearly different from the type species of the genus
581 (*Eumegamys paranensis*), which has a pentalophodont m2 (Fig. 9.E). Kraglievich
582 (1926) stated that the type of *E. scalabrinianus* has an evident pathology between the

m1 and m2 that could have affected the development of the m2. Until more material of this species is known, the validity is here maintained.

FIGURE 9

Genus ***Isostylomys*** Kraglievich, 1926

1926. *Megamys*, Ameghino, 1883: 269. Kraglievich: 125.

1926. *Isostylomys* Kraglievich: 125.

1979. *Eumegamysops*, Fernández de Álvarez, 1958: 87–88, fig. 1 (in part). Mones & Castiglioni: 84.

Megamys, Ameghino, 1889 (in part).

Type and only species. *Isostylomys laurillardi* (Ameghino, 1883) (see Rinderknecht *et al.*, 2018).

Distribution. Late Miocene of Argentina and Uruguay (Nasif *et al.*, 2013; Rinderknecht *et al.*, 2018), and Pliocene? of Argentina (Rusconi,1945).

Isostylomys laurillardi (Ameghino, 1883)

Figure 10.A–10.H

1926. *Megamys laurillardi* Ameghino, 1883: 269–270. Kraglievich: 1926: 125, lam. 3, figs. 1–2.

1979. *Isostylomys ameghinoi* Kraglievich, 1932. Mones & Castiglioni: 82, 84

1979. *Isostylomys laevis* Rusconi, 1945. Mones & Castiglioni: 82, 84.

2018. *Isostylomys intermedius* Mones & Castiglioni, 1979: 81–82, fig. 4. Rinderknecht *et al.*: 248.

2018. *Isostylomys magnus* Mones & Castiglioni, 1979: 84. Rinderknecht *et al.*: 248.

Megamys depressidens, Ameghino, 1889, lam. 26, fig. 4 (in part).

Pentastylodon racedi, Fernández de Álvarez, 1947: 62–64 (in part).

Type material. MACN-A 5823, anterior portion of a left mandible, with p4 (Fig. 10.A).

Referred material. MACN-A 5832, isolated left p4 (Fig. 10.B–10.D); MACN-PV 3473, isolated right p4 (Fig. 10.E–10.G); MLP-PV 15-425, fragment of left mandible with m1 and part of m2 (Fig. 10.H).

Geographic occurrence. Entre Ríos Province (Nasif *et al.*, 2013) and Buenos Aires Province (Rusconi, 1945), Argentina, and San José Department, Uruguay (Rinderknecht *et al.*, 2018).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al.*, 2013), Camacho Formation (Late Miocene; Rinderknecht *et al.*, 2018), and "*Arenas Puelchenses*" (Pliocene?; Rusconi, 1945).

Description. MACN-A 5832 is an isolated left p4, euhypsodont and pentalophodont, with the first two lophids joined labially, and the last three lophids separated (Fig. 10.B–10.C); these correspond to metalophulid I, metalophulid II, mesolophid, hypolophid, and posterolophid.

MACN-PV 3473 is a right p4, euhypsodont and pentalophodont, with the first and second lophids joined labially, and the last three lophids separated (Fig. 10.E–10.F).

MLP-PV 15-425 is a portion of a left mandible with complete m1 and the anterior portion of the m2. The m1 is pentalophodont, with the first three lophids joined labially and the last two separated, and the preserved portion of the m2 is constituted by three lophids joined labially (Fig. 10.H).

Comments. The isolated p4, MACN-A 5832, was previously referred to "*Megamys depressidens*" (see Ameghino, 1889) and is here referred to *Isostylomys laurillardi* given that it shares the same morphology of the type of this species.

MACN-PV 3473 was labeled as a left M3 but corresponds to a right p4, given the slight curvature of the crown (Fig. 10.G). It was referred to "*Pentastylodon racedi*" (see Fernández de Álvarez, 1947), but it shares morphology with *Isostylomys laurillardi*, the only species in which the p4 is pentalophodont with the first two lophids joined labially throughout ontogeny (see Rinderknecht *et al.*, 2018).

MLP-PV 15-425, labeled as *Isostylomys* sp., is assigned to *Isostylomys laurillardi*; it has the same morphology with other specimens referred to this species (see Kraglievich, 1926; Rinderknecht *et al.*, 2018), which is the only recognized for the genus (Rinderknecht *et al.*, 2018).

The wide range of size observed in the described p4s was already noted by Rinderknecht *et al*. (2018), who reported specimens of very different size. This species is one of the best known dinomyids thanks to descriptions of associated crania and mandibles from Uruguay (Rinderknecht *et al*., 2018).

FIGURE 10

Genus ***Rusconia*** Kraglievich, 1931

1931. *Rusconia* Kraglievich: 392. Kraglievich, 1932: 180.

Neoepiblema, Ameghino, 1889: 906 (in part).

Pentastylodon Fernández de Álvarez, 1947: 62-64, fig. 4 (in part); new synonymy.

Type and only species. *Rusconia crassidens* Kraglievich (1931).

Distribution. Late Miocene of Entre Ríos Province, Argentina.

Rusconia crassidens Kraglievich, 1931

Figure 11.A–11.G

1931. *Rusconia crassidens* Kraglievich: 392. Kraglievich, 1932: 180–181, figs. 6h, 7d.

Neoepiblema? *contorta* Ameghino, 1889: 906, lam. 80, fig. 14 (in part); new synonymy.

Pentastylodon racedi, Fernández de Álvarez 1947: 62-64, fig. 4 (in part); new synonymy.

Type material. MACN-PV 9116, portion of left mandible with m1–m2 (Fig. 11.A–11.C).

Referred material. MACN-PV 4575 (holotype of "*Neoepiblema*? *contorta*"), anterior portion of a left lower molar (Fig. 11.D–11.E); MACN-PV 2608, isolated m2 or m3 (Fig. 11.F–11.G).

Geographic occurrence. Entre Ríos Province, Argentina (Nasif *et al.*, 2013).

Stratigraphic occurrence. Ituzaingó Formation (Late Miocene; Nasif *et al.*, 2013).

Description. The cheek teeth of the holotype (MACN-PV 9116) are euhypsodont and sub-quadrangular. The m1 is pentalophodont, with the first four lophids (metalophulid I, neolophid, metalophulid II, hypolophid) joined labially, and the last lophid (posterolophid) separated (Fig. 11.A, 11.C). The third and fourth lophids of the m1 have deep indentations (Fig. 11.C). The m2 is also pentalophodont, but with the first three lophids (metalophulid I, neolophid, metalophulid II) joined labially, and the last two (hypolophid, posterolophid) separated (Fig. 11.A, 11.C). The walls of the lophids are sinuous.

The mandible is low, unlike the extant *Dinomys branickii*. The notch for the tendon of the *masseter medialis pars infraorbitalis* is large and anteroposteriorly long, located below the m2 (Fig. 11.B).

MACN-PV 4575 is an anterior portion of a left lower molar, with three lophids joined labially (Fig. 11.D–11.E), that resembles the m2 of *Rusconia crassidens*, m2–m3 of *Eumegamys paranensis*, and m1-m3 of *Diaphoromys gamayensis* and *Isostylomys laurillardi*. It is referred to *R. crassidens* because of the straight lophids with sinuous margins.

MACN-PV 2608 is an isolated m2 or m3, euhypsodont and pentalophodont, with the first three lophids joined labially and the last two separated. There are deep indentations in the second and fifth lophids (Fig. 11.F–11.G).

Comments. This genus and species was known by its holotype alone. It differs from all other euhypsodont dinomyids in having a pentalophodont m1 with the first four lophids joined labially. In most dinomyids with pentalophodont lower molars (‘gyriabrines’ and ‘eumegamyines’), only the first three lophids are joined labially.

Specimen MACN-PV 4575, part of the type series of "*Neoepiblema*? *contorta*" (Ameghino, 1889: lam. 80, fig. 14), is here referred to *Rusconia crassidens*.

MACN-PV 2608 was referred by Fernández de Álvarez (1947) to "*Pentastylodon racedi*". Its morphology is similar to the lower molars of several dinomyids (*i.e.* *Isostylomys*, *Eumegamys*, *Rusconia*, *Diaphoromys*), but the marked indentations in the lophids permit referral to *Rusconia crassidens*. These isolated indentations differ from the crenulations observed in *Potamarchus murinus* and *Eumegamys paranensis*.

FIGURE 11

Genus ***Eumegamysops*** Kraglievich in Fernández de Álvarez, 1947

1947. *Megamys*, Ameghino, 1889; Fernández de Álvarez: 61–62, fig. 3.

1947. *Eumegamysops* Kraglievich in Fernández de Álvarez: 61–62, fig. 3.

Pentastylodon Fernández de Álvarez, 1947: 62–64, fig. 4 (in part).

Type and only species. *Eumegamysops praependens*.

Distribution. Late Miocene of Entre Ríos Province, Argentina.

Eumegamysops praependens (Ameghino, 1889)

Figure 12.A–12.D

1947. *Megamys praependens* Ameghino, 1889. Fernández de Álvarez: 61–62, fig. 3.

1947. *Eumegamysops praependens* (Ameghino, 1889). Fernández de Álvarez: 61–62, fig. 3.

Pentastylodon racedi, Fernández de Álvarez, 1947: 62–64, fig. 4 (in part).

Type material. MACN-PV 4584, isolated left M2 (Fig. 12.B).

Referred material. MACN-PV 13353, isolated right M2 (Fig. 12.C–12.D).

Description. MACN-PV 13353 is a hexalophodont M2, with the first two lophs separated and the last four lophs joined lingually (Fig. 12.C–12.D).

