

Cavioids, Chinchilloids, and Erethizontoids (Hystricognathi, Rodentia, Mammalia) of the Early Miocene Pampa Castillo Fauna, Chile

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ABSTRACT

Caviomorph rodents became important components of South American faunas after their Eocene arrival from Africa. Here we describe the cavioid, chinchilloid, and erethizontoid caviomorphs of the early Miocene Pampa Castillo fauna of southern Chile. This fauna's age and location make it key for resolving outstanding biostratigraphic questions concerning early Miocene Patagonian fossiliferous strata.

Each of the four major caviomorph clades ("superfamilies") is represented in the Pampa Castillo fauna, three whose members are detailed here: cavioids (3 genera; 3 species), chinchilloids (3 genera; 6 species), and erethizontoids (2 genera; 2 species).

Abundantly represented taxa, e.g., *Neoreomys australis*, *Perimys erutus*, and *Prolagostomus pusillus*, corroborate previous work assigning the Pampa Castillo fauna to the Santacrucian South American Land Mammal "Age" (SALMA; inclusive of the "Pinturan"). Several taxa, including *Eosteiomys*, *Perimys intermedius*, and *Perimys* sp. nov.?, are also found in the lower and middle Pinturas Formation (ImPF) but not "core" Santacrucian faunas (from the Santa Cruz Formation [SCF] along the Río Santa Cruz and Atlantic coast), suggesting a distinctive

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resemblance between ImPF and Pampa Castillo rodents. Some authors consider the fauna from the ImPF to form the basis of a “Pinturan” SALMA or subage, considered to slightly predate core Santacrucian faunas, but which has yet to be formally recognized. The taxonomic composition of rodent fauna from Pampa Castillo, as well as relative abundance data, indicated a paleoenvironment intermediate between the closed forests of the ImPF and the mosaic of open and closed habitats of the core Santacrucian faunas from the SCF.

INTRODUCTION

Prior to the Great American Biotic Interchange, South American Cenozoic terrestrial faunas were largely composed of endemic taxa (e.g., Simpson, 1940; Flynn et al., 2012; Croft, 2016). Caviomorph rodents first appear in South America in the middle Eocene, likely after rafting across the Atlantic Ocean from Africa (Lavocat, 1974; Martin, 1994; Mouchaty et al., 2001; Rowe et al., 2010; Marivaux and Boivin, 2019). Initially, they diversified in low latitudes before dispersing southward (Vucetich et al., 2010a; Antoine et al., 2012; Bertrand et al., 2012; Boivin et al., 2017, 2021). The four major clades (“superfamilies”) of caviomorphs diverged from one another by the late Eocene or early Oligocene: Cavoidea (cavies, capybaras, agoutis, and kin), Chinchilloidea (chinchillas and kin), Erethizontoidea (porcupines), and Octodontoidea (spiny rats, tuco-tucos, degus, and kin) (Wood, 1965; Vucetich et al., 1999; Voloch et al., 2013; Boivin et al., 2019a). Members of the first three of these clades will be discussed herein, whereas the octodontoids of Pampa Castillo will be discussed in a subsequent paper. By the early Miocene, caviomorphs were diverse and abundant components of South American mammal communities (Vucetich et al., 2010b, 2015; Candela et al., 2012; Arnal et al., 2019).

The early Miocene Santacrucian South American Land Mammal “Age” (SALMA) is likely the best-understood pre-Quaternary interval in the Cenozoic of South America, but its precise duration and the faunas assigned to it are disputed. Most Santacrucian SALMA localities are in Argentine Patagonia. These include the localities on which Ameghino (1889) originally based his “Santacrucense,” which come from the Santa Cruz Formation (SCF) along the Río Santa Cruz (RSC; fig. 1) in Santa Cruz Province, and span ~17.2–15.6 Ma (e.g., Barrancas Blancas, Segundas Barrancas Blancas, and Yaten Huageno; Cuitiño et al., 2016; Fernicola et al., 2019). The best-studied Santacrucian localities, sometimes referred to as the “classic Santacrucian” localities, are from exposures of the SCF along the Atlantic Coast (fig. 1; e.g., Monte León, Cerro Observatorio, and Killik Aike). They average slightly older (~17.8–16.2 Ma) than the RSC localities, but their faunas are nearly identical (Flynn and Swisher, 1995; Perkins et al., 2012; Trayler et al., 2020; Kay et al., 2021). For ease of reference, throughout this work we collectively term SCF localities and faunas from along the Río Santa Cruz, plus those from the Atlantic coast, as “core Santacrucian” localities/faunas. The descriptor “Santacrucian” alone will be used to refer to all faunas assigned to the Santacrucian SALMA.

Other Santacrucian faunas from the SCF in western Santa Cruz Province, such as Karaiken and Río Bote, seem to be slightly older than their eastern counterparts and are sometimes considered to represent a “Notohippidian stage” (“étage Notohippidien”) within the Santacrucian SALMA (González Ruiz and Scillato-Yané, 2009; Fernicola et al., 2014; Cuitiño

et al., 2016). At Lago Posadas, in the northwestern part of Santa Cruz Province, SCF strata span a broad temporal range from ~18–14.2 Ma (Blisniuk et al., 2005; Cuitiño et al., 2015). Rodents from Pampa Castillo (Flynn et al., 2002a), a southern Chilean Santacrucian SALMA site recovered from strata that may correspond to the SCF, are described below. Santacrucian faunas also occur in the Pinturas Formation, which is divided into three stratigraphic sequences (upper, middle, and lower). The fauna of the upper sequence of the Pinturas Formation (uPF) is similar to those from localities bearing core Santacrucian faunas, whereas the fauna of the lower and middle sequences of the Pinturas Formation (lmPF) comprises a mix of Colhuehuapian SALMA (also early Miocene, but slightly older) and Santacrucian taxa (fig. 1); these lower sequences are also geochronologically older than localities bearing core Santacrucian faunas (Kramarz and Bellosi, 2005; Fleagle et al., 2012; Perkins et al., 2012). Faunal differences between the lmPF and core Santacrucian localities have long been recognized, leading some authors to recognize the fauna from the lmPF as a biostratigraphically distinct interval, the “Pinturan,” though this biochron has never been formalized (Castellanos, 1937; Kramarz and Bellosi, 2005; Kramarz and Bond, 2005; Kramarz et al., 2010; Dunn et al., 2013). The Upper Faunal Zone (UFZ) of the Colhue-Huapi Member of the Sarmiento Formation at Gran Barranca was assigned to the “Pinturan” interval by Kramarz et al. (2010; fig. 1). It is unclear whether Santacrucian faunas from elsewhere in South America (e.g., those from Chucal and from certain fossil horizons in the Cura-Mallín Formation near Laguna del Laja in Chile; Cerro Boleadoras Formation, Chinchas Formation, and Mariño Formation at Divisadero Largo in Argentina, and Castilletes Formation in Colombia) might pertain to this “Pinturan” interval, as they lack taxa that have been used to discriminate between “Pinturan” and core Santacrucian faunas (Vucetich, 1994; Scillato-Yané and Carlini, 1998; Flynn et al., 2002b, 2008; Cerdeño and Vucetich, 2007; Wertheim, 2007; López et al., 2011; Luna, 2015; Carrillo et al., 2018; Solórzano et al., 2020).

The Pampa Castillo fauna can help resolve the confused chronology of Santacrucian faunas. The name of the mammal-bearing unit at Pampa Castillo is unsettled with different authors referring it to the Río Zeballos (Niemeyer, 1975), Santa Cruz (de la Cruz et al., 2004; Ugalde et al., 2015; Encinas et al., 2019), Galera (Niemeyer et al., 1984; Flynn et al., 2002a), and Pampa Castillo (Scalabrino, 2009; Folguera et al., 2018) formations. Since this issue remains unresolved, we refer to this unit in this work as the Galera Formation to be consistent with our previous publications (Flynn et al., 2002a; McGrath et al., 2020). Pampa Castillo is located in southern Chile at a latitude (~47° S) equivalent to the northern Santa Cruz Province in Argentina (fig. 1). Pampa Castillo, and exposures of the lmPF exposures in the upper Pinturas River valley are nearer to each other (~130 km) than either is to the core Santacrucian faunas (>350 km). Geochronological age estimates suggest that Pampa Castillo is also closer temporally to “Pinturan” faunas than either is to core Santacrucian faunas. Folguera et al. (2018) reported a U/Pb date of 18.7 +/-0.3 Ma from a reworked tuff directly below strata bearing the Pampa Castillo fauna. “Pinturan” faunas of the lmPF and Upper Fossil Zone at Gran Barranca are ~19.0–17.9 Ma (Perkins et al., 2012; Dunn et al., 2013), whereas core Santacrucian faunas are ~17.5–15.6 Ma (Cuitiño et al., 2016; Trayler et al., 2020). Notably, fossiliferous strata between

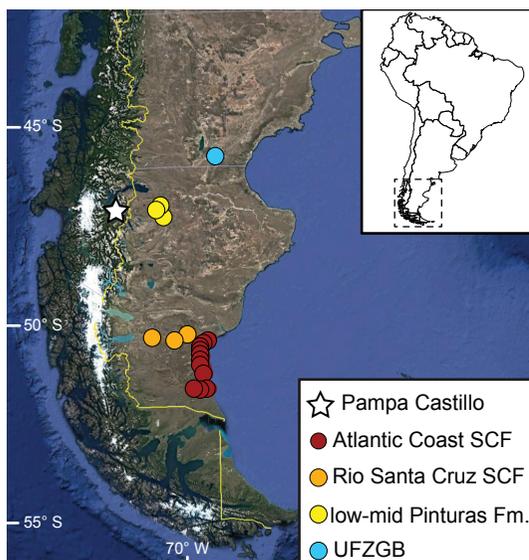


FIG. 1. Map showing location of Pampa Castillo and other localities mentioned in the text. Abbreviations: Fm., Formation; SCF, Santa Cruz Formation; UFZGB, Upper Fossil Zone at Gran Barranca.

and a detailed description of the palaeothentid marsupials. They assigned the mammalian fauna to the Santacrucian SALMA based on the presence of characteristic taxa such as *Nesodon* Owen, 1846, *Perimys* Ameghino, 1887a, and *Homalodotherium* Flower, 1873. McGrath et al. (2020) described the litopterns from Pampa Castillo, finding them consistent with assignment to the Santacrucian SALMA. In this work, we describe the cavioids, chinchilloids, and erethizontoids of Pampa Castillo and discuss their biochronologic and paleoenvironmental implications.

MATERIALS AND METHODS

Fossil rodents from Pampa Castillo were compared firsthand to related forms housed in the American Museum of Natural History and Yale Peabody Museum and others described in the literature. Measurements were taken using Mitutoyo CD-8" digital calipers to the nearest 0.1 mm.

We follow the dental nomenclature of Boivin and Marivaux (2020), and note differences from the terminology of Rasia et al. (2021) where relevant. We use the term "hypsodont" to refer to teeth that are rootless and ever growing. We refer to rooted cheekteeth with relatively tall crowns as "hypsodont," which some authors alternatively refer to as "protohypsodont" (e.g., Mones, 1982, but see Janis and Fortelius, 1988).

In the Systematic Paleontology section, Referred Material and Locality and Horizon refer to specimens from Pampa Castillo newly described in this contribution, whereas Age and

19 and 17.5 Ma crop out at other SCF localities such as Río Bote, Karaiken, and Lago Posadas, but these faunas are less studied than their core Santacrucian counterparts along the RSC and Atlantic coast and/or past collections have lacked stratigraphic control (Fericola et al., 2014; Cuitiño et al., 2015, 2016, 2019a; Vizcaíno et al., 2021). Pampa Castillo is closer geographically and in age to "Pinturan" faunas than to core Santacrucian faunas but is not stratigraphically associated with either the ImPF (Pinturas Formation) or strata of the Upper Fossil Zone at Gran Barranca (Sarmiento Formation).