Comments. The specimen MACN-PV 13353, originally assigned to "*Pentastylodon racedi*" (see Fernández de Álvarez, 1947), is labeled as a right M1 but is more likely a right M2, given its similarities with the M2 (MLP-PV 41-XII-13-237) of

Eumegamysops praependens, in which the first three lophs are separated and the last three are joined lingually (Fig. 12.A). Also, MACN-PV 13353 is slightly larger than the M2 of MLP-PV 41-XII-13-237.

Many specimens were assigned to this species by Fernández de Álvarez (1947, 1958), including a partially complete cranium (MLP-PV 41-XII-13-237); these are not redescribed in this work given that the status of this species is not in doubt.

FIGURE 12

Genus ***Arazamys*** Rinderknecht, Bostelmann & Ubilla, 2011

2011. *Arazamys* Rinderknecht, Bostelmann & Ubilla: 170–171.

Pentastylodon Fernández de Álvarez, 1947: 62–64 (in part).

Type and only species. *Arazamys castiglionii* Rinderknecht *et al*., 2011.

Distribution. Late Miocene of Uruguay and Argentina.

Arazamys castiglionii Rinderknecht, Bostelmann & Ubilla, 2011

Figure 12.E–12.G

2011. *Arazamys castiglionii* Rinderknecht, Bostelmann & Ubilla: 171–175, figs. 2, 3c, 4c, 6, 7, 8.

Pentastylodon seriei, Fernández de Álvarez, 1947: 62–64 (in part).

Type material. MNHN 2521, posterior portion of the skull, left P4–M3, right M1–M3, right incisor and atlas.

Referred material. MACN-PV 13354, isolated left M3.

Description. MACN-PV 13354 is a euhypsodont and pentalophodont M3, with the first three lophs separated, and the last two joined lingually (Fig. 12.F–12.G).

Comments. MACN-PV 13354 was referred to "*Pentastylodon racedi*" by Fernández de Álvarez (1947). Although it is an M3, its morphology does not match the description of Fernández de Álvarez (1947) of "*Pentastylodon racedi*", which has the first two lophs separated and the last three joined lingually. Rather, it is identical to the M3 (Fig. 12.E) of the holotype and only known material of *Arazamys castiglionii*. This species is the

only “eumegamyid” with a simple M3; it has five parallel lophs of similar morphology rather than the more complex posterior lophs typical of “eumegamyids” (see Rinderknecht *et al*., 2011, 2018). The specimen also resembles the holotype of *A. castiglionii* (MNHN 2521) in size (MDW 26.51 mm compared to MDW 26.3 and 26.7 mm).

This is the first record of *Arazamys castiglionii* in Argentina.

“***Briaromys trouessartianus***” Ameghino, 1889 *nomen dubium*

1889. *Briaromys trouessartianus* Ameghino: 904–905, lam. 72, fig. 15; Ameghino, 1906: 417, fig. 304.

Comments. Ameghino (1889) erected this genus and species based on a right mandible with the incisor and three cheek teeth (p4–m2), the latter all with five lophids, the first two joined labially and the last three separated, with narrow flexids. Later, Ameghino (1906, fig. 304) illustrated three right lower cheek teeth of this species, probably m1–m3, all tetralophodont, with the first three lophids joined labially and the fourth lophid separated. According to the description (Ameghino, 1906: 417), the cheek teeth have short roots. These cheek teeth are very similar to those of *Potamarchus murinus*, *P. sigmodon* and *Olenopsis aequatorialis* (Anthony, 1922).

In the collection of the MACN, only one specimen is catalogued as “*Briaromys trouessartianus*” (MACN-A 5882), a fragment of a lower molar with two lophids joined labially, probably the first two.

The two descriptions and illustrations of this genus and species (Ameghino, 1889, 1906) are completely different even though they partially refer to the same teeth (p4–m2 in Ameghino, 1889 and m1–m3 in Ameghino, 1906). None of the specimens described and figured by Ameghino could be found in the collections of MACN. Future studies might be able to clarify the validity of this taxon.

“***Megamys racedi***” Ameghino, 1885 *nomen vanum*

1885. *Megamys racedi* Ameghino: 34.

1947. *Pentastylodon racedi* (Ameghino, 1885). Fernández de Álvarez: 62–64, fig. 4.

Comments. Ameghino (1885) described a new species, *Megamys racedi*, based on an isolated left lower incisor and one isolated cheek tooth (MACN-A 5819). Later, Fernández de Álvarez (1947) erected the new genus *Pentastylodon* to include *P. racedi*; she defined a new holotype (MACN-PV 4587) without any comment or justification and referred numerous isolated cheek teeth to this species (MACN-PV 13348, 13474, 3473, 13353, 13354, 13358, 2608). Some of these specimens are referred to other species above, and are addressed again below.

The incisor could not be found in the collections at MACN; nevertheless, no incisor characters can be used to distinguish Dinomyidae species or genera. Ameghino (1885) remarked that its size was distinctive (MDW 29 mm, LLW 30 mm), but these dimensions are similar to those of other giant dinomyids such as *Arazamys castiglionii* (MDW 21 mm, LLW 24.6 mm), *Eumegamysops praependens* (MDW 22.5 mm, LLW 22.2 mm), *Isostylomys laurillardi* (MDW 25.1 mm, LLW 23.2 mm), and *Josephoartigasia monesi* (MDW 33.65 mm) (see Fernández de Álvarez, 1958; Rinderknecht & Blanco, 2008; Rinderknecht *et al*., 2011, 2018).

The cheek tooth (MACN-A 5819; Fig. 13.A–13.C) originally described by Ameghino (1885) as a right p4 was later figured (Ameghino, 1889), but it corresponds to a left upper cheek tooth, most likely a P4 given its occlusal morphology and crown curvature. It is very similar in size and morphology to the P4 of *Eumegamysops praependens* and *Arazamys castiglionii*.

The specimen MACN-PV 4587 (Fig. 13.D–13.F), figured and considered the holotype by Fernández de Álvarez (1947), is identified as a left P4. It is pentalophodont, with the last three lophs joined lingually, like MACN-A 5819, but it is more quadrangular, with similar mesiodistal and labiolingual widths. The morphology of MACN-PV 4587 is similar to that of *Eumegamysops praependens* but not identical; it

786 also resembles *Arazamys castiglionii* and *Josephoartigasia monesi* Rinderknecht &
787 Blanco, 2008.
788 MACN-PV 13348 (Fig. 13.G–13.I) is labeled as a M2. It is identical to the M1 of
789 *Eumegamysops praependens* and the M1-M2 of *Isostylomys laurillardi*.
790 MACN-PV 13474 (Fig. 13.J–13.L) is labeled as a m2, and the attached dentary
791 fragment confirms this locus. It is tetralophodont with the first three lophids joined
792 labially. This morphology is present in the lower molars of *Isostylomys*, *Diaphoromys*,
793 *Eumegamys* and *Rusconia*.
794 Most of the specimens mentioned above (MACN-A 5819, MACN-PV 4587,
795 13348, and 13474) are considered as Dinomyidae indet. (Fig. 13). MACN-PV 3473,
796 labeled as a M3, is a p4 that is referred above to *Isostylomys laurillardi*. MACN-
797 PV13353, labeled as a right M1 but more likely a M2, is referred above to
798 *Eumegamysops praependens*. MACN-PV 13354, a left M3, is referred above to
799 *Arazamys castiglionii*. MACN-PV 13358 is a m1 referred above to *Telodontomys*
800 *compressidens*. MACN-PV 2608, labeled as a m2, is a m2 or m3 referred above to
801 *Rusconia crassidens*.
802 Given that none of the material on which this species is based can be
803 differentiated from other species, "*Megamys racedi*" is considered here a *nomen vanum*.
804 In addition, many specimens previously assigned to this species (Fernández de Álvarez,
805 1947) are here referred to other taxa. The genus "*Pentastylodon*" is also considered a
806 *nomen vanum*, since it does not include any valid species.
807 FIGURE 13
808 "***Megamys depressidens***" Ameghino, 1885 *nomen vanum*
809 1885. *Megamys depressidens* Ameghino: 30–31.
810 1981. "*Megamys*" *depressidens* Ameghino, 1885. Mones: 613.
811 2005. "*Eumegamys*" *depressidens* (Ameghino, 1885). Candela: 44.

Comments. This species was erected by Ameghino (1885) based on an isolated incisor (MACN-A 5824). Ameghino (1885) stated that it was 50% larger than the extant capybara (*Hydrochoerus hydrochaeris*), and with an incisor more labio-lingually compressed (MDW 13 mm, LLW 9 mm) than in other dinomyids. These features suggest than the specimen might correspond to a large caviid (*e.g.*, *Cardiatherium paranensis*), and there is no sufficient evidence to maintain this species, lacking characters that permit to differentiate it from any other caviomorphs of equivalent size. Therefore, "*Megamys depressidens*" is here considered a *nomen vanum*.

Later, Ameghino (1889, lam. 21, fig. 12) referred and figured a right M3 to this species that could not be found in MACN collections. This material is identical to the M3 of *Eumegamysops praependens* based on the information in Ameghino (1889).

The specimen MACN-A 5832 was also referred to this species and figured by Ameghino (1889, lam. 26, fig. 4). It is a euhypsodont and pentalophodont p4, with the first two lophids joined labially. Its morphology permits referral to *Isostylomys laurillardi* (see above).

DISCUSSION

The study of material (including holotypes and referred material) of dinomyid rodents from the Ituzaingó Formation (Late Miocene of Entre Ríos Province, northeastern Argentina) allowed the taxonomic status of several doubtful taxa to be reevaluated.

"*Tetrastylomys castellanosi*", based on a single tooth, is here considered a juvenile specimen of a large species of *Tetrastylus* due to similarities with juvenile individuals of larger species of this genus.

The three isolated teeth that comprise the type series of "*Neoepiblema*? *contorta*" (="*Eumegamys contortus*") are here referred to *Carlesia pendolai* (MACN-PV 4576,

837 4067) and *Rusconia crassidens* (MACN-PV 4575), given similarities in size and
838 morphology with these species.
839 "*Pentastylomys seriei*", based on a single tooth, is here considered a juvenile
840 specimen of *Gyriabrus holmbergi*, given its size and morphology and comparisons with
841 juvenile individuals of *Tetrastylus*.
842 "*Protomegamys*" *coligatus* is here transferred to *Gyriabrus*, given its identical
843 morphology but larger size, resulting in the proposal of the new combination *Gyriabrus*
844 *coligatus*. "*Doellomys parcus*" is considered a junior synonym of *G. coligatus*, due to
845 its similar size and morphology.
846 "*Diaphoromys compressidens*" and "*Eumegamys dubius*" are considered
847 synonyms of *Diaphoromys gamayensis*, by comparison with fairly complete specimens
848 attributed to *D. gamayensis*.
849 "*Briaromys trouessartianus*" is considered a *nomen dubium* until the holotype or
850 new material are found. "*Megamys racedi*" and "*Megamys depressidens*" are considered
851 *nomina vana*, given that the material referred to these species cannot be differentiated
852 from other taxa. Some specimens previously assigned to "*Megamys racedi*" are here
853 referred to *Eumegamysops praependens*, *Arazamys castiglionii*, *Telodontomys*
854 *compressidens*, and *Rusconia crassidens*, and specimens previously considered
855 "*Megamys depressidens*" are here referred to *Eumegamysops praependens* and
856 *Isostylomys laurillardi*, given the similar size and morphology.
857 This taxonomic revision reduces the diversity of the family Dinomyidae in the
858 Ituzaingó Formation (and therefore the diversity of Caviomorpha as a whole). On the
859 other hand, *Pseudosigmomys paranensis*, *Telodontomys compressidens Diaphoromys*
860 *mesopotamicus*, *Eumegamys scalabrinianus*, and *Rusconia crassidens* are confirmed as
861 valid taxa; although they are known from a single or a few specimens (and in some

862 cases, very incomplete ones), they are different from all other known dinomyids.
863 *Arazamys castiglionii* is reported for the first time for the Ituzaingó Formation, which
864 also constitutes the first report of this species for Argentina.
865 Candela (2005) was the first comprehensive summary of the caviomorph rodents
866 from the Ituzaingó Formation. Counting 19 genera and 34 species, it was the highest
867 recorded diversity for dinomyids in a single locality and formation. The results of the
868 present study (building on Ameghino, 1891; Nasif *et al.*, 2013; Rinderknecht *et al.*,
869 2018; Rasia, 2023; see Tab. 1), establish a diversity of 13 genera and 19 species for the
870 Ituzaingó Formation.
871 The diversity of dinomyids from the Ituzaingó Formation remains notably higher
872 than other coeval units like Urumaco (five genera), Solimões (nine genera), Camacho
873 (four genera) and Cerro Azul (four genera) formations (see Appendix 1).
874 As previously noted (Rasia *et al.*, 2025b), the dinomyid assemblages of Late
875 Miocene (Chasicoan and Huayquerian stages/ages) levels of central Argentina differ
876 from those of lower latitudes, not only in the number of taxa (see Appendix 1), but also
877 in the absence of protohypsodont taxa (traditionally considered Potamarchinae). The
878 absence of protohypsodont dinomyids is also observed in the Late Miocene Camacho
879 Formation in Uruguay, but all the species of this unit are also recorded in the Ituzaingó
880 Formation (see Appendix 1).
881 A constant occlusal pattern for the cheek teeth has been proposed for some
882 euhypsodont dinomyids like *Isostylomys laurillardi* (see Rinderknecht *et al.*, 2018),
883 with juveniles and adults sharing the same pattern. On the other hand, an occlusal
884 pattern changing with wear has been proposed for several taxa, such as *Gyriabrus*
885 *holmbergi* (see Rasia, 2023), *Diaphoromys gamayensis* (see Sostillo *et al*., 2022),
886 *Bondesiomys chasiquensis* (see Rasia *et al.*, 2025b), and the extant *Dinomys branickii*

(see Nasif & Abala, 2015). The fact that some specimens of *Gyriabrus holmbergi* and *Bondesiomys chasiquensis* have different occlusal patterns in the right and left cheek teeth of the same locus (see Rasia, 2023, fig. 4b; Rasia *et al.*, 2025b, fig. 7c, d) indicates intraspecific variation that could be interpreted as different stages of wear.

In this work, a changing occlusal pattern is proposed for *Gyriabrus coligatus*, *Telodontomys compressidens*, and *Eumegamysops praependens*, based on different specimens. Future discoveries of more complete material would help lead to a better understanding of ontogenetic changes in the occlusal pattern of euhypsodont dinomyids.

CONCLUSIONS

The study of the type material of several dinomyid species from the Ituzaingó Formation lead to conclude that: "*Tetrastylomys castellanosi*" should be considered *Tetrastylus* sp.; the type series of "*Eumegamys contortus*" pertains to *Carlesia pendolai* and *Rusconia crassidens*; "*Pentastylomys seriei*" is a junior synonym of *Gyriabrus holmbergi*; "*Protomegamys*" *coligatus* should be included in the genus *Gyriabrus*; "*Doellomys parcus*" is a junior synonym of *Gyriabrus coligatus* (new combination); "*Diaphoromys compressidens*" and "*Eumegamys dubius*" are junior synonyms of *Diaphoromys gamayensis*; "*Briaromys trouessartianus*" is *nomen dubium*; "*Megamys racedi*" and "*Megamys depressidens*" are *nomina vana*; and *Pseudosigmomys paranensis*, *Telodontomys compressidens*, *Diaphoromys mesopotamicus*, *Eumegamys scalabrinianus*, and *Rusconia crassidens* are valid taxa. Finally, *Arazamys castiglionii* is recognized for the first time in the Ituzaingó Formation and in Argentina.

This taxonomic revision reduces the diversity of Dinomyidae in the Ituzaingó Formation to 13 genera and 19 species. This diversity is still higher than in other coeval

911 units of South America (*e.g.*, Urumaco, Solimões, Camacho, and Cerro Azul
912 formations) and represents the highest diversity for the family during its history.
913
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Figure captions

Figure 1. Map of South America showing localities discussed in the text. The star indicates location of the Ituzaingó Formation in Entre Ríos Province. 1, Urumaco Formation, Urumaco; 2, Solimões Formation, Acre Region; 3, Ipururo Formation, Fitzcarrald Arch; 4, Camacho Formation, Colonia Department; 5, Cerro Azul Formation, Pampean Region.

Figure 2. Nomenclature of cheek teeth structures. **A,** upper premolar; **B,** upper molar; **C,** lower premolar; **D,** lower molar. Abbreviations: **anl,** anteroloph; **hyp,** hypolophid; **mes,** mesolophid; **met I,** metalophulid I; **met II,** metalophulid II; **msl/mlf,** mesoloph/mesolophule; **mtl,** metaloph; **neo,** neolophid; **pol,** posteroloph; **pos,** posterolophid; **prl,** protoloph.

Figure 3. Cheek teeth of ***Potamarchus murinus*** and ***Tetrastylus*****. A–D, *P. murinus*. A, MACN-A** 5870, right P4-M3 in occlusal view**; B**–**D, MACN-A** 1498 (holotype of **"*Discolomy cuneus*"**), right upper cheek tooth in **B,** occlusal, **C,** schematic outline, and **D,** labial view; **E–F,** ***Tetrastylus*** sp., **MACN-PV** 3332 (holotype of **"*Tetrastylomys castellanosi*"**), left p4 in **E,** occlusal view and **F,** schematic outline; **G,** ***T. laevigatus*****, MACN-PV** 2610, right p4 schematic occlusal outline; **H–I,** ***Tetrastylus*** sp., **MACN-PV** 2596, right P4 in **H,** occlusal view and **I,** schematic outline. Scale bar equals 1 cm in A, E–I and 0.5 cm in B–D.

Figure 4. Lower cheek teeth of ***Carlesia pendolai*****. A**–**B, MACN-A** 4576, right lower molar in **A,** occlusal view and **B,** schematic outline; **C**–**D, MACN-PV** 4067, right lower

molar in **C,** occlusal view and **D,** schematic outline; **E, MACN-A** 3986 (holotype), right m2–m3 occlusal schematic outline. Scale bar equals 1 cm.

Figure 5. Lower cheek teeth of ***Pseudosigmomys paranensis*** and ***Gyriabrus holmbergi*****. A**–**B, *Pseudosigmomys paranensis*, MACN-PV** 3453, left lower molar in **A,** occlusal view and **B,** schematic outline; **C–E, *Gyriabrus holmbergi*; C–D, MACN-PV** 3468 (holotype of "***Pentastylomys seriei***"), left p4 in **C,** occlusal view and **D,** schematic outline; **E, MLP-PV** 15-252, right p4 occlusal schematic outline. Scale bar equals 0.5 cm.