The Pampa Castillo fauna was first described by Flynn et al. (2002a), who provided an overview of the locality's geology, a composite taxonomic list of the fossil macroinvertebrates from underlying marine strata, a list and brief description of the fossil mammal fauna,

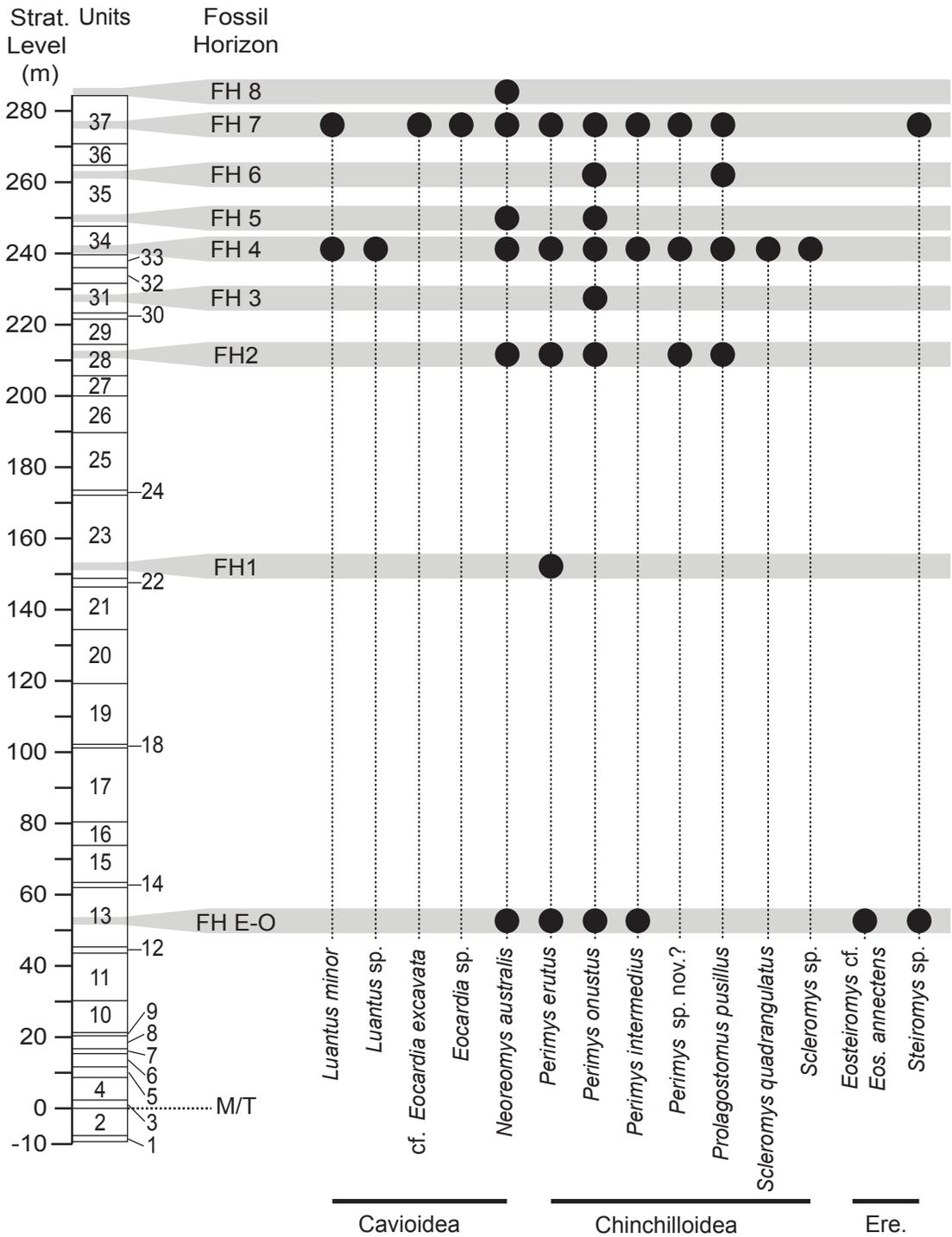


FIG. 2. Simplified stratigraphic column showing lithological units and fossil horizons per Flynn et al. (2002a) and stratigraphic position of rodents at Pampa Castillo. Abbreviations: **Ere**, Erethizontoidea; **M/T**, marine/terrestrial transition; **strat**, stratigraphic.

Distribution refers to the full geographic and temporal range of the taxon. Flynn et al. (2002a) noted nine distinct fossil-bearing layers at Pampa Castillo, which they referred to as “levels” 0 (lowest in section) through 8 (highest; fig. 2). In this work, we refer to these intervals as fossil horizons to emphasize that they are characterized by fossils, not lithology, thickness, or absolute age.

We recognize that “Eocardiidae” is a paraphyletic grade of cavioids, but we still employ this name as a useful shorthand for this nonmonophyletic grouping of anatomically similar taxa (Pérez, 2010a; Pérez and Vucetich, 2012a; Boivin et al., 2019a).

We compared the relative abundance of different caviomorph genera at Pampa Castillo and two other well-studied Santacrucian rodent faunas. For Pampa Castillo, we treated all octodontoids together as they will be described in detail in a future analysis. Taxon identity and abundance for the lower and middle sequences of the Pinturas Formation were taken from Kramarz (2001a, 2002, 2004, 2006a, 2006b). Taxon identities and abundances for the Santa Cruz Formation along the Río Santa Cruz were taken from Arnal et al. (2019).

ABBREVIATIONS

ANATOMICAL: M/m: upper/lower molar; P/p: upper/lower premolar.

INSTITUTIONAL: SGOPV: Vertebrate Paleontology collections, Museo Nacional de Historia Natural, Santiago, Chile.

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Eutheria Huxley, 1880

Rodentia Bowdich, 1821

Hystriognathi Tullberg, 1899

Caviomorpha Wood and Patterson in Wood, 1955

Cavioidea Fischer de Waldheim, 1817

Luantus Ameghino, 1899

TYPE SPECIES: *Luantus propheticus* Ameghino, 1899.

INCLUDED SPECIES: The type species, *L. initialis* Ameghino, 1902, *L. toldensis* Kramarz, 2006b, *L. minor* Pérez et al., 2010, and *L. sompallwei* Solórzano et al., 2020.

AGE AND DISTRIBUTION: Colhue-Huapi and Trelew members, Sarmiento Formation, Colhuehupian SALMA, Chubut Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Tcm3 unit, Cura-Mallín Formation, Santacrucian? SALMA, Biobío Region, Chile.

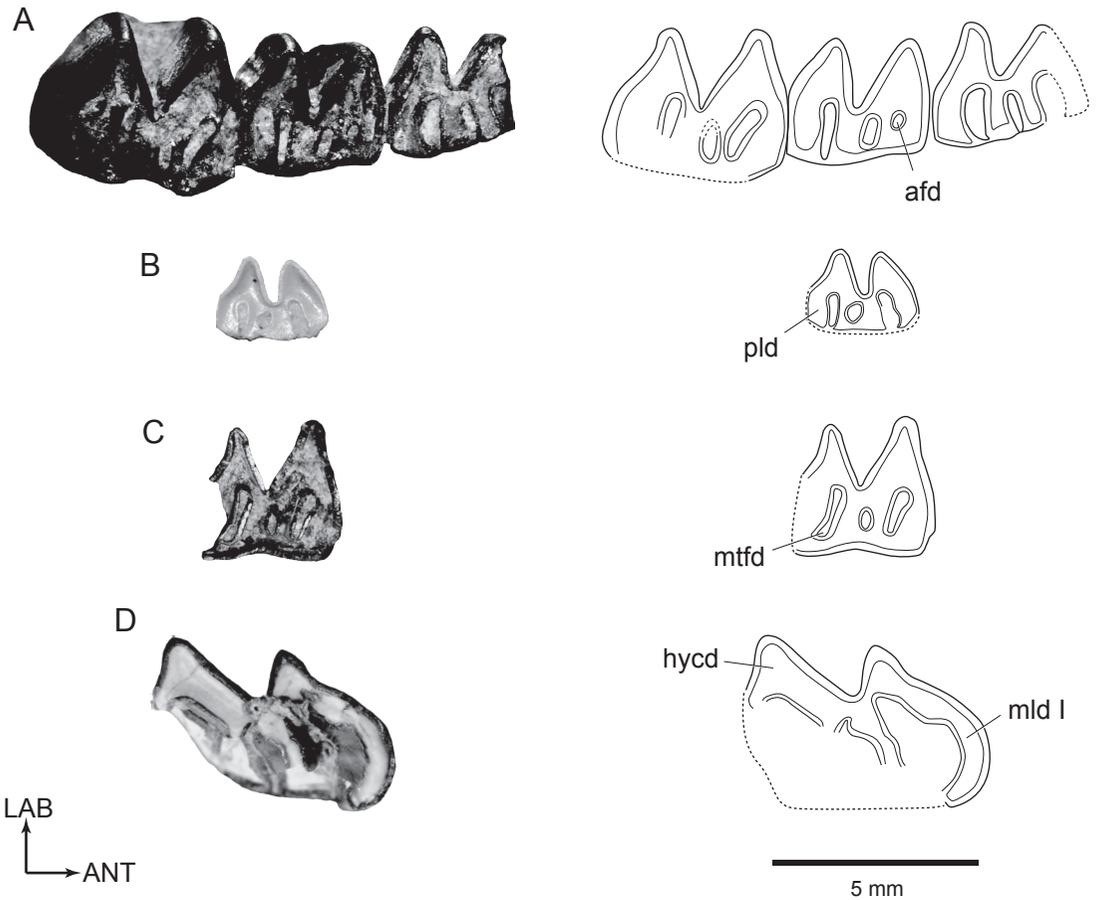


FIG. 3. *Luantus* specimens from Pampa Castillo. *Luantus minor*: **A**, SGOPV 2691, right partial p4 and m1–2 (reversed); **B**, cast of SGOPV 2134, left p4; **C**, SGOPV 2697, left m1 or 2. *Luantus* sp.: **D**, SGOPV 2698, right p4 (reversed). Dashed lines represent presumed outlines of damaged teeth. Abbreviations: **afd**, anterofossettid; **ANT**, anterior; **hycd**, hypoconid; **LAB**, labial; **mld I**, metalophulid I; **mtfd**, metafossettid; **pld**, posterolophid.

Luantus minor Pérez et al., 2010

Figure 3A–C

REFERRED MATERIAL: SGOPV 2134, right m1 or 2 (fig. 3B); SGOPV 2691, right p4–m2 (fig. 3A); SGOPV 2697, left m1 or 2 (fig. 3C).

LOCALITY AND HORIZON: Fossil Horizon 4 (SGOPV 2691, 2697) and Fossil Horizon 7 (SGOPV 2134); Galera Formation, Pampa Castillo, Chile.

AGE AND DISTRIBUTION: Trelew Member, Sarmiento Formation, Colhuehuapian SALMA, Chubut Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile.

DESCRIPTION: All Pampa Castillo specimens here referred to *Luantus minor* represent lower cheekteeth (fig. 3A–C; table 1). They are bilobed, bear pointed protoconids and hypoconids, and are hypsodont, being higher crowned than *Luantus initialis* (Pérez et al., 2010).

Enamel covers much of the lingual wall of the only specimen that preserves this region, SGOPV 2697 (fig. 3C). However, the base of this isolated tooth is incomplete, so we cannot assess whether enamel discontinuities were present in life or represent taphonomic damage. Cement is present in the lingual fossettids of all specimens, with a small amount of cement in some of their hypoflexids as well.

SGOPV 2691 bears a moderately worn p4, the metalophulid I of which is damaged (fig. 3A). SGOPV 2134, conversely, is complete (fig. 3B). These teeth resemble each other in all aspects but size. All three lingual flexids are open. The anterior wall of the V-shaped hypoflexid is slightly longer than its posterior counterpart. The posterolophid is straight and obliquely oriented. The m1–2 of SGOPV 2691 resemble one another save that m2 is larger and less worn. The anterofossettids and mesofossettids are closed on both teeth. The metaflexid remains open in m1, but damage obscures this part of m2. These fossettids and the flexids are labiolingually elongate, except for the circular anterofossettids of m1. Both the anterior and posterior surfaces of the tooth are convex. Much like in p4, the walls of the molar hypoflexids are straight, though the hypoflexids of the molars are more symmetric. SGOPV 2697 (fig. 3C), representing either m1 or 2, is more heavily worn than the teeth of SGOPV 2691, as indicated by its completely closed metafossettids. The lingual border of this tooth curves labially opposite the mesofossettids.

REMARKS: We refer these specimens to *Luantus* based on their rooted cheekteeth, persistent lingual fossettids, and presence of enamel covering the lingual surface of the lower molars, a combination of features distinguishing them from other early Miocene “eocardiids” such as *Eocardia*, *Phanomys*, and *Schistomys* (Kramarz, 2006a; Pérez, 2010b; Pérez and Vucetich, 2012b). The p4 mesoflexid of SGOPV 2691 is much shorter than in the late Oligocene “eocardiid” *Asteromys* (Pérez et al., 2019; Candela et al., 2021). Compared to late Oligocene *Chubutomys*, the hypiconid and protoconid are oriented more directly labially and the hypoflexid extends less far lingually in these Pampa Castillo specimens (Pérez et al., 2012). We assign these specimens to *L. minor* based on their degree of hypsodonty, enamel coverage, and size (fig. 3A–C; table 1). The Colhuehuapian-aged *Luantus initialis* is much lower crowned than other members of the genus (Pérez et al., 2010), including all specimens from Pampa Castillo. The lower molars of *L. propheticus*, from the lower and middle Pinturas Formation and Upper Fossil Zone of the Sarmiento Formation, *L. toldensis*, and *L. sompallwei* bear larger patches of exposed dentine on their lingual walls unlike specimens from Pampa Castillo (Kramarz, 2006a). Teeth of *L. initialis*, *L. propheticus*, *L. toldensis*, and *L. sompallwei* are all larger than the *Luantus* specimens recovered from Pampa Castillo (Kramarz, 2006a; Pérez, 2010b; Pérez et al., 2010; Solórzano et al., 2020). *Luantus* specimens from Pampa Castillo match *L. minor* in all respects, including size.