Figure 6. Upper cheek teeth of ***Gyriabrus*****. A**–**H, K**–**M,** upper cheek teeth of ***Gyriabrus coligatus*****; A**–**C, MACN-PV** 4727 (holotype of "***Protomegamys*****" *coligatus***), left M2 in **A,** occlusal, **B,** schematic, **C,** and lingual views; **D**–**E, MACN-PV** 4071 (holotype of "***Doellomys parcus***") palate with right M1–M2 in **D,** occlusal view and **E,** schematic outline; **F**–**H, MLP-PV** 41-XII-3-183, left P4 in **F,** occlusal, **G,** schematic, and **H,** lingual views; **I**–**J,** upper cheek teeth of ***Gyriabrus holmbergi*****; I, MACN-A** 5879, occlusal outline of right P4–M3 (reversed); **J, MNHN** 1342, occlusal outline of left P4–M3; **K, MACN-PV** 4071, occlusal outline of right M1–M2 (reversed); **L, MLP-PV** 41-XII-3-183, occlusal outline of left P4; **M, MACN-PV** 4727, occlusal outline of left M2. Black arrows indicate different degree of fusion of lophs in P4. Grey arrows indicate different degree of fusion of lophs in M2. Scale bar equals 1 cm.

Figure 7. Lower molars of ***Telodontomys compressidens*****. A**–**C, MACN-PV** 4567 (holotype), left lower molar in **A,** occlusal view, **B,** schematic outline, and **C,** mesio-

lingual view; **D–H, MACN-PV** 13358, left lower molar in **D,** occlusal view, **E,** labial view, **F,** lingual view, **G,** basal view, and **H,** schematic outline. Scale bar equals 1 cm.

Figure 8. Mandibles and lower cheek teeth of ***Diaphoromys*. A–L, *Diaphoromys gamayensis*; A–B, MACN-PV** 3969 (holotype of **"*Eumegamys dubius*"**), right mandible in **A,** occlusal and **B,** lateral view; **C, MACN-PV** 4055 (topotype of **"*E. dubius*"**), right mandible in occlusal view; **D–F, MACN-PV** 13357 (holotype of **"*D. compressidens*"**), right m1 in **D,** occlusal view, **E,** schematic outline, and **F,** lingual view; **G–I, MACN-PV** 4581 (topotype of ***D. mesopotamicus***), left m1 in **G,** occlusal view, **H,** schematic outline, and **I,** lingual view; **J–L, MACN-PV** 9028, right m1 in **J,** occlusal view, **K,** schematic outline, and **L,** lingual view; **M–O, *Diaphoromys mesopotamicus*, MACN-PV** 9029 (holotype), left m1 in **M,** occlusal view, **N,** schematic outline, and **O,** lingual view. Scale bar equals1 cm.

Figure 9. Cheek teeth schematic outline of ***Diaphoromys*** and ***Eumegamys***. **A–D, *Diaphoromys gamayensis*; A, MACN-PV** 6742 (holotype), right p4–m3 (m2–m3 reversed); **B, GHUNLPam** 5133, right p4–m3; **C, MMH-CH** 88-6-66, right p4–m1; **D, MACN-PV** 3969 (holotype of **"*Eumegamys dubius*"**), right m1–m3; **E, *Eumegamys paranensis*, MLP-PV** 15-245, right p4–m3**; F, *Eumegamys scalabrinianus***, right m1–m2**.** Scale bar equals 1 cm.

Figure 10. Lower cheek teeth of ***Isostylomys laurillardi*. A, MACN-A** 5823 (holotype), left p4 in occlusal view; **B–D, MACN-A** 5832, left p4 in **B,** occlusal view, **C,** schematic outline, and **D,** lingual view; **E–G, MACN-PV** 3473, right p4 in **E,** occlusal view, **F,**

schematic outline, and **G,** labial view; **H, MLP-PV** 15-425, 1, left mandible with m1–m2. Scale bar equals 1 cm.

Figure 11. Mandible and lower molars of ***Rusconia crassidens*****. A**–**C, MACN-PV** 9116 (holotype), left mandible in **A,** occlusal, and **B,** lateral view, **C,** occlusal outline of m1–m2; **D**–**E, MACN-A** 4575, left lower molar in **D,** occlusal view and **E,** schematic outline; **F–G, MACN-PV** 2608, left m2 or m3 in **F,** occlusal view and **G,** schematic outline. Scale bar equals 1 cm.

Figure 12. Upper cheek teeth of ***Eumegamysops praependens*** and ***Arazamys castiglionii*****. A**–**D, *Eumegamysops praependens*; A, MLP-PV** 41-XII-13-237, right P4–M3 schematic outline; **B, MACN-PV** 4584 (holotype), left M2 occlusal outline; **C–D, MACN-PV** 13353, right M2 in **C,** occlusal view and **D,** schematic outline**; E**–**G, *Arazamys castiglionii*; A, MNHN** 2521 (holotype), left P4–M3 ; **F–G, MACN-PV** 13354, left M3 in **F,** occlusal view and **G,** schematic outline. Scale bar equals 1 cm.

Figure 13. Cheek teeth of indeterminate Dinomyidae. **A–C, MACN-A** 5819, left P4 in **A,** occlusal; **B,** schematic outline; **C,** lingual view; **D–F, MACN-PV** 4587, right P4 in **D,** occlusal; **E,** schematic outline; **F,** lingual view; **G–I, MACN-PV** 13348, right M2 in **G,** occlusal; **H,** schematic outline; **I,** lingual view; **J–L, MACN-PV** 13474, right m2 in **J,** occlusal; **K,** schematic outline; **L,** lingual view. Scale bar equals 1 cm.