Luantus minor was previously reported only from the Colhuehuapian-aged Trelew Member of the Sarmiento Formation at Bryn Gwyn, Chubut Province, Argentina (Pérez et al., 2010). Given this temporal and geographic distribution, it is surprising that *L. minor* is the only *Luantus* species present at Pampa Castillo, given that two others, *L. propheticus* and *L. toldensis*, are known from the geographically proximal and temporally similar Pinturas Formation (Kramarz, 2006a; fig. 1).

Luantus sp.

Figure 3D

REFERRED MATERIAL: SGOPV 2698, partial left p4 (fig. 3D).

LOCALITY AND HORIZON: Fossil Horizon 4, Galera Formation, Pampa Castillo, Chile.

DESCRIPTION: SGOPV 2698 is a left p4 missing most of its lingual and posterior regions, and the preserved regions exhibit light to moderate wear (fig. 3D). The protoconid is triangular and the wide, curved metalophulid I extends from it. There is no trace of an anterior flexid on this lophid. Enamel present on the end of metalophulid I suggests that the anteroflexid was not completely closed in this specimen. The second transverse lophid is incomplete but appears to have been sinuous, suggesting that it was formed by both the posterior arm of the protoconid and the neomesolophid (sensu Boivin and Marivaux, 2020). The hypoflexid is wide and has straight sides. The hypoconid is triangular like the protoconid, but it is larger and extends further labially than the protoconid. Only the most labial parts of the hypolophid and posterolophid are preserved, but the region joining the posterolophid and hypoconid is much thinner than the anterior arm of the hypoconid. The tooth is fairly high crowned, though rooted, and enamel is present around the entire tooth.

REMARKS: We refer SGOPV 2698 to *Luantus* because it is rooted, has persistent fossetids, a wide hypoflexid with straight sides, and a triangular protoconid and hypoconid with the latter being larger (fig. 3D). Due to its size, we think that this tooth represents a second species of *Luantus* at Pampa Castillo. Although the tooth is too damaged to record a definitive measurement, it is larger than the p4s we assign to *L. minor*. *Luantus propheticus* is known from the lower and middle sequences of the Pinturas Formation, and *L. toldensis* is known from the upper sequence of the Pinturas Formation (Kramarz, 2006a). Those species are similar in size and differ primarily in crown height. We were unable to examine isolated cheek teeth of either of those species to compare their hypsodonty to SGOPV 2698, so we refrain from assigning this specimen to either species and refer to it as currently indeterminate, as *Luantus* sp.

Eocardia Ameghino, 1887b

TYPE SPECIES: *Eocardia montana* Ameghino, 1887b.

INCLUDED SPECIES: The type species, *Eoc. fissa* Ameghino, 1891, *Eoc. excavata* Ameghino, 1891, *Eoc. robusta* Vucetich, 1984, and *Eoc. robertoi* Vucetich, 1984. We follow the taxonomy of Pérez (2010a) for this genus.

AGE AND DISTRIBUTION: Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina; Chinchas Formation; Santacrucian SALMA, San Juan Province, Argentina; Collón Curá Formation, Colóncuran SALMA, Chubut, Neuquén, and Río Negro provinces, Argentina.

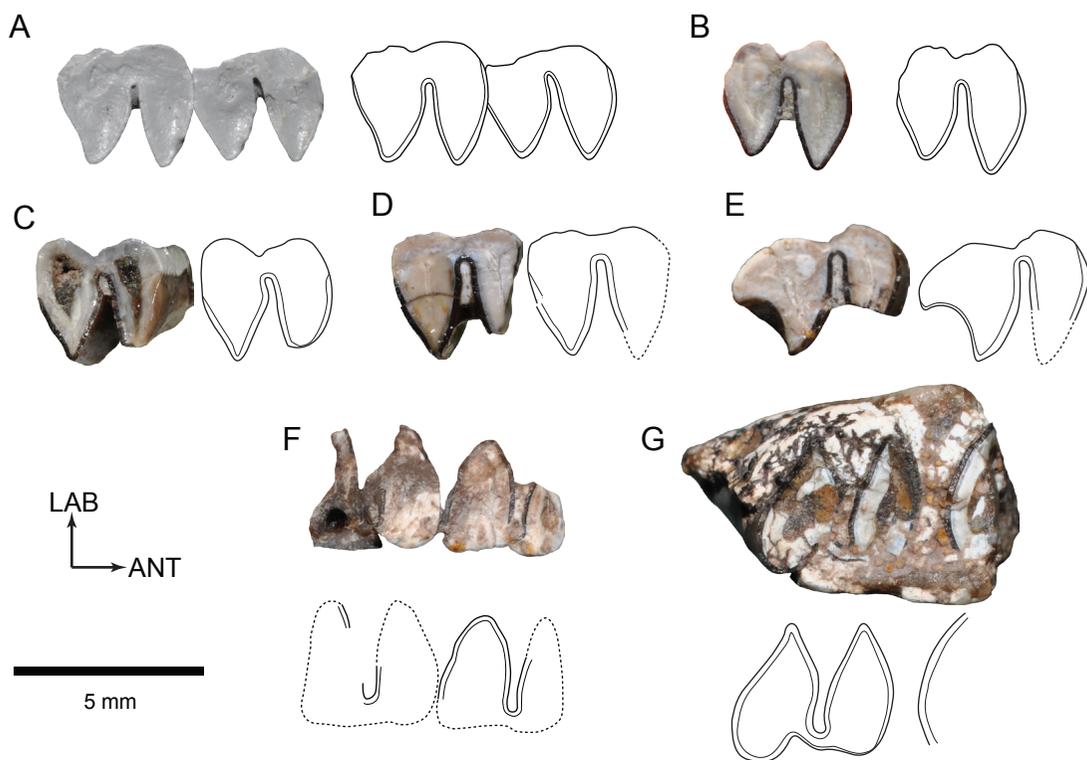


FIG. 4. *Eocardia* specimens from Pampa Castillo. cf. *Eocardia excavata*: A, cast of SGOPV 2133, left M1–2 (reversed); B, SGOPV 2693, left M1 or 2 (reversed); C, SGOPV 2694, right M2; D, SGOPV 2696, right M1; E, SGOPV 2692, right M3; F, SGOPV 2690, partial left m1–2 (reversed). cf. *Eocardia* sp.: G, SGOPV 2695, partial left m2 and complete m3 in mandibular fragment. Dashed lines represent presumed outlines of damaged teeth. Abbreviations: ANT, anterior; LAB, labial.

cf. *Eocardia excavata* Ameghino, 1891

Figure 4A–F

Eocardia perforata Flynn et al., 2002a: 289 (partim), table 1.

REFERRED MATERIAL: SGOPV 2133, left M1–2 (fig. 4A); SGOPV 2690, left m1–2 (fig. 4F); SGOPV 2692, right M3 (fig. 4E); SGOPV 2693, left M1 or 2 (fig. 4B); SGOPV 2694, right M2 (fig. 4C); and SGOPV 2696, right M1 (fig. 4D).

LOCALITY AND HORIZON: Fossil Horizon 7, Galera Formation, Pampa Castillo, Aysén Region, Chile.

AGE AND DISTRIBUTION: Chinchas Formation; Santacrucian SALMA, San Juan Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina.

DESCRIPTION: Save for SGOPV 2133, all referred specimens were recovered in close proximity, include no overlapping elements, and are similar in size, indicating they may represent a single individual (fig. 4B–F). The teeth are bilobed and hypselodont (= euhypselodont). In the

M1 and M2, the anterior and posterior walls of the lobes are slightly convex, with their pointed apices directed lingually (fig. 4A–D). No labial fossettes are present. The labial walls of these teeth lack enamel and bear a slight sulcus opposite the hypoflexus. The hypoflexus extends nearly to the labial edge of the tooth, and its walls are essentially straight. At its apex, the hypoflexus turns slightly posteriorly. Cementum occurs inside the hypoflexus. SGOPV 2692, an M3, is similar to M1 and M2, except that its posterior lobe has a posterior projection (fig. 4E). This projection curves slightly lingually, nearly reaching the labiolingual midpoint of the tooth. Additionally, the apex of the posterior lobe points posteriorly. The apex of the anterior lobe is damaged.

SGOPV 2690 consists of two poorly preserved lower molariforms in a mandibular fragment (fig. 4F). We presume these teeth represent the left m1–2 but are not certain. These teeth are bilobed, lack enamel lingually, and contain cementum within hypoflexids that nearly reach the labial wall.

REMARKS: We assign these specimens to cf. *Eocardia excavata*. The lack of labial fossettes, slightly convex anterior and posterior edges, pointed molar lobes, and deeply penetrating hypoflexi/ids rule out assignment to the cavioids “*Chubutomys leucoreios* Pérez et al., 2010, *Luantus*, and *Phanomys* Ameghino, 1887c (fig. 4A–F; Kramarz, 2006b; Pérez, 2010a; Pérez et al., 2010; Pérez and Vucetich, 2012a). The hypselodont nature of these teeth indicates that they do not pertain to *Asteromys*, *Chubutomys*, *Phanomys*, or *Luantus*. We further rule out *Eocardia fissa*, *Eoc. montana*, *Eoc. robertoi*, *Eoc. robusta*, *Matiamys elegans* Vucetich, 1984, and *Schistomys erro* Ameghino, 1887c, based on the posterior lobe of M3 being less extended in SGOPV 2692 than in these other taxa (fig. 4E; Vucetich, 1984; Pérez, 2010a; A.J.M., personal obs.). Teeth of these species also are larger than the specimens described here, other than for *Eoc. fissa* and *Sch. erro* (table 1). This material most likely pertains to *Eocardia excavata* or *Schistomys rollinsii* Scott, 1905, both of which resemble these Pampa Castillo specimens in their similarly developed M3 posterior lobes and absence of enamel on the antero- and posterolabial corners and labial walls of their upper molars (Pérez, 2010b). These taxa are best distinguished from one another by their premolars. *Eocardia excavata* (and other species of *Eocardia*) have a unilobed P4 and bilobed p4, whereas in *Sch. rollinsii* (and *Sch. erro*) P4 is bilobed (Scott, 1905; Pérez, 2010b). The p4 of *Sch. rollinsii* is unknown, but the tooth is unilobular in worn specimens of *Sch. erro*. The thinner, more gently convex molar lobes of these teeth more closely match *Eoc. excavata* than *Sch. rollinsii*, but we cannot rule out assignment to *Sch. rollinsii* without knowing the premolar morphology.

Eocardia excavata has previously been reported from various localities in the Santa Cruz Formation in eastern and central Santa Cruz Province but not from western localities such as Lago Posadas, Karaiken, and Sierra Baguales, which are geographically closer to Pampa Castillo (fig. 1; Scott, 1905; Pérez, 2010; Bostelmann et al., 2013; Arnal et al., 2019; Cuitiño et al., 2019a). *Eocardia excavata* has also been recovered at Las Hornillas in the Chinchas Formation of west-central Argentina (San Juan Province; López et al., 2011). If our tentative assignment is correct, this and the specimen noted below are the first documented occurrences of any species of *Eocardia* outside Argentina.

TABLE 1. Summary statistics of lower tooth measurements of Pampa Castillo cavioids, chinchilloids, and erethizontoids. See table S1 in the online supplement (<https://doi.org/10.5531/sd.sp.53>) for measurements of individual specimens. Measurements reported in mm.

Taxon		p4		m1		m2		m1 or m2		m3	
		AP	LL	AP	LL	AP	LL	AP	LL	AP	LL
<i>Luantus minor</i>	N	0	1	1	1	1	1	2	2	0	0
	MEAN	—	2.9	3.6	3.3	4.3	3.8	3.0	2.9	—	—
	MAX	—	2.9	3.6	3.3	4.3	3.8	3.5	3.6	—	—
	MIN	—	2.9	3.6	3.3	4.3	3.8	2.5	2.1	—	—
<i>Eocardia cf. Eoc. excavata</i>	N	0	0	1	1	0	1	0	0	0	0
	MEAN	—	—	3.2	3.1	—	3.3	—	—	—	—
	MAX	—	—	3.2	3.1	—	3.3	—	—	—	—
	MIN	—	—	3.2	3.1	—	3.3	—	—	—	—
cf. <i>Eocardia</i> sp.	N	0	0	0	0	0	0	0	0	1	1
	MEAN	—	—	—	—	—	—	—	—	4.5	4.2
	MAX	—	—	—	—	—	—	—	—	—	—
	MIN	—	—	—	—	—	—	—	—	—	—
<i>Perimys erutus</i>	N	8	8	2	2	1	1	4	4	2	2
	MEAN	3.2	3.1	3.4	3.5	3.8	3.8	3.1	3.6	3.4	3.4
	MAX	4.0	3.7	3.5	3.7	—	—	3.6	4.1	3.5	3.5
	MIN	2.3	3.0	3.3	3.2	—	—	2.4	3.3	3.2	3.3
<i>Perimys onustus</i>	N	5	5	2	2	4	4	10	10	2	2
	MEAN	5.8	6.0	6.5	6.5	5.5	6.0	5.3	6.1	4.8	5.4
	MAX	7.3	6.8	6.5	6.9	6.2	6.7	7.7	7.1	5.8	7.1
	MIN	4.6	4.7	6.4	6.1	3.9	4.1	3.3	5.2	3.7	3.7
<i>Perimys intermedius</i>	N	1	1	3	3	2	2	0	0	2	2
	MEAN	3.8	3.5	3.7	3.4	3.4	3.3	—	—	5.0	4.3
	MAX	—	—	3.8	3.7	3.9	3.5	—	—	5.0	5.2
	MIN	—	—	3.7	2.9	2.9	3.0	—	—	4.9	3.3
<i>Perimys</i> , sp. nov.?	N	1	1	1	2	2	3	4	4	4	4
	MEAN	4.4	3.7	3.7	4.5	4.3	4.0	4.2	4.4	4.2	3.9
	MAX	—	—	—	4.8	4.8	4.5	4.6	4.9	4.9	4.5
	MIN	—	—	—	4.2	3.8	3.3	3.4	3.9	3.1	3.3
<i>Prologostomus pusillus</i>	N	6	6	0	0	0	0	4	4	0	0
	MEAN	3.3	3.1	—	—	—	—	3.1	3.6	—	—
	MAX	4.3	3.8	—	—	—	—	3.5	4.0	—	—
	MIN	2.6	2.6	—	—	—	—	2.5	3.3	—	—

TABLE 1. *continued*

Taxon		p4		m1		m2		m1 or m2		m3	
		AP	LL	AP	LL	AP	LL	AP	LL	AP	LL
<i>Scleromys quadrangulatus</i>	N	2	2	1	1	2	2	2	2	0	0
	MEAN	6.2	4.8	4.8	4.4	4.9	4.7	4.9	4.6	—	—
	MAX	6.6	4.9	—	—	4.9	4.9	5.2	5.1	—	—
	MIN	5.7	4.6	—	—	4.8	4.5	4.5	4.0	—	—
<i>Eosteiomys</i> cf. <i>Eos. annectens</i>	N	2	2	1	1	1	1	0	0	0	0
	MEAN	6.2	3.3	4.5	4.0	4.8	4.0	—	—	—	—
	MAX	7.1	3.5	—	—	—	—	—	—	—	—
	MIN	5.3	3.0	—	—	—	—	—	—	—	—
<i>Steiromys</i> sp.	N	0	0	0	0	0	0	0	0	1	1
	MEAN	—	—	—	—	—	—	—	—	6.1	5.9
	MAX	—	—	—	—	—	—	—	—	—	—
	MIN	—	—	—	—	—	—	—	—	—	—

cf. *Eocardia* sp.

Figure 4G

Eocardia perforata Flynn et al., 2002a: 289 (partim), table 1.

REFERRED MATERIAL: SGOPV 2695, partial left m2 and left m3 in mandibular fragment (fig. 4G).

LOCALITY AND HORIZON: Fossil Horizon 7, Galera Formation, Pampa Castillo, Chile.

DESCRIPTION: SGOPV 2695 consists of a mandibular fragment in which unerupted parts of two cheekteeth are visible (fig. 4G). The teeth appear to be euhypsodont (i.e., ever growing), given that they are fairly large and have a simplified coronal morphology similar to *Eocardia*. The complete tooth represents m3, as evidenced by the wide, shallow flexid on its posterior lobe, which is slightly longer and wider than the anterior lobe. This tooth bears a thin layer of enamel labially.

REMARKS: The lower cheekteeth of SGOPV 2695 approximately match in size their counterparts in material from elsewhere assigned to *Schistomys* and *Eocardia* (table 1), the two euhypsodont “eocardiid” genera known from the early Miocene of Patagonia (Scott, 1905; Pérez, 2010b). It cannot be determined which of these genera SGOPV 2695 represents, as premolars are generally necessary to distinguish them. However, SGOPV 2695 is smaller than nearly all known specimens of *Sch. erro* and *Sch. rollinsii*, favoring assignment to cf. *Eocardia* sp. Of the known *Eocardia* species, SGOPV 2695 falls within the adult size range of *Eoc. excavata* and *Eoc. fissa* but could represent a juvenile of a larger species.

Dasyproctidae Smith, 1842

Neoreomys Ameghino, 1887a

TYPE SPECIES: *Neoreomys australis* Ameghino, 1887a.

INCLUDED SPECIES: The type species, *N. pinturensis* Kramarz, 2006b, and possibly “*N.*” *huilensis* Fields, 1957.

AGE AND DISTRIBUTION: Cerro Boleadoras Formation, Santacrucian SALMA, Santa Cruz Province, Argentina; Chinchas Formation, Santacrucian SALMA, San Juan Province, Argentina; Chucal Formation, Santacrucian SALMA, Arica y Parinacota Region, Chile; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina; Colhue-Huapi Member, Sarmiento Formation, Santacrucian (“Pinturan”) SALMA, Chubut Province, Argentina; Cura-Mallín Formation, Santacrucian? SALMA, Biobío Region, Chile; Collón Curá Formation, Colloncuran SALMA, Chubut, Neuquén, and Río Negro provinces, Argentina; Río Mayo or Pedregoso Formation, Mayoan? SALMA, Santa Cruz or Chubut Province, Argentina; La Victoria Formation, Laventan SALMA, Huila Department, Colombia.

Neoreomys australis Ameghino, 1887a

Figure 5A

LOCALITY AND HORIZON: Fossil horizons E-0, E-2, 4, 5, 7, and 8, Pampa Castillo, Galera Formation, Aysén Region, Chile.

AGE AND DISTRIBUTION: Chinchas Formation, Santacrucian SALMA, San Juan Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina; Collón Curá Formation, Colloncuran SALMA, Chubut, Neuquén, and Río Negro provinces, Argentina.

DESCRIPTION: A full specimen inventory and detailed description of *N. australis* from Pampa Castillo, including an analysis of ontogenetic changes in occlusal morphology, is the subject of another, ongoing project. The level of hypsodonty and overall size of specimens with their cheekteeth in the alveoli lead us to conclude that all Pampa Castillo specimens belong to *N. australis* rather than *N. pinturensis* or “*N.*” *huilensis*. Summary remarks are presented here as a preliminary review of all the cavioids from this fauna. Measurements of these specimens are not reported in tables 1 or 2 or in the online supplement.

REMARKS: *Neoreomys australis* is known from the Santa Cruz and Pinturas formations (Ameghino, 1887b; Scott, 1905; Kramarz, 2006b; Arnal et al., 2019). Material from the Chinchas and Collón Curá formations, which crop out in more northerly Patagonia, is referred to *Neoreomys* cf. *N. australis* (Vucetich et al., 1993; López et al., 2011). In the past, a variety of *Neoreomys* species were recognized (Ameghino, 1887b; Scott, 1905), but most contemporary authors follow Fields (1957) in recognizing *N. australis* as the sole species

represented in the Santa Cruz Formation (Kramarz, 2006b; Croft, 2013; Arnal et al., 2019). *Neoreomys pinturensis* is known from the lower sequence of the Pinturas Formation, where it cooccurs with *N. australis*, and the Upper Faunal Zone of the Sarmiento Formation at Gran Barranca (Kramarz and Bellosi, 2005; Kramarz, 2006b; Kramarz et al., 2010). Two non-Patagonian taxa include “*Neoreomys*” *huilensis* (Fields, 1957) from the middle Miocene of La Venta, Colombia, though this taxon’s assignment to *Neoreomys* is uncertain (Walton, 1997; Kramarz, 2006b), and an undescribed taxon from the Cura-Mallín Formation of central Chile (Flynn et al., 2008).

Neoreomys australis is the most abundantly recovered fossil mammal from Pampa Castillo, comprising more than half of all specimens recovered and including a nearly complete skull (fig. 5A). It is also the most abundant rodent in the Santa Cruz Formation (Scott, 1905; Croft, 2013; Arnal et al., 2019; Zurita-Altamirano et al., 2019) but is much less abundant in the Pinturas Formation (Kramarz and Bellosi, 2005; Kramarz, 2006b). Even if the number of specimens of *N. australis* and *N. pinturensis* are combined, they do not dominate the fauna of the Pinturas Formation to the degree that *N. australis* does at Pampa Castillo or localities in the Santa Cruz Formation (Arnal et al., 2019).

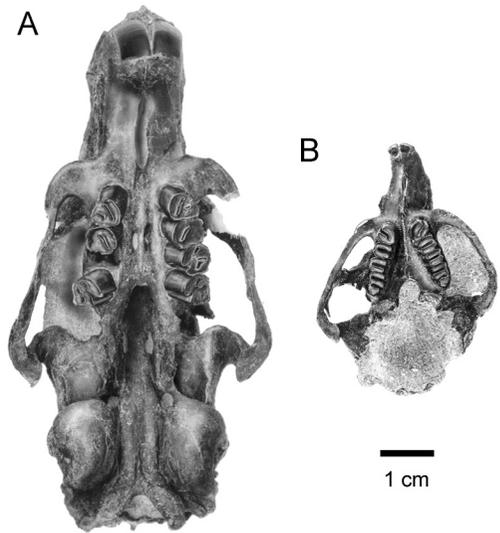


FIG. 5. Ventral view of **A**, *Neoreomys australis* (SGOPV 2212) and **B**, *Perimys erutus* (SGOPV 2361) crania from Pampa Castillo (modified from Flynn et al., 2002a).

Chinchilloidea Bennett, 1833

Neopiblemidae Kraglievich, 1926

Perimys Ameghino, 1887a

TYPE SPECIES: *Perimys erutus* Ameghino, 1887a.

INCLUDED SPECIES: The type species, *Per. onustus* Ameghino, 1887a, *Per. planaris* Ameghino, 1891, *Per. perpinguis* Ameghino, 1891, *Per. zonatus* Ameghino, 1894, *Per. impactus* Ameghino, 1894, *Per. dissimilis* Ameghino, 1902, *Per. incavatus* Ameghino, 1902, *Per. ameghinoi* Scott, 1905, *Per. intermedius* Kramarz, 2002, and *Perimys* sp. nov.? Kramarz, 2002.

AGE AND DISTRIBUTION: Colhue-Huapi and Trelew members, Sarmiento Formation, Colhuehuapian SALMA, Chubut Province, Argentina; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina.

AFFINITIES: *Perimys* is generally considered a member of the extinct chinchilloid subgroup Neoeplemidae; per Rasia and Candela (2018), Neoeplemidae includes the early Miocene, medium-sized *Perimys* and *Doryperimys* Kramarz et al., 2015, and the late Miocene, gigantic rodents *Phoberomys* Kraglievich, 1926, and *Neoeplema* Ameghino, 1889. Most phylogenetic analyses place *Perimys* as the earliest diverging neoeplemid (Rasia and Candela, 2018; Busker et al., 2019; Kerber and Sánchez-Villagra, 2019; Rasia et al., 2021). However, Boivin et al. (2019a), the only study to include *Perimys* in an analysis of all caviomorphs, recovered it as a stem cavioid. Other studies presumed a priori that *Perimys* is a chinchilloid, including only one or two nonchinchilloids as outgroups and not testing chinchilloid monophyly.