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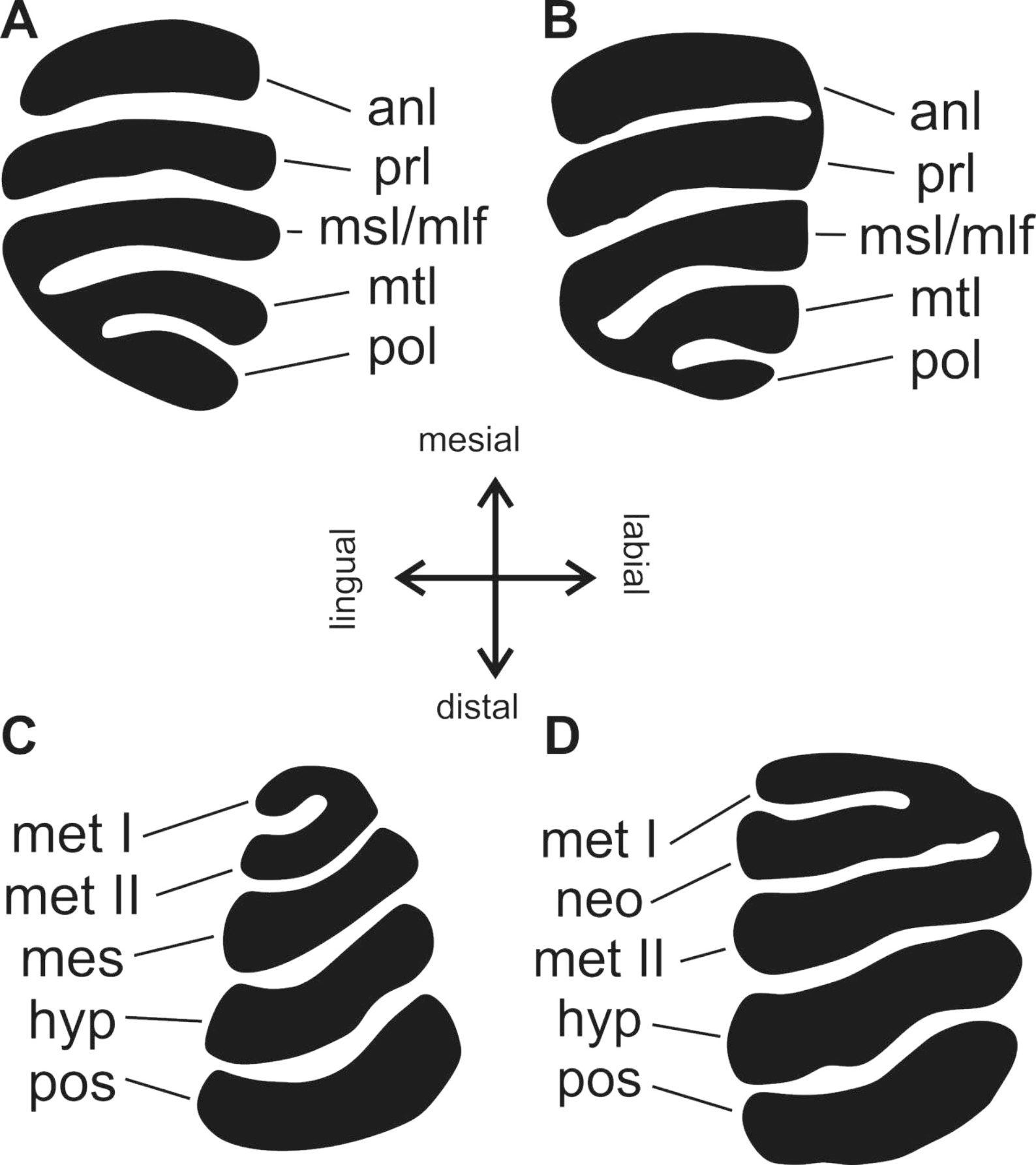
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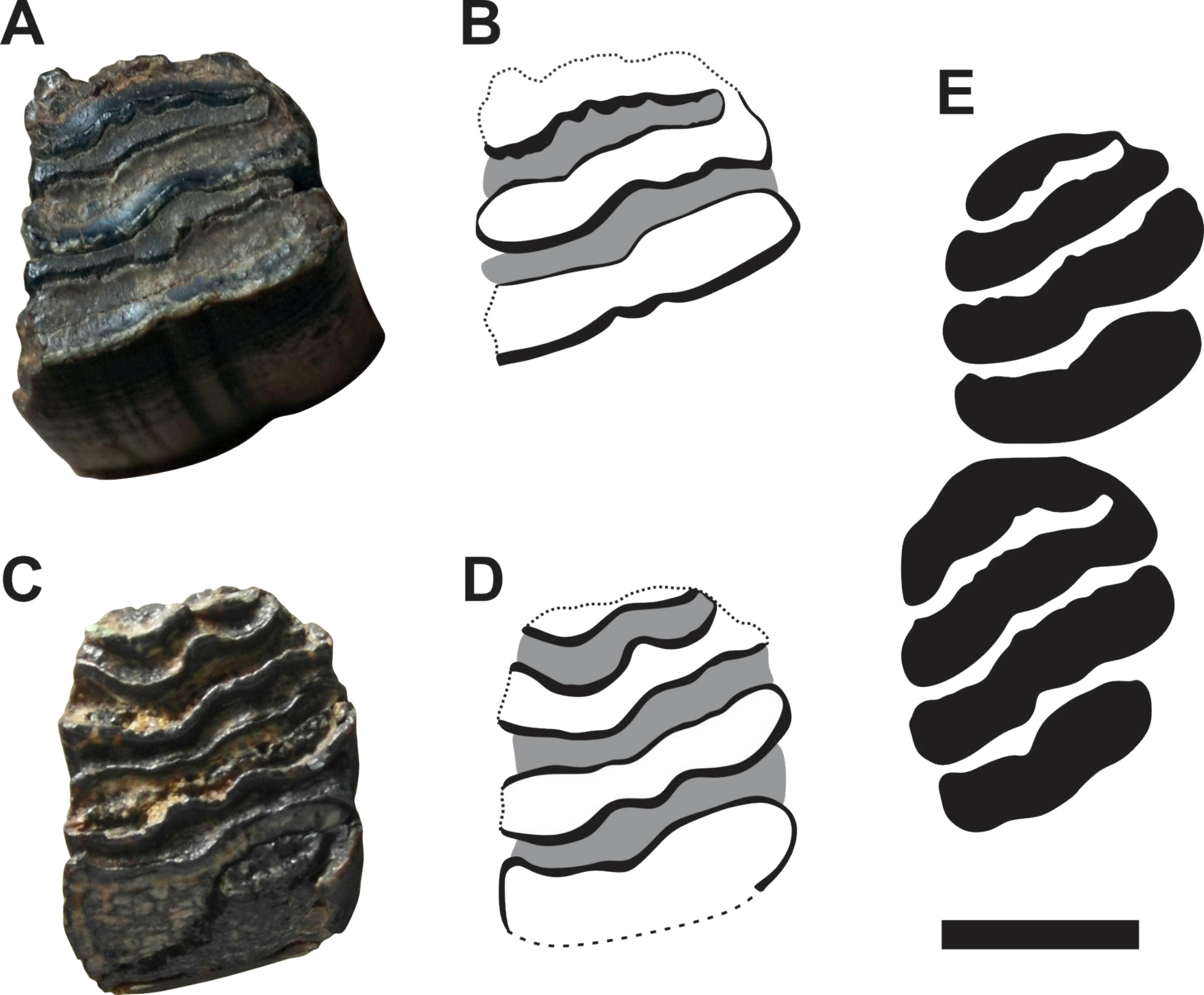
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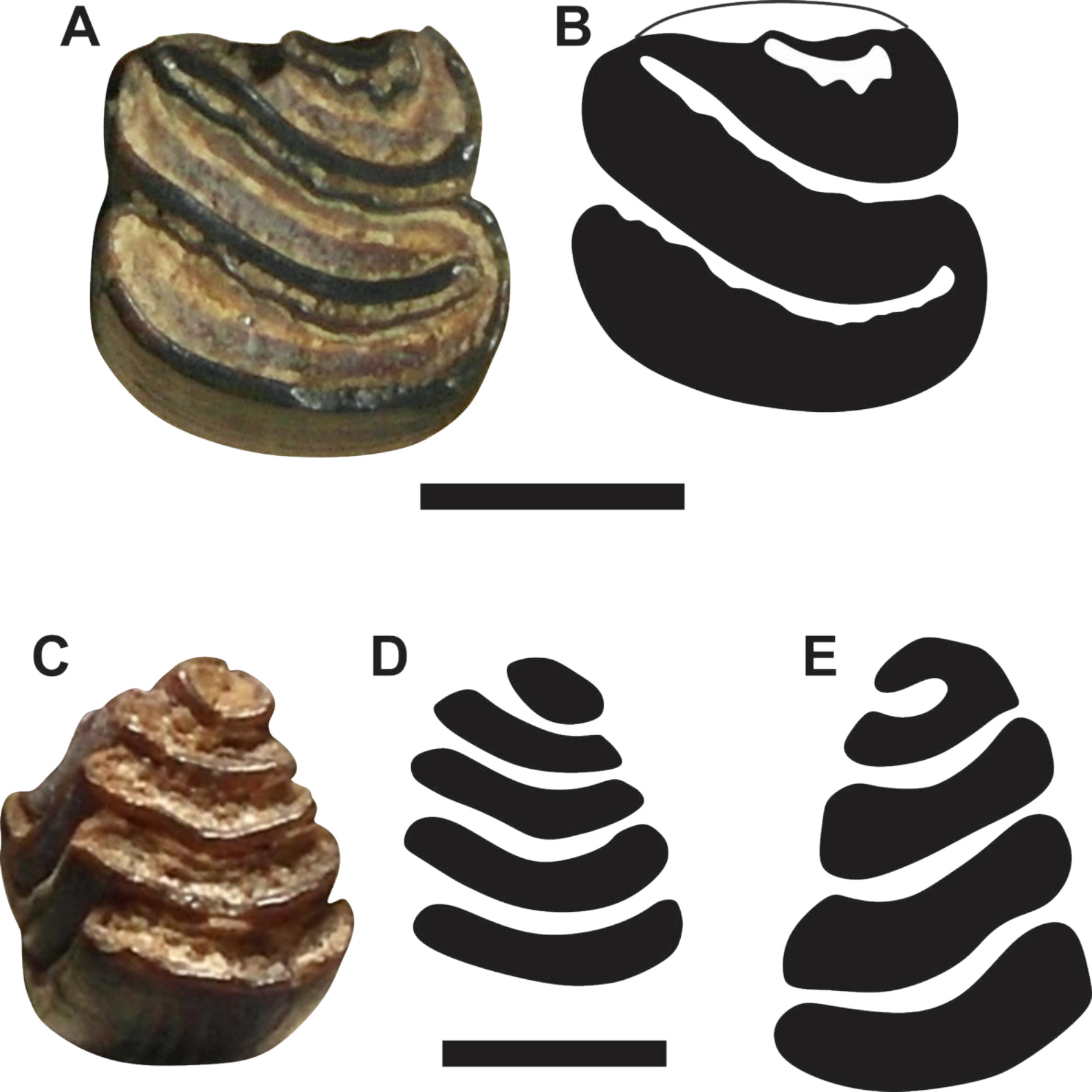
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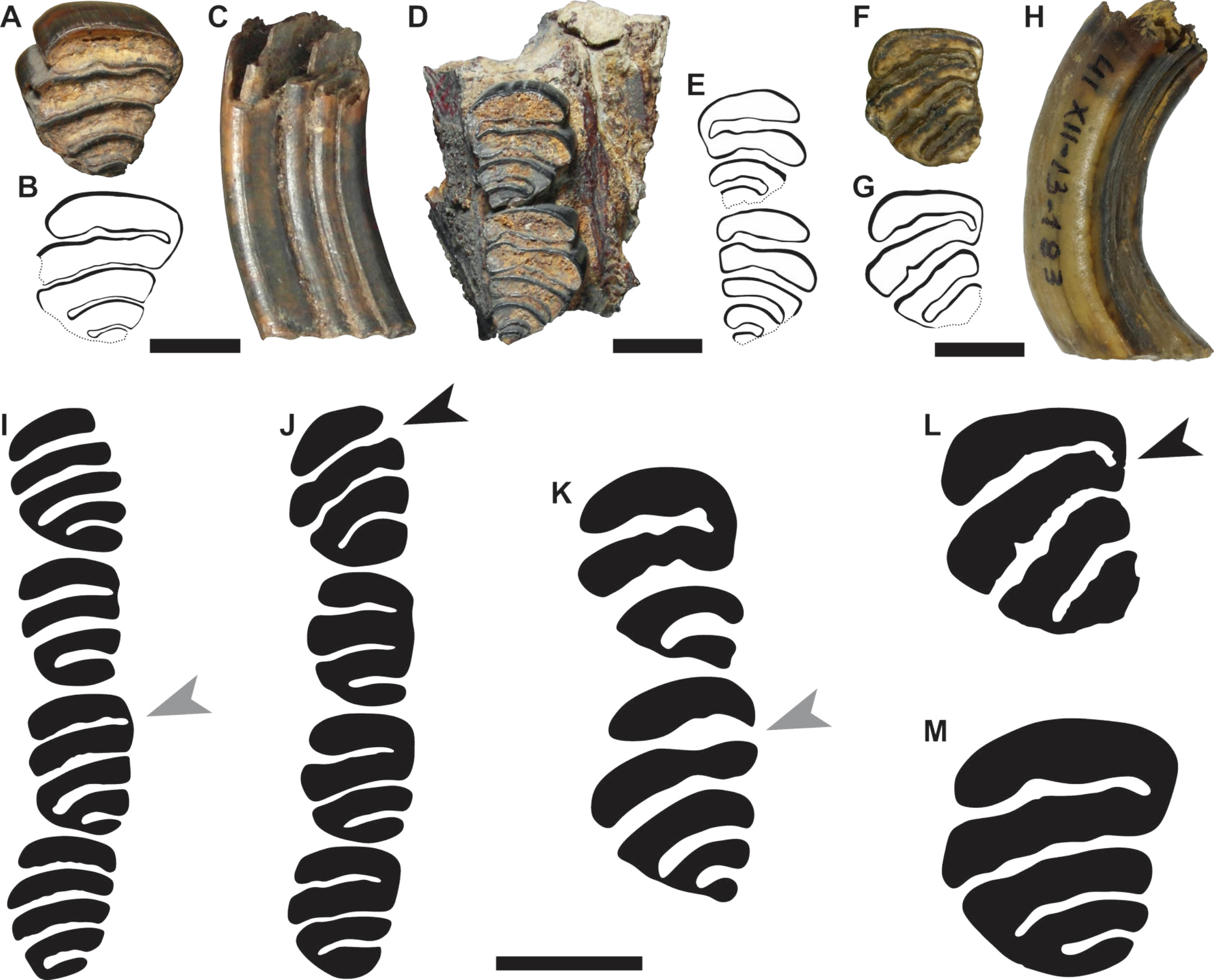
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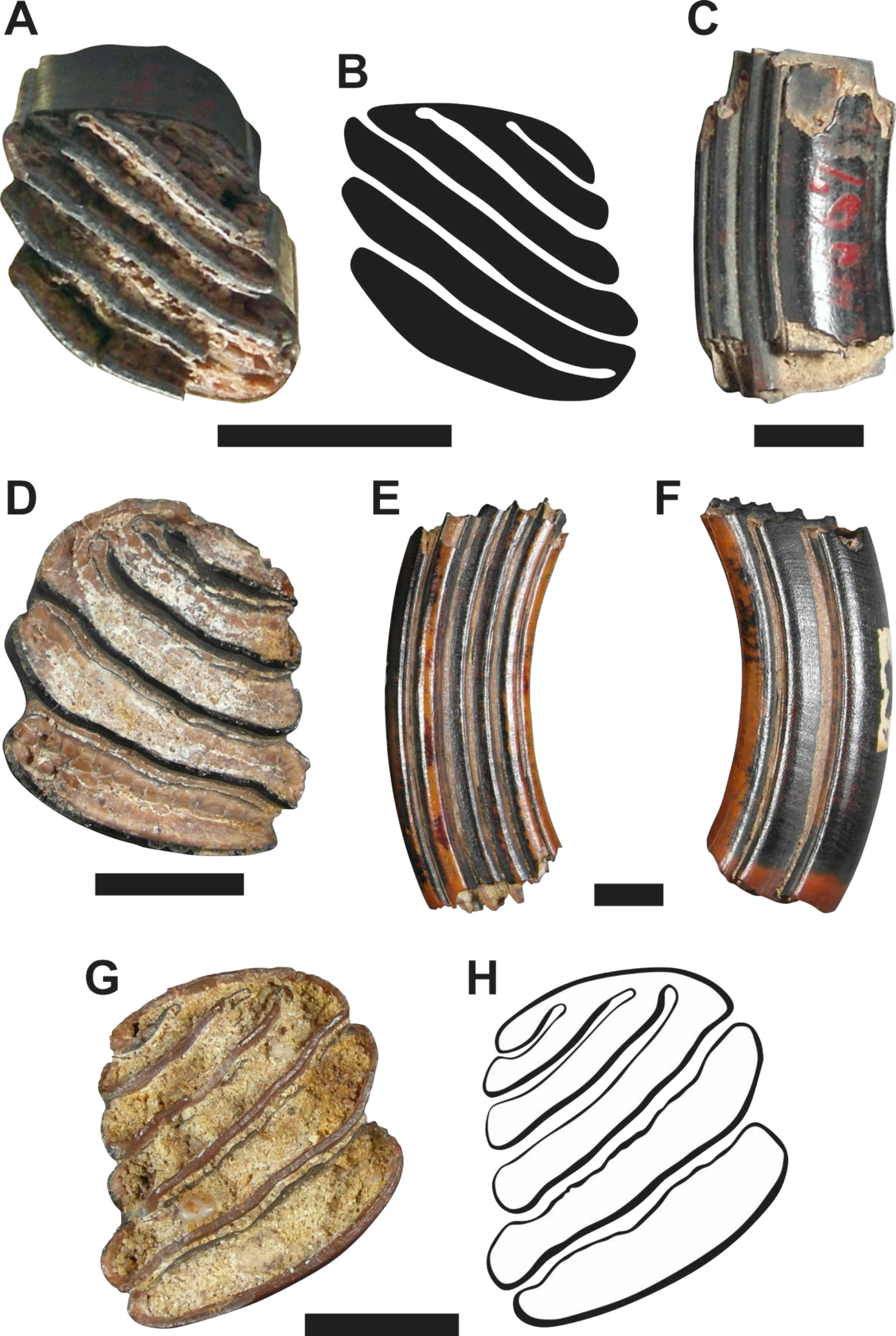