GENERAL DESCRIPTION: Here we summarize features shared by species referred to *Perimys*. The differences between these species are detailed subsequently. The cheekteeth of *Perimys* are hypselodont. When freshly erupted, they consist of four lophs/ids that quickly merge into two such structures, though M3 becomes trilophodont (Boivin et al., 2019b; Rasia and Candela, 2019a). Unlike most caviomorphs, the P4 opens labially with a wide flexus (likely the mesoflexus), the apex of which projects posteriorly. The M1 and M2 are bilophodont; their hypoflexi open lingually and are wider than those of *Prolagostomus* and *Pliolagostomus*. The anterior loph is composed of the anteroloph and protocone, while the posterior one includes the mesolophule, metaloph, hypocone, and posteroloph. The mesolophule and hypocone make up the central loph on the trilophodont M3, while the metaloph and posteroloph comprise the posterior loph. The lower cheekteeth are generally quite similar, being bilophodont with anterolabially opening hypoflexids. Teeth generally increase in size posteriorly within the toothrow. Currently recognized species of *Perimys* are distinguished by the borders of their hypoflexi/ids, the distribution of enamel around their teeth, and the presence of “columns” (i.e., stylids or cuspules) on the labial surfaces of upper molars and lingual surfaces of lower molars.

REMARKS: Among other early Miocene chinchilloid caviomorphs, *Perimys* most closely resembles the neoeplemid *Doryperimys olscheri* and the chinchillids *Prolagostomus* and *Pliolagostomus*. The labially opening P4 is the clearest distinction between *Perimys* and chinchillids (Arnal et al., 2019; Rasia and Candela, 2019b). The third loph of M3 reaches the lingual edge of the tooth in species of *Perimys* but not in chinchillids. The lophs/ids and hypoflexi/ids are generally broader in *Perimys* than in *Prolagostomus* and *Pliolagostomus*. *Perimys* mostly notably differs from *Doryperimys* of the Cerro Bandera Formation (most likely Colhuehuapian SALMA) in the more rounded ends of its lower molar lophs. A suite of additional distinguishing features are detailed by Kramarz et al. (2015).

Flynn et al. (2002a) assigned Pampa Castillo *Perimys* specimens to five species (*Per. onustus*, *Per. perpinguis*, and *Per. impactus*, *Perimys* “*scalaris*,” and *Perimys* “*procerus*”), whereas we recognize only four species: *Per. erutus*, *Per. onustus*, *Per. intermedius*, and *Perimys* sp. nov.?. This difference is largely due to the revision of this genus by Kramarz (2002). In that study, he named *Per. intermedius* as a new species. Kramarz (2002) also described a set of *Perimys* teeth that did not match any known species, which he recognized as a potentially new species but chose to call them *Perimys* sp. We will refer to this potentially valid taxon as *Perimys* sp. nov.?. Additionally, Kramarz (2002) synonymized two *Perimys* species recognized by Flynn et al. (2002a), *Per.* “*sca-*

laris” and *Per. “procerus”* (along with *Perimys “angulatus,”* *Perimys “diminutus,”* and *Perimys “reflexus”*), with the genotype species *Per. erutus*. Kramarz (2001a) commented that the other three species identified by Flynn et al. (2002a), *Per. onustus*, *Per. perpinguis*, and *Per. impactus* (plus *Per. planaris*, *Per. zonatus*, and *Per. ameghinoi*), were synonymous with *Per. onustus*.

Perimys erutus Ameghino, 1887a

Figures 5B, 6A–E

Perimys procerus Flynn et al., 2002a: 289, table 1.

Perimys scalaris Flynn et al., 2002a: 289, table 1.

REFERRED MATERIAL: SGOPV 2294, left p4; SGOPV 2361, partial skull with complete upper dentition (fig. 5B; identified as *Perimys “procerus”* therein); SGOPV 2386, left p4–m1 (fig. 6C); SGOPV 2391, right p4; SGOPV 2616, right P4–M1; SGOPV 2617, right m2–3 (fig. 6E); SGOPV 2618, right M1 or 2; SGOPV 2619, left P4–M2 (fig. 6A); SGOPV 2620, right m1 or 2; SGOPV 2621, right M1 or 2; SGOPV 2622, left M1 or 2; SGOPV 2623, right p4–m1 (fig. 6D); SGOPV 2624, left M1–3; SGOPV 2625, right P4; SGOPV 2626, left M1 or 2; SGOPV 2627, left M3; SGOPV 2628, right M3 (fig. 6B); SGOPV 2629, right M1–2; SGOPV 2630, right lower molar; SGOPV 2631, right p4; SGOPV 2632, left M3; SGOPV 2633, right M1 or 2; SGOPV 2634, left p4 in mandibular fragment with incisor root; SGOPV 2635, right M3; SGOPV 2636, right m3; SGOPV 2637, right P4; SGOPV 2638, left M1 or 2; SGOPV 2639, left p4 in mandibular fragment with incisor root; SGOPV 2640, right p4 in mandibular fragment with incisor root; SGOPV 2641, right m1 or 2; SGOPV 2642, left M1 or 2; SGOPV 2643, right m1 or 2; SGOPV 2644, right M1 or 2; SGOPV 2672, right P4; SGOPV 2722, right m1 or 2.

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon E-0 (SGOPV 2386, 2618, 2627, 2628, 2631, 2632, 2633, 2634, 2635, 2636, 2637, 2638, 2639, 2640, 2672, 2722), Fossil Horizon 1A (SGOPV 2361), Fossil Horizon E-2 (SGOPV 2616), Fossil Horizon 4 (SGOPV 2617, 2617, 2621, 2623, 2624, 2625, 2629, 2630), Fossil Horizon 7 (SGOPV 2641, 2642, 2643, 2644), “Glyptodont Glen” (SGOPV 2294, 2620, 2626), and unknown Fossil Horizon (SGOPV 2391, 2622), Galera Formation, Pampa Castillo, Chile.

AGE AND DISTRIBUTION: Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina.

DESCRIPTION: Specimens of *Per. erutus* from Pampa Castillo resemble those from other sites. *Perimys erutus*, the smallest-bodied species of *Perimys* at Pampa Castillo (tables 1, 2), is distinguished from other members of the genus by the following dental characters. The hypoflexi/ids of M1–3 and p4–m3 have straight or nearly straight borders (figs. 5B, 6A–E). Enamel surfaces on M1–3 labially, and p4–m3 lingually, usually complete or lacking only a narrow vertical band. M1–2 usually bear “pillars” opposite the anterior loph on the labial surface (figs. 5B, 6A). The m3 is the only lower tooth that possesses a small lingual flexid (fig. 6E).

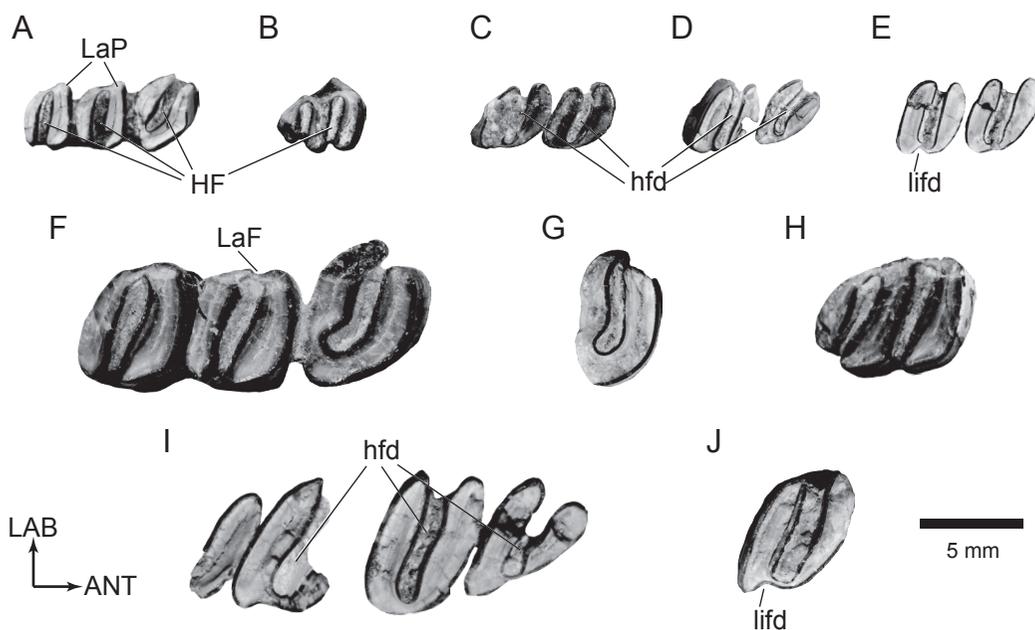


FIG. 6. *Perimys erutus* and *Perimys onustus* specimens from Pampa Castillo. *Perimys erutus*: A, GOPV 2619, left P4–M2 (reversed); B, GOPV 2628, right M3; C, GOPV 2386, left p4–m1; D, GOPV 2623, right p4–m1 (reversed); E, GOPV 2617, right m2–3 (reversed). *Perimys onustus*: F, GOPV 2661, left P4–M2 (reversed); G, GOPV 2655, right P4; H, GOPV 2662, left M3 (reversed); I, GOPV 2273, right p4–m1 and partial m2–3 (reversed); J, GOPV 2030, left m3. Abbreviations: ANT, anterior; HF, hypoflexus; hfd, hypoflexid; LAB, labial; LaF, labial flexus; LaP, labial pillar; lifd, lingual flexid.

REMARKS: *Perimys erutus* is one of the most abundant rodents recovered from Pampa Castillo, trailing only *Perimys onustus* and *Neoreomys australis* in the number of specimens identified (table S1 in the online supplement, <https://doi.org/10.5531/sd.sp.53>). It occurs throughout the stratigraphic section, but most abundantly in the lowest fossiliferous horizon, Fossil Horizon E-0 (fig. 2). This taxon is also known from throughout the Santa Cruz Formation and from the upper sequence of the Pinturas Formation (Ameghino, 1887b; Scott, 1905; Kramarz, 2002; Arnal et al., 2019). Two of the five *Perimys* species recognized from Pampa Castillo by Flynn et al. (2002a), *Perimys “scalaris”* and *Perimys “procerus,”* were identified as junior synonyms of *Per. erutus* by Kramarz (2002).

Perimys onustus Ameghino, 1887a

Figure 6F–J

Perimys perpinguis Flynn et al., 2002a: 289, table 1.

Perimys impactus Flynn et al., 2002a: 289 (partim), table 1.

Perimys onustus Flynn et al., 2002a: 289 (partim), table 1.

REFERRED MATERIAL: GOPV 2014, right p4–m2 and left m2; GOPV 2030; left m3 (fig. 6J); GOPV 2045, left P4–M3, right P4–M2, and partial right M3; GOPV 2056, left m1 or 2;

SGOPV 2080, lower incisors and fragments of right p4–m3; SGOPV 2273, right p4–m1 and partial right m2–3 (fig. 6I); SGOPV 2378, left m1 or 2; SGOPV 2421, right P4; SGOPV 2655, right P4 (fig. 6G); SGOPV 2656, right M3; SGOPV 2657, left P4; SGOPV 2658, left M3; SGOPV 2659, right M1 or 2; SGOPV 2660, right M1 or 2; SGOPV 2661, left P4–M2 (fig. 6F); SGOPV 2662, left M3 (fig. 6H); SGOPV 2663, right P4; SGOPV 2664, right M1 or 2; SGOPV 2665, left m1 or 2; SGOPV 2666, right p4; SGOPV 2667, right m1 or 2; SGOPV 2668, left p4; SGOPV 2669, left m1 or 2; SGOPV 2670, left m3?; SGOPV 2671, left m1 or 2; SGOPV 2673, right M1 or 2; SGOPV 2674, right m1 or 2; SGOPV 2675, right m2–3; SGOPV 2676, right lower molar; SGOPV 2677, left lower molar; SGOPV 2678, right M3; SGOPV 2680, right P4; SGOPV 2681, right P4; SGOPV 2682, right m1 or 2; SGOPV 2683, right P4–M2; SGOPV 2684, left m1 or 2; SGOPV 2685, m1 or 2; SGOPV 2687, left M1 or 2.

LOCALITY AND HORIZON: Fossil Horizon E-0 (SGOPV 2421, 2673) Fossil Horizon E-2 (SGOPV 2101, 2675), Fossil Horizon 2 (SGOPV 2014), Fossil Horizon 3 (SGOPV 2030), Fossil Horizon 4 (SGOPV 2045, 2056, 2060, 2273, 2661, 2662, 2663, 2664, 2671, 2674, 2681, 2682), Fossil Horizon 5 (SGOPV 2080, 2665, 2687), Fossil Horizon 6-7 (SGOPV 2655, 2656, 2657, 2658, 2659, 2660), Fossil Horizon 7 (SGOPV 2121, 2378, 2666, 2667, 2668, 2669, 2670, 2677, 2678, 2680), “Glyptodont Glen” (SGOPV 2676), and unknown Fossil Horizon (SGOPV 2683), Galera Formation, Pampa Castillo, Chile.

AGE AND DISTRIBUTION: Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina.

DESCRIPTION: Specimens of *Perimys onustus* from Pampa Castillo closely match those reported from the Santa Cruz Formation. This taxon is the largest-bodied species of *Perimys*, though little worn teeth fall within the size range exhibited by other *Perimys* species (tables 1, 2). The edges of the hypoflexi/ids of *Per. onustus* are often sinuous (fig. 6F–J). Enamel on the labial surfaces of M1–3 and the lingual surfaces of p4–m3 is usually complete or missing a narrow vertical band. M1–3 bear labial flexi, and p4–m3 bear lingual flexids (becoming more pronounced posteriorly). The upper molars are characterized by the anterolabial “pillars” mentioned previously (fig. 6F).

REMARKS: *Perimys onustus* is the most commonly preserved species of *Perimys* in the Pampa Castillo fauna, slightly more abundant than *Per. erutus* (table S1). After *Neoreomys australis*, *Per. onustus*, the second most commonly recovered species at Pampa Castillo, occurs throughout the section. This is the first detailed description of material assigned to *Per. onustus* outside of the Santa Cruz Formation of Argentina (Scott, 1905; Croft, 2013; Arnal et al., 2019). Flynn et al. (2002a) reported *Per. onustus* from Pampa Castillo, as well as two species synonymized with it in an unpublished Ph.D. dissertation (Kramarz, 2001a), *Perimys “impactus”* and *Perimys “perpinguis.”*

Perimys intermedius Kramarz, 2002

Figure 7A–D

Perimys onustus Flynn et al., 2002a: 289 (partim), table 1.

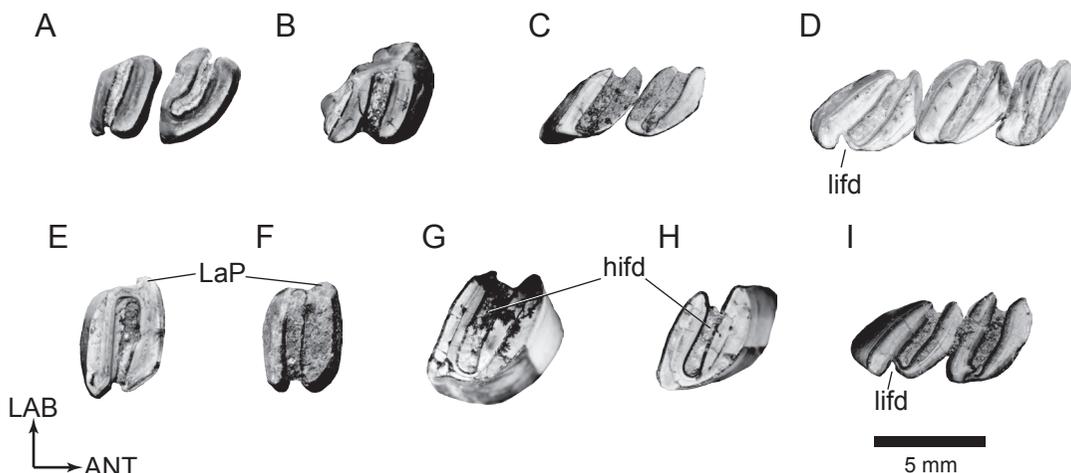


FIG. 7. *Perimys intermedius* and *Perimys* sp. nov.? specimens from Pampa Castillo. *Perimys intermedius*: A, SGOPV 2651, right P4–M1; B, SGOPV 2653, partial right M3; C, SGOPV 2281, left p4–m1; D, SGOPV 2652, right m1–3 (reversed). *Perimys* sp. nov.?: E, SGOPV 2679, left M1 or 2 (reversed); F, SGOPV 2285, right M1 or 2; G, SGOPV 2684, left p4; H, SGOPV 2649, right m1 or 2 (reversed); I, SGOPV 2267, right m2–3 (reversed). Abbreviations: ANT, anterior; hifd, hypoflexid; LAB, labial; LaP, labial pillar; lifd, lingual flexid.

REFERRED MATERIAL: SGOPV 2281, left p4–m1 (fig. 7C); SGOPV 2299, right m3; SGOPV 2645, right M3; SGOPV 2651, right P4–M1 (fig. 7A); SGOPV 2652, right m1–3 (fig. 7D); SGOPV 2653, partial right M3 (fig. 7B); SGOPV 2654, right m1–2.

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon E-0 (SGOPV 2299), Fossil Horizon 4 (SGOPV 2651, 2652, 2653), Fossil Horizon 4abc (SGOPV 2281), and Fossil Horizon 7 (SGOPV 2645, 2654), Galera Formation, Pampa Castillo, Aysén Region, Chile.

AGE AND DISTRIBUTION: Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile.

DESCRIPTION: As its name suggests, *Perimys intermedius* is intermediate in size between *Per. erutus* and *Per. onustus* (tables 1, 2; Kramarz, 2002). The molar hypoflexi/id borders are straight, unlike in *Per. onustus* (fig. 7A–D). *Per. intermedius* is most obviously distinguished from other species of the genus by the lack of enamel on the lingual faces of its lower molars and the labial faces of M1–2 (the labial wall of M3 in *Per. intermedius* generally bears enamel but in a narrower band than other species; fig. 7A–B). The upper molars of *Per. intermedius* lack labial flexi, while p4–m2 lack lingual flexids. Specimens from Pampa Castillo here assigned to *Per. intermedius* are closely similar to those from the Pinturas Formation described by Kramarz (2002).

REMARKS: *Perimys intermedius* is the least abundant of the four *Perimys* species at Pampa Castillo (table S1). Of the four specimens whose precise provenance is known, three were recovered low in the section (Fossil Horizon E-0), and one high (Fossil Horizon 7). Besides Pampa Castillo, *Per. intermedius* has only been identified in the lower and middle sequences of the Pinturas Formation (ImPF), where it is the most abundant species of *Perimys* (Kramarz, 2002).

Perimys sp. nov.? Kramarz, 2002

Figure 7E–I

Perimys sp. Kramarz, 2002: 175–176.

Perimys impactus Flynn et al., 2002a: 289 (partim), table 1.

REFERRED MATERIAL: SGOPV 2267, right m2–3 (fig. 7I); SGOPV 2285, right M1 or 2 (fig. 7F); SGOPV 2401, right m3; SGOPV 2431, right m3; SGOPV 2646, right m1 or 2; SGOPV 2647, right m1–2; SGOPV 2648, right m1 or 2; SGOPV 2649, left m1 or 2 (fig. 7H); SGOPV 2650, right m2–3; SGOPV 2679, left M1 or 2 (fig. 7E); SGOPV 2684, left p4 (fig. 7G); SGOPV 2686, left p4–m1.

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon E-0 (SGOPV 2285, 2401, 2650), Fossil Horizon E-2 (SGOPV 2267, 2686), Fossil Horizon 4 (SGOPV 2646, 2647, 2648, 2649, 2684), and Fossil Horizon 7 (SGOPV 2431, 2679), Galera Formation, Pampa Castillo, Aysén Region, Chile.

AGE AND DISTRIBUTION: Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina.

DESCRIPTION: These specimens from Pampa Castillo are similar in size (tables 1, 2) and morphology to the unnamed new species of *Perimys* from the Pinturas Formation mentioned by Kramarz (2002) and differ from other *Perimys* species in several respects. The labial edges of the upper molars are marked by narrow band of enamel, and a narrow band of enamel occurs on the lingual surface of the lower molars unlike *Per. intermedius*. The edges of the hypoflexi/ids are straight in these specimens unlike *Per. onustus* (fig. 7E–I).

REMARKS: Owing to their poor match to described species, Kramarz (2002) assigned four distinctive specimens from the Pinturas Formation to *Perimys* sp. but declined to recognize a new species given the limited and fragmentary sample. The specimens from Pampa Castillo here assigned to *Perimys* sp. nov.? match Kramarz’s (2002) description. *Perimys* sp. nov.? is distinguished from other members of the genus by a unique combination of features that are seen individually in other species (size, sinuosity of lophs, and enamel distribution). Unfortunately, our material is equally unsatisfactory for diagnosing a new species. In view of this, and an inability to directly examine the material described by Kramarz (2002), we similarly opt against naming a new taxon at this time.

Perimys sp. nov.? is the third most abundant species of *Perimys* at Pampa Castillo, after *Per. onustus* and *Per. erutus* (table S1). In the Pinturas Formation, it is also the third most abundant, although it is far less common than *Per. intermedius* and *Per. erutus* (Kramarz, 2002).

Chinchillidae Bennett, 1833

Lagostominae Wiegmann, 1835

Prolagostomus Ameghino, 1887a

TYPE SPECIES: *Prolagostomus pusillus* Ameghino, 1887a.

INCLUDED SPECIES: The type species, *Pro. obliquidens* Scott, 1905, *Pro. rosendoi* Vucetich, 1984, and *Prolagostomus* sp. nov.?, Kramarz, 2002.

AGE AND DISTRIBUTION: Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Cerro Boleadoras Formation, Santacrucian SALMA, Neuquén Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina; Cura-Mallín Formation, Santacrucian? SALMA, Biobío Region, Chile; Collón Curá Formation, Colloncuran SALMA, Chubut, Neuquén, and Río Negro provinces, Argentina; Río Frías Formation, Colloncuran SALMA, Aysén Region, Chile, and Chubut Province, Argentina; unnamed formation (Quebrada Honda), Laventan SALMA, Tarija Department, Bolivia.

Prolagostomus pusillus Ameghino, 1887a

Figure 8

Pliolagostomus notatus Flynn et al., 2002a: 289, table 1.

Prolagostomus divisus Flynn et al., 2002a: 289, table 1.

Prolagostomus profluens Flynn et al., 2002a: 289, table 1.

Prolagostomus pusillus (sic) Flynn et al., 2002a: 289, table 1.

REFERRED MATERIAL: SGOPV 2427, left M1 or 2; SGOPV 2599, partial right P4–M2; SGOPV 2600, left lower molariform; SGOPV 2601, left lower molariform; SGOPV 2602, left p4 with root of left lower incisor (fig. 8C); SGOPV 2603, partial left P4–M1; SGOPV 2604, left p4 (fig. 8D); SGOPV 2605, right lower molariform; SGOPV 2606, left p4 with root of left lower incisor; SGOPV 2607, right P4–M1 (fig. 8B); SGOPV 2608, right M2–M3 (fig. 8A); SGOPV 2609, partial left M1 or 2?; SGOPV 2610, partial left P4–M1; SGOPV 2611, right p4 and root of right lower incisor (fig. 8E); SGOPV 2612, left lower molariform; SGOPV 2613, right p4; SGOPV 2614, left p4; SGOPV 2615, right p4.

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon E-2 (SGOPV 2612), Fossil Horizon 4 (SGOPV 2613), Fossil Horizon 6-7 (SGOPV 2427, 2607, 2608, 2609, 2610, 2611), and Fossil Horizon 7 (SGOPV 2599, 2600, 2601, 2602, 2603, 2604, 2605, 2606, 2614, 2615), Galera Formation, Pampa Castillo, Chile.

AGE AND DISTRIBUTION: Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina; Cura-Mallín Formation, Santacrucian? SALMA, Biobío Region, Chile; Collón Curá Formation, Colloncuran SALMA, Chubut, Neuquén, and Río Negro provinces, Argentina; Río Frías Formation, Colloncuran SALMA, Aysén Region, Chile, and Chubut Province, Argentina.

DESCRIPTION: The cheekteeth of *Pro. pusillus* are hypselodont with two simple laminae, except M3, which has three laminae (fig. 8). Although broadly similar to *Perimys*, the laminae and hypoflexi/ids of *Pro. pusillus* are much narrower anteroposteriorly. Moreover, the hypoflexus of the P4 of *Pro. pusillus* opens lingually, like M1–3, differing from *Perimys* (where the flexus of P4 open labially). The hypoflexi of P4–M3 are oriented transversely and filled with cementum (fig. 8A–B). The molars of *Pro. pusillus* differ from those of *Pliolagostomus* in the former’s slightly more convex anterior and posterior borders. Additionally, the anterior lophes (anteroloph, per Rasia and Candela, 2019a) of the upper molars project further labially than

the posterior lophs in *Pro. pusillus*, whereas they extend equally far in *Pliolagostomus*. The anterior and lingual faces of the lower molars have a smooth transition in *Pro. pusillus*, whereas in *Pliolagostomus* the interface is more angular.