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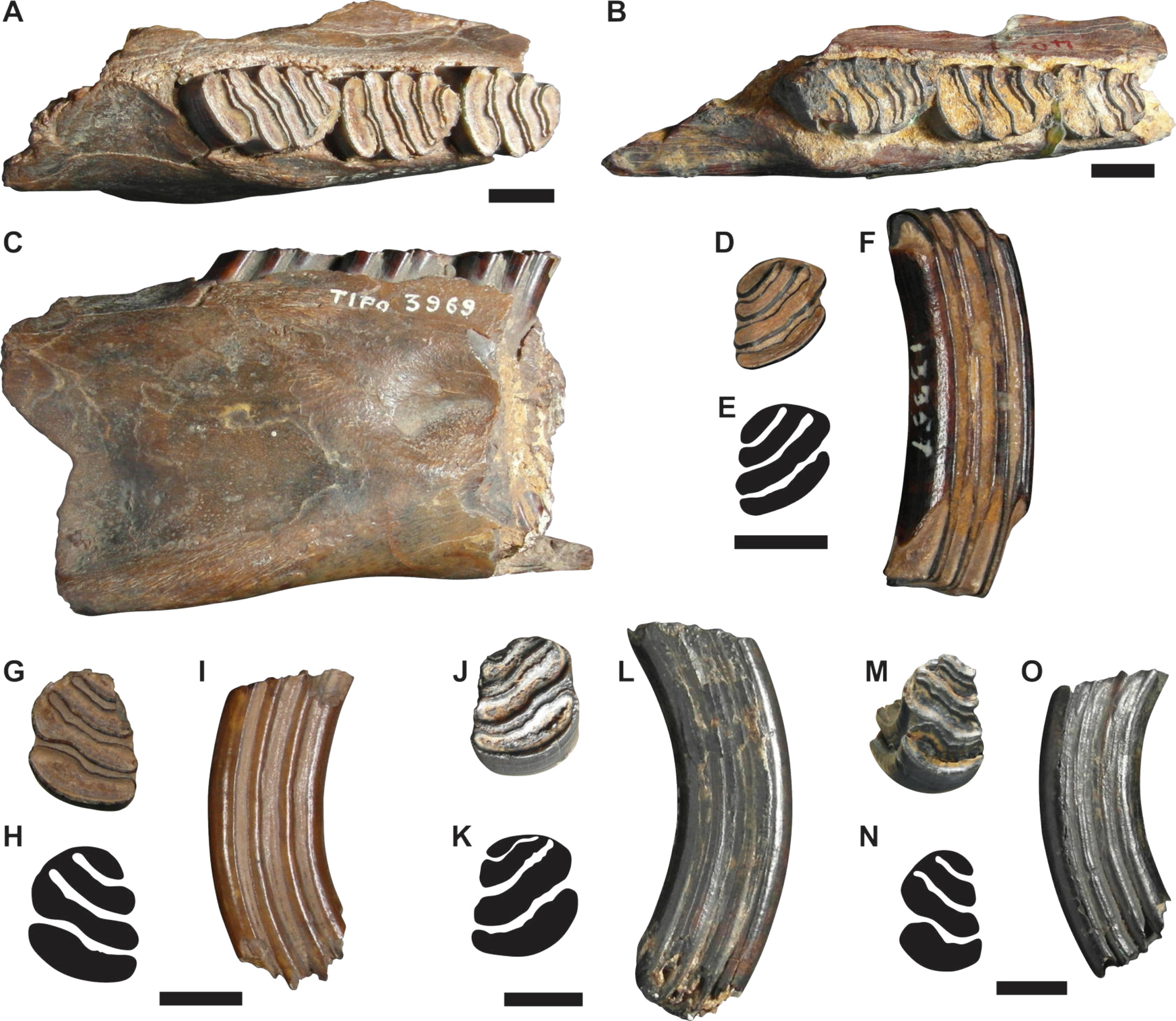
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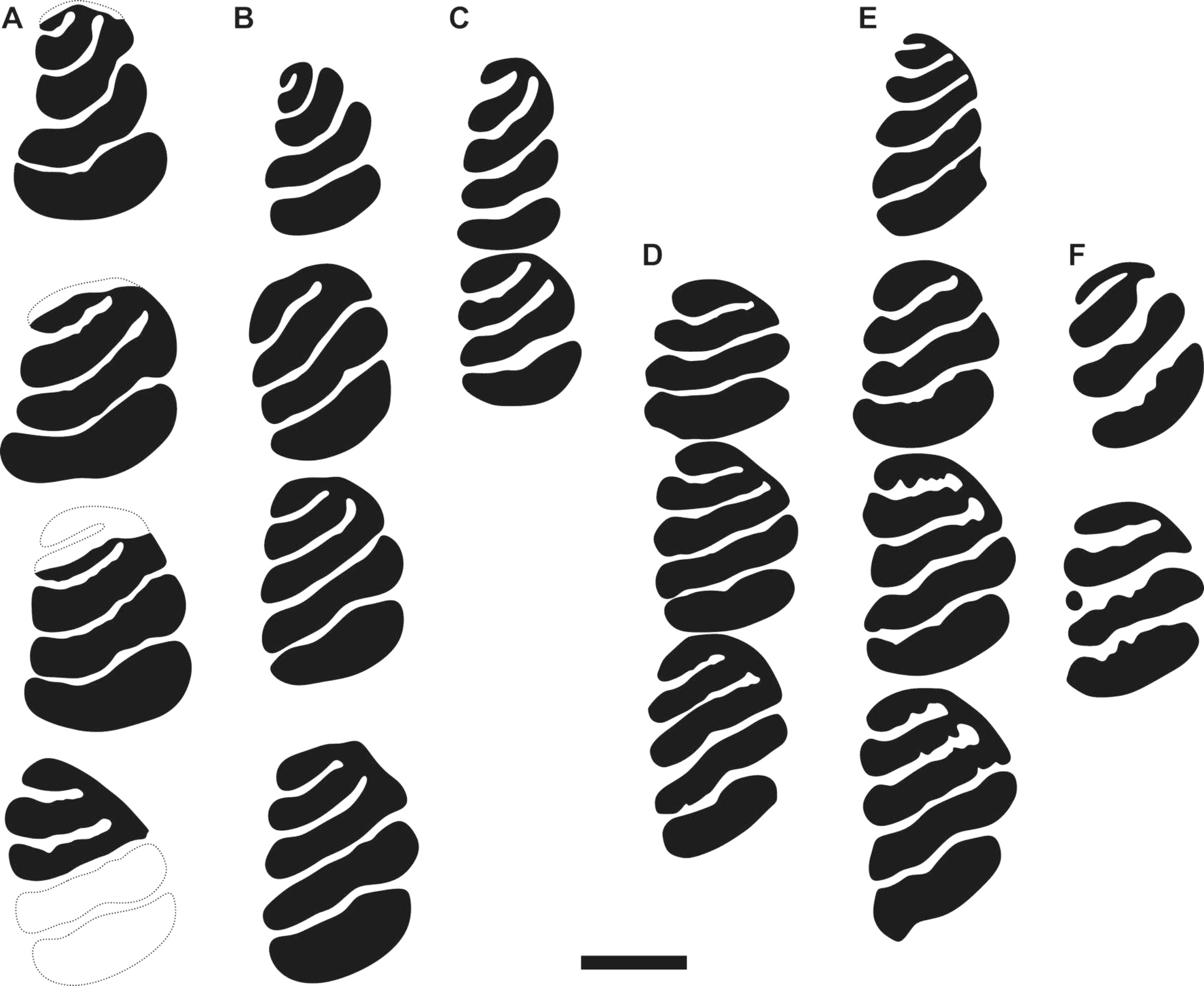
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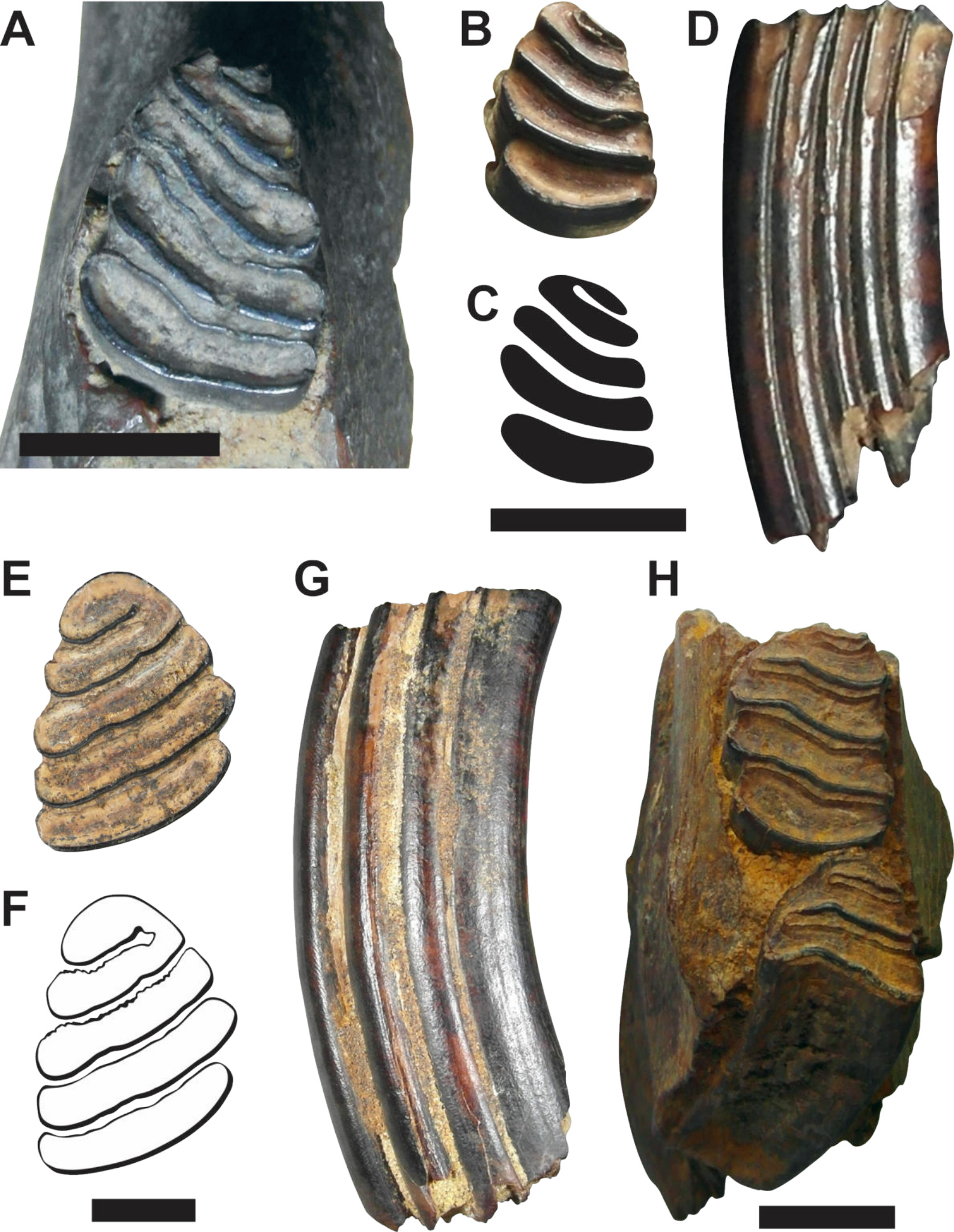
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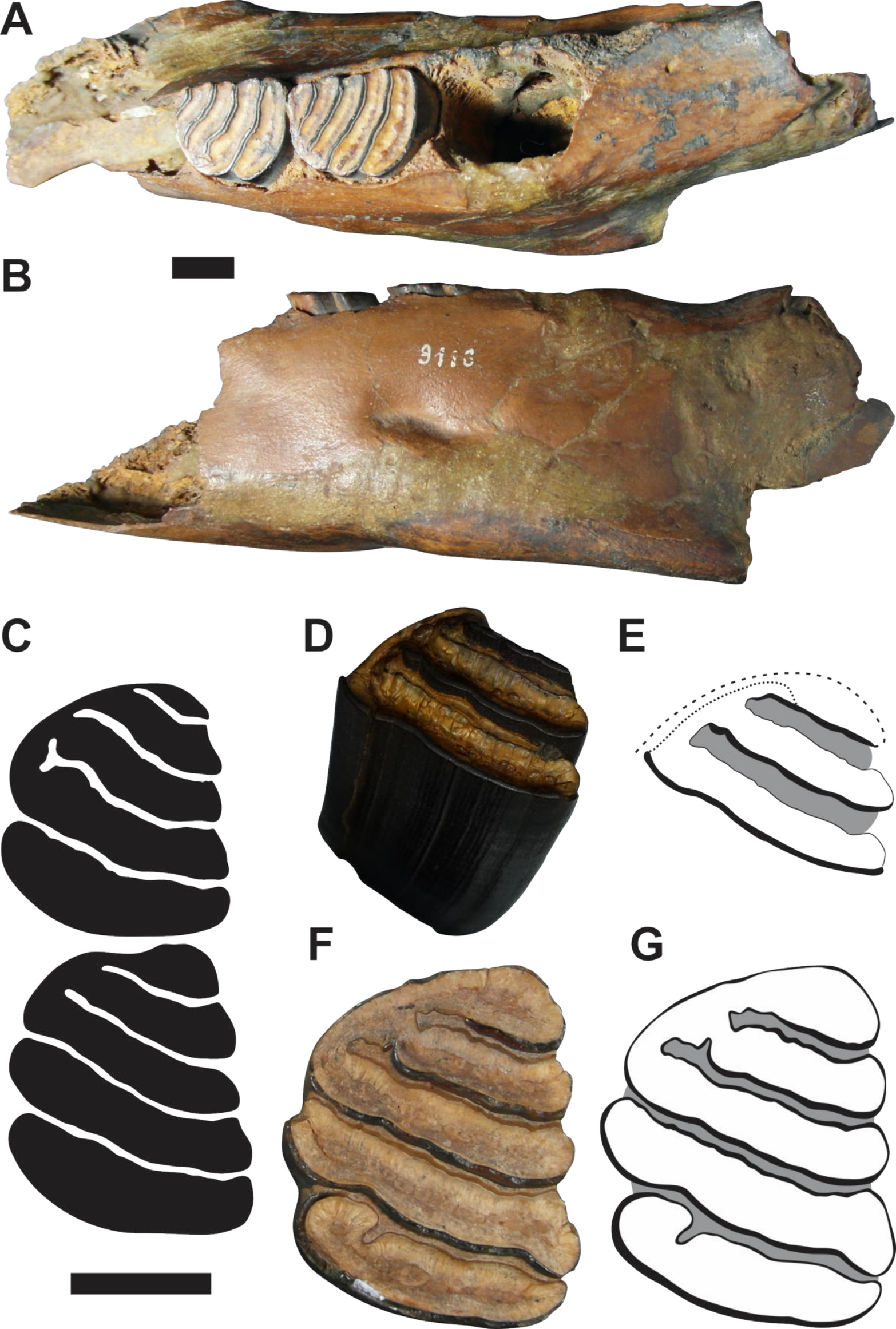
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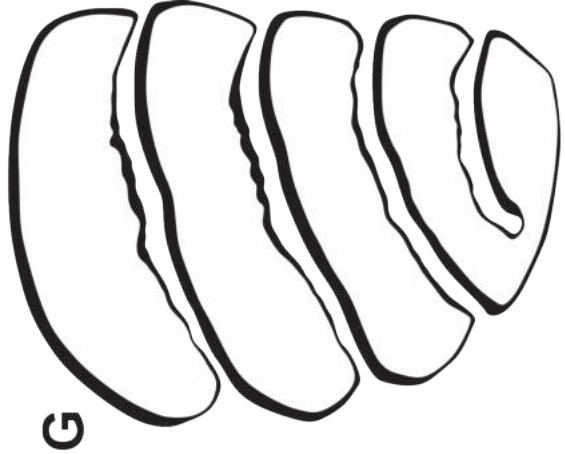