Lower molars of the Colloncuran-aged *Pro. rosendoi* are unknown (Vucetich, 1984), and the lower molars of a possibly new *Prolagostomus* species from the Pinturas Formation are indistinguishable from those of *Pro. pusillus* (fig. 8C–E; Kramarz, 2002; Rasia, 2016). We assign these lower molar specimens from the Pampa Castillo fauna to *Pro. pusillus*, however, because it is the most parsimonious conclusion given their morphological match with *Pro. pusillus* and the presence of upper teeth only referable to *Pro. pusillus* in the same fossil horizon.

REMARKS: In an unpublished Ph.D. thesis, Rasia (2016) recognized two, or possibly three, *Prolagostomus* species from the Santacrucian SALMA, many fewer than previous authors (e.g., Ameghino, 1887a; Scott, 1905), by synonymizing most previously recognized species with the type, *Pro. pusillus*. *Prolagostomus obliquidens* was left valid, but one of the authors of this study (A.J.M.) was unable to locate the type and sole specimen of *Pro. obliquidens* in the collections of the Yale Peabody Museum. Rasia (2016) concurred with Kramarz (2002) that the *Prolagostomus* specimens from the Pinturas Formation seem distinct from all known species but cautioned that better-quality specimens were needed to verify this hypothesis.

Prolagostomus pusillus is common at Pampa Castillo, its abundance trailing only that of *N. australis*, *Per. onustus*, *Per. erutus*, and *Perimys* sp. nov.? among rodents (table S1). *Prolagostomus pusillus*, previously reported from the Santa Cruz, Río Frías, and Collón Curá formations and the Honda Group (Bolivia) (Ameghino, 1887b; Scott, 1905; Vucetich, 1984; Bamba and Croft, 2015; Rasia, 2016), is likely the only species of the genus recorded at Pampa Castillo.

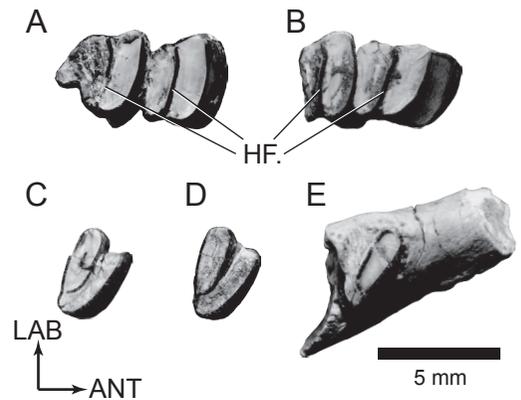


FIG. 8. *Prolagostomus pusillus* specimens from Pampa Castillo. A, SGOPV 2608, right M2–3; B, SGOPV 2607, right P4–M1; C, SGOPV 2602, left p4; D, SGOPV 2604, left p4; E, SGOPV 2611, partial right p4 in mandibular fragment (reversed). Abbreviations: ANT, anterior, HF, hypoflexus, LAB, labial.

Dinomyidae Alston, 1876

Scleromys Ameghino, 1887a

TYPE SPECIES: *Scleromys angustus* Ameghino, 1887a.

INCLUDED SPECIES: The type species, *Scl. osbornianus* Ameghino, 1894, and *Scl. quadrangulatus* Kramarz, 2006a. Note: Although “*Scleromys*” *colombianus* Fields, 1957, and “*Scleromys*” *schurmanni* Stehlin, 1940, from northern South America appear more closely related to the extant Dinomyidae than to extinct species of *Scleromys* from Patagonia, they have not yet been formally reassigned to another taxon (Patterson and Wood, 1982; Walton,

1997; Kramarz et al., 2013). As they are clearly distinct from *Scleromys* sensu stricto, they will not be considered here.

AGE AND DISTRIBUTION: Chambira Formation, Deseadan SALMA, Peru; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina; Cura-Mallín Formation, Santacrucian? SALMA, Biobío Region, Chile; Chinchas Formation, Santacrucian SALMA, San Juan Province, Argentina.

Scleromys quadrangulatus Kramarz, 2006a

Figure 9A–E

Scleromys sp. Flynn et al., 2002a: 289 (partim), table 1.

REFERRED MATERIAL: SGOPV 2699, roots of left p4 and complete left m1–2 (fig. 9A); SGOPV 2700, complete right p4 (fig. 9B) and partial right m1–2; SGOPV 2701, left m1 or 2 (fig. 9C); SGOPV 2702, left p4 (fig. 9D); SGOPV 2703, left m1 or 2 (fig. 9E).

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon 4 (SGOPV 2699, 2700, 2702, 2703) and unknown Fossil Horizon (SGOPV 2701), Galera Formation, Pampa Castillo, Aysén Region, Chile.

AGE AND DISTRIBUTION: Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Galera Formation, Santacrucian SALMA, Aysén Region, Chile.

DESCRIPTION: Two specimens, SGOPV 2700 and SGOPV 2702, preserve p4 (fig. 9B, 9D). Although this tooth in SGOPV 2700 is slightly longer anteroposteriorly than that of SGOPV 2702, these teeth are otherwise remarkably similar (table 1). Metalophulid I is straight and transversely oriented in both. The posterolophid of p4 in SGOPV 2700 is straighter and more transverse than in SGOPV 2702, but this difference likely reflects the latter specimen’s lesser wear, as evidenced by its open anteroflexid. The m1 and m2 of *Scl. quadrangulatus* closely resemble one another; both are preserved in SGOPV 2699 and SGOPV 2700 (fig. 9A–B). SGOPV 2701 and 2703, isolated teeth, thus may represent either tooth position (fig. 9C, 9E). As on p4, the metalophulid I of m1 and m2 are straight and transversely oriented. In the m1–2 of SGOPV 2703, and the m1 of SGOPV 2699, the anterofossettid is completely separated from the mesoflexid/fossettid by the neomesolophid (= metalophulid II sensu Rasia et al., 2021), but in m1–2 of SGOPV 2701 and the m2 of SGOPV 2699 the neomesolophid does not join metalophulid I, so the fossettids are merged. The anterolabial corners of m1 and m2 of SGOPV 2700 are damaged, so their details are unknown.

REMARKS: We assign these specimens to *Scleromys quadrangulatus* based on the diagnostic straight, transverse metalophulid I (fig. 9A–E). This is the only known record of *Scl. quadrangulatus* apart from the lower and middle part of the Pinturas Formation (Kramarz, 2006b). *Scleromys angustus* and *Scleromys osbornianus* are known from the Santa Cruz Formation (Ameghino, 1887b; Scott, 1905; Arnal et al., 2019), and the latter species also occurs in the upper Pinturas Formation (Kramarz, 2006b). A fourth species, “*Scleromys*” *praecursor*, was named from the late

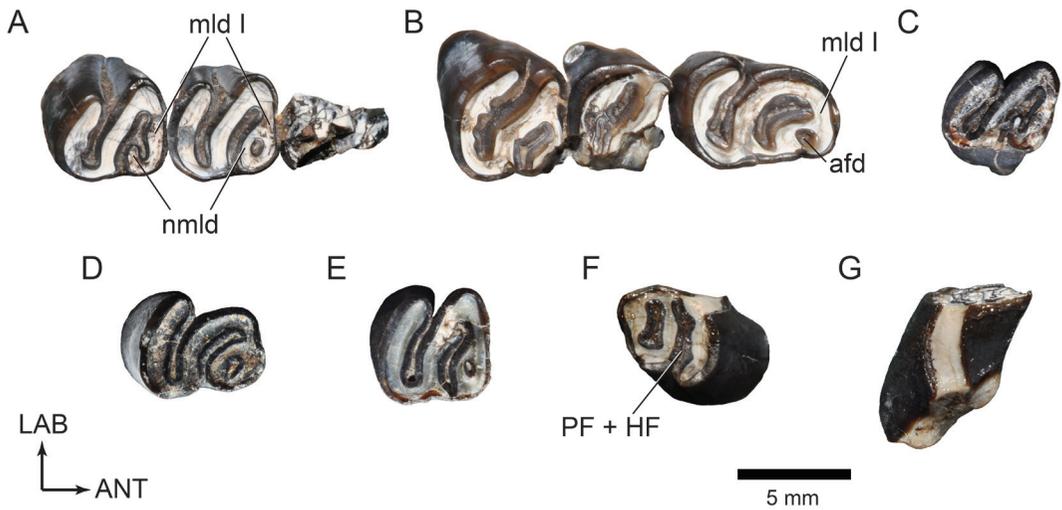


FIG. 9. *Scleromys* specimens from Pampa Castillo. *Scleromys quadrangulatus*: **A**, SGOPV 2699, roots of left p4 and complete m1–2; **B**, SGOPV 2700, right p4 and partial m1–2 (reversed); **C**, SGOPV 2701, left m1 or 2; **D**, SGOPV 2702, left p4; **E**, SGOPV 2703, left m1 or 2. *Scleromys* sp.: SGOPV 2704, left upper molar in occlusal (**F**, reversed) and labial view. Abbreviations: **afd**, anterofossettid; **ANT**, anterior; **LAB**, label; **mld I**, metalopholid I; **nmld**, neomesolophid; **PF + HF**, combined paraflexus and hypoflexus.

Oligocene (Deseadan SALMA) of Contamana, Peru (Boivin et al., 2017), but later work reassigned this species to the monotypic genus *Maquiamys* (Boivin et al., 2019a).

Scleromys sp.

Figure 9F–G

Scleromys sp. Flynn et al., 2002a: 289 (partim), table 1.

REFERRED MATERIAL: SGOPV 2704, right lower molar (fig. 9F–G).

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon 4, Galera Formation, Pampa Castillo, Aysén Region, Chile.

DESCRIPTION: SGOPV 2704 likely represents a left upper cheektooth (fig. 9F–G). The paraflexus and hypoflexus are merged, and the metafossette is hourglass shaped. No trace of the posterofossette is preserved. The posterior border of the paraflexus-hypoflexus is irregular rather than smoothly curved or sinuous. The anteroloph is broad and smoothly convex on its anterior side but has an uneven posterior border (which is the anterior border of paraflexus-hypoflexus). The posteroloph is straight and extends posterolabially from the hypocone. The labial end of the posteroloph is notably thicker than where it joins the hypocone, likely reflecting that it has merged with the mesoloph (Boivin and Marivaux, 2020; Rasia et al., 2021). The protocone extends farther lingually than the hypocone. The most notable aspect of this tooth is its lack of enamel around its anterolabial corner (fig. 9G). We are uncertain whether this feature was present in life or is a preservational artifact. The former hypothesis is supported by the consistent width of this gap from the occlusal surface to the root of the tooth and that some anatomically derived chinchilloids have similar

enamel gaps, such as *Ferigolomys pacarana* Kerber et al., 2018 (Dinomyidae), *Arazamys castiglionii* Rinderknecht et al., 2011 (Dinomyidae), *Eoviscaccia boliviana* Vucetich, 1989 (Chinchillidae), and others. The relatively abrupt transition from enamel to dentine on the edge of this tooth supports the preservational artifact hypothesis. This feature has not been reported in Santacrucian or Laventan species of *Scleromys* or “*Scleromys*” (Scott, 1905; Fields, 1957; Walton, 1997; Kramarz, 2006b; Cerdeño and Vucetich, 2007).

REMARKS: SGOPV 2704 most closely resembles an upper molar of *Scleromys* spp. The protocone extends farther lingually than the hypocone, unlike in the lower cheekteeth where the corresponding features, the posteroloph and metaconid, are generally even or the metaconid may extend farther labially (Kramarz, 2006b). Additionally, the posteroloph is straight and oblique, whereas the corresponding metalophulid I in a lower cheektooth is curved in *Scl. angustus* and *Scl. osbornianus* or straight and labiolingually oriented in *Scl. quadrangulatus* (Kramarz, 2001a, 2006b; Rasia and Candela, 2019a). Despite being similar in size to the upper molars of *Scl. quadrangulatus* (table 2; Kramarz, 2006b), SGOPV 2704 bears some morphological differences. Kramarz (2006b) only depicted two little-worn upper cheekteeth of *Scl. quadrangulatus*, but in his unpublished PhD dissertation (Kramarz, 2001a), more specimens were illustrated, allowing us to compare more broadly. The absence of enamel on the anterolabial corner of SGOPV 2704 is the most notable difference, but as stated previously, this could be preservational damage. The metafossette is oriented labiolingually, whereas in *Scl. quadrangulatus* (and *Scl. angustus* and *Scl. osbornianus*), the labial end of this feature is typically anterior to the lingual end. Alternatively, if our preferred orientation (i.e., rotation) of the specimen is inaccurate and the metafossette is oriented similarly to *Scl. quadrangulatus*, then the protocone of SGOPV 2704 would extend farther lingually, relative to the hypocone, than is seen in *Scl. quadrangulatus*.