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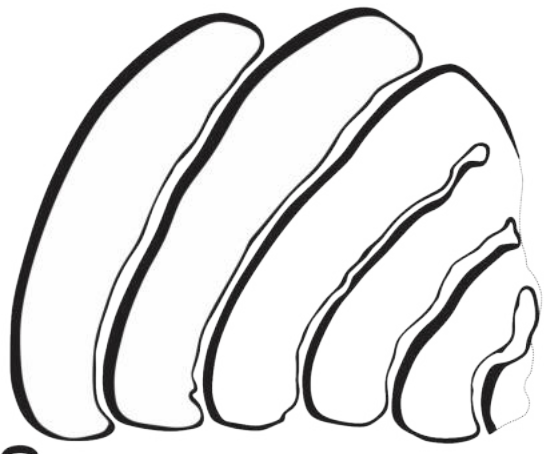

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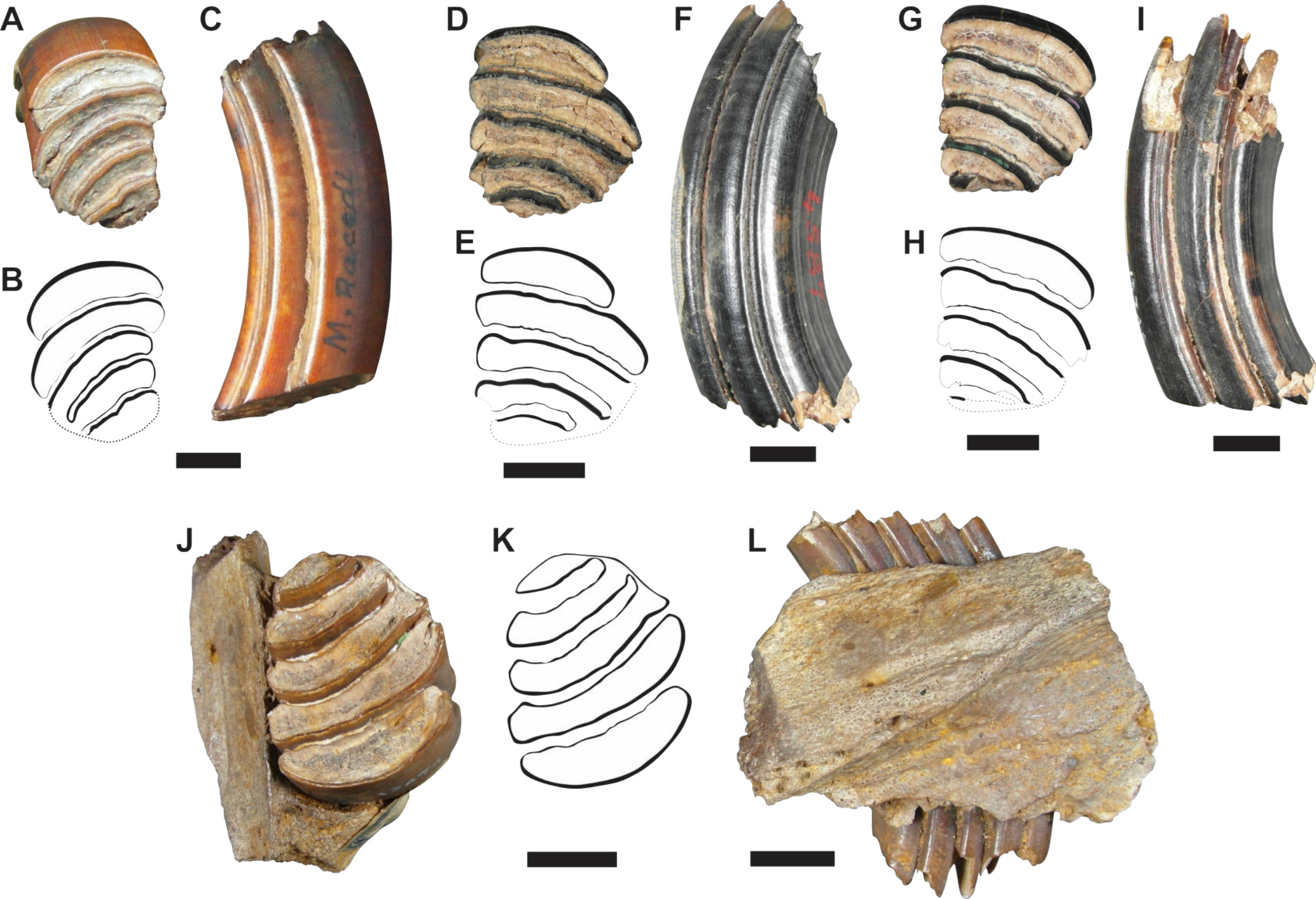
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TABLE 1. List of genera and species of dinomyids from the Ituzangó Formation.

Candela, 2005	[a]Nasif *et al*., 2013; [b]Ameghino, 1891; [c]Rasia, 2023; [d]Rinderknecht *et al.*, 2018	This study
Briaromys		***"Briaromys"*** *nomen dubium*
B. trouessartianus		***"B. trouessartianus"*** *nomen dubium*
Carlesia	***Carlesia***[a]	
C. pendolai	***C. pendolai***[a]	
Diaphoromys		***Diaphoromys***
D. compressidens		***D. gamayensis***
D. gamayensis		***D. gamayensis***
D. mesopotamicus		***D. mesopotamicus*** and ***D. gamayensis***
"Discolomys"	***Potamarchus***[b]	***Potamarchus***
"D". cuneus	***P. murinus***[b]	***P. murinus***
Doellomys		***Gyriabrus***
D. parcus		***G. coligatus***
Eumegamys	***Eumegamys***[a]	***Eumegamys***
E. contortus		***Carlesia pendolai*** and ***Rusconia crassidens***
E. scalabrinianus		***E. scalabrinianus***
E. paranensis	***E. paranensis***[a]	
E. dubius		***Diaphoromys gamayensis***
"E". depressidens		***"Megamys depressidens"*** *nomen vanum* (***Eumegamysops praependens*** and ***Isostylomys laurillardi***)
Eumegamysops	***Eumegamysops***[a]	
E. praependens	***E. praependens***[a]	
Gyriabrus	***Gyriabrus***[a, c]	
G. glutinatus	***G. holmbergi***[c]	
G. holmbergi	***G. holmbergi***[a, c]	
G. indivisus	***G. holmbergi***[c]	
G. rebagliattii	***G. holmbergi***[c]	
Isostylomys	***Isostylomys***[a, d]	
I. ameghinoi	***I. laurillardi***[d]	
I. laurillardi	***I. laurillardi***[a, d]	
Paranamys	***Paranamys***[a]	
P. typicus	***P. typicus***[a]	
Pentastylodon		***"Pentastylodon"*** *nomen vanum*
P. racedi		***"Megamys racedi"*** *nomen vanum* (***Eumegamusops praependens***, ***Arazamys castiglionii***, ***Telodontomys compressidens***, ***Rusconia crassidens***)
Pentastylomys		***Gyriabrus***

P. seriei		***G. holmbergi***
Potamarchus	***Potamarchus***[a]	
P. murinus	***P. murinus***[a]	
P. sigmodon	***P. sigmodon***[a]	
Protomegamys		***Gyriabrus***
P. coligatus		***G. coligatus***
Pseudosigmomys		***Pseudosigmomys***
P. paranensis		***P. paranensis***
Rusconia		***Rusconia***
R. crassidens		***R. crassidens***
Telodontomys		***Telodontomys***
T. compressidens		***T. compressidens***
Tetrastylomys		***Tetrastylus***
Tetrastylomys castellanosi		***Tetrastylus*** sp.
Tetrastylus	***Tetrastylus***[a]	
T. laevigatus	***T. laevigatus***[a]	
T. aguilari	*nomen nudum*[a]	
T. diffisus	***"T". diffisus***[a]	
T. robustus	***Carlesia*** sp.[a]	
T. (Protelicomys) atavus	***"T". (Protelicomys) atavus***[a]	