We refer SGOPV 2704 to *Scleromys* sp. rather than *Scl. quadrangulatus* because of its slight morphological differences from that species, as detailed above. Furthermore, we cannot be certain of its locus, because SGOPV 2704 was found as a single, isolated tooth. Cheekteeth of different loci from other early Miocene chinchilloids bear some resemblance to SGOPV 2704, such as the upper cheekteeth of *Garridomys curunuquem* Kramarz et al., 2013, and the p4 of *Saremmys ligcura* Busker et al., 2019. This additional uncertainty provides further reason to refrain from identifying SGOPV 2704 more definitively to the species level.

Erethizontoidea Bonaparte, 1845

Erethizontidae Bonaparte, 1845

Eosteioromys Ameghino, 1902

TYPE SPECIES: *Eosteioromys homogenidens* Ameghino, 1902.

INCLUDED SPECIES: The type species, *Eos. annectens* Ameghino, 1899, and *Eos. segregatus* Ameghino, 1902.

AGE AND DISTRIBUTION: Colhue-Huapi Member, Sarmiento Formation, Colhuehuapian and Santacrucian (“Pinturan”) SALMAs, Chubut Province, Argentina; Cerro Bandera Formation, Colhuehuapian(?) SALMA, Neuquén Province, Argentina; Galera Formation, Santacru-

cian SALMA, Aysén Region, Chile; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina.

Eosteiomys cf. *Eos. annectens* Ameghino, 1899

Figure 10A–B

Steiromys new sp. Flynn et al., 2002a: 289, table 1.

REFERRED MATERIAL: SGOPV 2157, right mandibular fragment with roots of the incisor and p4, and complete m1–2 (fig. 10B); SGOPV 2688, partial right (d?)p4 (fig. 10A).

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon E-0 (SGOPV 2157, 2688) and unknown level (SGOPV 2752), Galera Formation, Pampa Castillo, Aysén Region, Chile.

AGE AND DISTRIBUTION: Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina.

DESCRIPTION: SGOPV 2157 preserves the root of the lower right incisor. This incisor seems slightly labiolingually flattened (although the specimen may be slightly deformed), but it is still convex labially (externally/ventrally), and slightly thicker labiolingually than wide mesiodistally.

The crown of (d?)p4 of SGOPV 2157 is obliterated (fig. 10B), whereas SGOPV 2688 represents a heavily worn partial (d?)p4 (fig. 10A). SGOPV 2688 is tetralophodont and bears a small spur within the anterofossettoid, likely representing a neolophid (Candela, 2002; Boivin and Marivaux, 2020). The neomesolophid splits before reaching the lingual edge of the dp4 to meet the metaconid and mesostylid, producing a small fossettoid. The mesolophid is small and weakly joined to the mesostylid. The hypolophid and posterolophid are both obliquely oriented, and the posterolophid is strongly curved.

SGOPV 2157 preserves m1 and m2, both of which are brachydont and tetralophodont (fig. 10B; table 1). The anterofossettoids and metafossettoids are closed, whereas the mesoflexids and hypoflexids remain open. All three lingual flexids/fossettoids are approximately equal in width. In m1, the anterofossettoid, mesoflexid, and metafossettoid extend approximately the same distance labially, but in m2, the anterofossettoid extends farther than the other two fossettoids. Metalophid I on both teeth is straight and transversely oriented, whereas the neomesolophid and hypolophid are somewhat sinuous. The posterolophid curves gently to join the hypoconid. Particularly in m2, the anterior arm of the hypoconid, separating the hypoflexid and metafossettoid, is thinner than the other lophids suggesting that these features were united in an earlier stage in wear.

REMARKS: We regard SGOPV 2157 as assignable to a species of *Eosteiomys* based on its tetralophodont molars, unlike *Branisamyopsis* Candela, 2003, which is pentalophodont. Additionally, the incisor in this specimen is transversely narrow, with a slightly convex labial (external) face, unlike in *Steiromys* Ameghino, 1887a, which has much broader (mesiodistally) incisors with flatter faces. Among named *Eosteiomys* species, SGOPV 2157 bears closest resemblance to *Eos. annectens* Kramarz, 2004. The weak connection between the hypoconid and hypolophid distinguishes this taxon from *Eosteiomys homogenidens*. Although SGOPV 2157 is smaller than all specimens of *Eos. annectens* from the Pinturas Formation (Kramarz, 2004), this difference is slight (~0.5 mm). In an

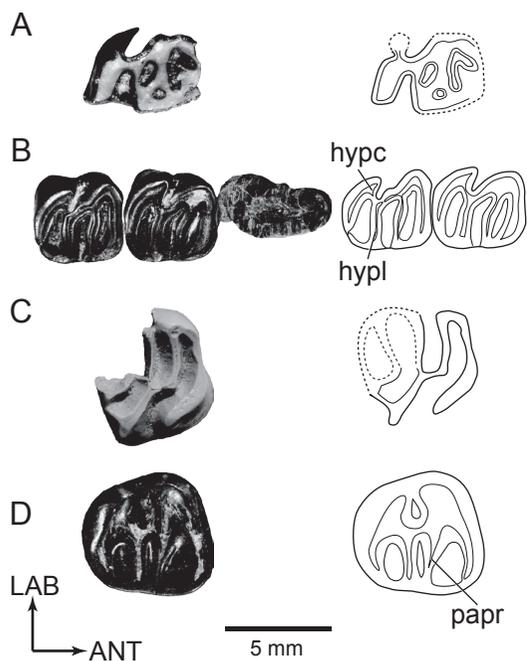


FIG. 10. Erethizontoid specimens from Pampa Castillo. *Eosteiomys* cf. *Eos. annectens*: **A**, SGOPV 2688, right dp4 (reversed); **B**, SGOPV 2157, roots of right p4 and complete m1–2. *Steiromys* sp.: **C**, cast of SGOPV 2190, partial left M3 (reversed); **D**, SGOPV 2689, right m3 (reversed). Abbreviations: **ANT**, anterior; **hycp**, hypoconid; **hypl**, hypolophid, **LAB**, labial; **papr**, posterior arm of the protoconid.

unpublished Ph.D. dissertation, Candela (2000) described a species smaller than *Eos. annectens* from the Colhuehuapian of Gran Barranca that also has a weak connection between the hypoconid and hypolophid (Kramarz, 2004; Vucetich et al., 2010b). Unfortunately, we were unable to study this material firsthand to compare it with SGOPV 2157 directly.

We also refer SGOPV 2688 to *Eosteiomys* cf. *Eos. annectens*. The p4s and dp4s of *Steiromys* and *Branisamyopsis* are hexalophodont, while those of *Hypsosteiomys* Patterson, 1958, are tetralophodont (Candela, 2002, 2003). The identification of SGOPV 2688 is tenuous due to its high degree of wear, but its size (larger than contemporaneous octodontoids) and known presence of *Eos.* cf. *Eos. annectens* in the fauna lead us to assign it to this taxon.

Eosteiomys species are known from Colhuehuapian and “Pinturan” localities throughout Patagonia (Kramarz, 2004; Kramarz et al., 2005, 2010; Vucetich et al., 2010b). *Eosteiomys annectens*, to which we provisionally refer the specimens from Pampa Castillo, was previously reported only from the lower and middle sequences of the Pinturas Formation (Kramarz and Bellosi, 2005).

Steiromys Ameghino, 1887a

TYPE SPECIES: *Steiromys detentus* Ameghino, 1887a.

INCLUDED SPECIES: The type species, *St. duplicatus* Ameghino, 1887a, and *St. principalis* Ameghino, 1899.

AGE AND DISTRIBUTION: Galera Formation, Santacrucian SALMA, Aysén Region, Chile; Pinturas Formation, Santacrucian (“Pinturan”) SALMA, Santa Cruz Province, Argentina; Santa Cruz Formation, Santacrucian SALMA, Santa Cruz Province, Argentina.

Steiromys sp.

Figure 10C–D

Steiromys duplicatus Flynn et al., 2002a: 289, table 1.

REFERRED MATERIAL: SGOPV 2190, cast of partial left M1 or M2 (fig. 10C); SGOPV 2689, right m3 (fig. 10D).

LOCALITY AND HORIZON OF REFERRED MATERIAL: Fossil Horizon E-0 (SGOPV 2689) and Fossil Horizon 7 (SGOPV 2190), Galera Formation, Pampa Castillo, Aysén Region, Chile.

DESCRIPTION: SGOPV 2190 is a little-worn brachydont upper molar that is missing the posterolabial corner (fig. 10C; table 2). The anteroloph is labiolingually oriented until it joins the protocone, which itself has an arm that projects posterolingually. The parafossette, enclosed labially, is continuous with the hypoflexus, but a small, low crest connecting the protocone and protoloph indicates that these features would become separated after additional wear. The protoloph and mesolophule parallel one another, and the mesoflexus is open. The hypocone is large and pointed.

The tetralophodont SGOPV 2689, a right m3, is low crowned, bears thick enamel bands around its perimeter, and is notably larger than the lower molars assigned to *Eosteiomys* cf. *Eos. annectens* (fig. 10D; table 1). Metalophulid I is straight and angled slightly anterolingually. The posterior arm of the protoconid, angled posterolingually, barely reaches the ectolophid despite the specimen's advanced wear stage. The hypolophid is labiolingually oriented and straight, whereas the posterolophid is curved. The anterofossettid, the anteroposteriorly widest of the lingual fossettids, broadens lingually. The metafossettid is the next widest lingual fossettid, and the mesofossettid is the narrowest. All three lingual fossettids are very shallow. The hypoflexid, which points directly lingually, is constricted at its labial edge by the protoconid and hypoconid.

Neither specimen preserves sufficient diagnostic morphology to assign it to one of the three recognized species of this genus.

REMARKS: These specimens are lower crowned than *Hypsosteiomys* (Candela and Vucetich, 2002) and notably larger than *Eosteiomys* (tables 1, 2; Kramarz, 2004). The flexi of SGOPV 2190 are deep and wide, unlike those of *Branisamyopsis* (fig. 10C; Kramarz, 2004). SGOPV 2689 is tetralophodont (fig. 10D), distinguishing it from *Branisamyopsis* and *Hypsosteiomys* (Candela and Vucetich, 2002; Candela, 2003).

Steiromys is a common rodent in faunas in the Santa Cruz and Pinturas formations (e.g., Scott, 1905; Kramarz, 2004; Croft, 2013; Arnal et al., 2019). *Steiromys detentus* and *St. principalis* are known exclusively from the Santa Cruz and Pinturas formations, respectively, whereas *St. duplicatus* has been recovered from both.

DISCUSSION

PAMPA CASTILLO COMPARED TO OTHER SANTACRUCIAN RODENT FAUNAS

CAVIOIDS: The cavioid assemblage from Pampa Castillo is largely what would be expected of a Santacrucian SALMA fauna, with the exception of *Luantus minor* being the only *Luantus* species in the assemblage. *Eocardia* (fig. 4) is fairly common in Santa Cruz Formation (SCF) faunas (fig. 11; Scott, 1905; Candela et al., 2012; Arnal et al., 2019) but absent from the Pinturas Formation (Kramarz, 2006a). *Luantus minor* (fig. 3A–C) was previously known only from the Colhuehuapian-aged fauna at Bryn Gwyn, which is older and approximately 800 km north of

the core Santacrucian faunas (fig. 1; Pérez et al., 2010). *Luantus* is abundant in the Pinturas Formation, where it is represented by two species (*L. propheticus* in lower-middle Pinturas Formation [lmPF] and *L. toldensis* in the upper Pinturas Formation), neither of which occurs at Pampa Castillo. *Phanomys* is known from the Santa Cruz and Pinturas formations, and *Schistomys* is known exclusively from the SCF (Scott, 1905; Kramarz, 2006a; Bostelmann et al., 2013; Arnal et al., 2019; Cuitiño et al., 2019a). Neither genus has yet been identified at Pampa Castillo, though the presence of *Schistomys* cannot be ruled out completely due to the lack of diagnostic premolars in specimens assigned to *Eocardia* (fig. 4). Overall, “eocardiids” are fairly uncommon at Pampa Castillo compared to other early Miocene Patagonian faunas (fig. 11).

Neoreomys australis (fig. 5A) is the most common rodent (and mammal) at Pampa Castillo, a pattern seen in many SCF faunas (fig. 11; Scott, 1905; Candela et al., 2012; Arnal et al., 2019). Two species of the genus are known from the lmPF, *N. australis* and *Neoreomys pinturensis*, with the latter more abundant in levels where they cooccur (Kramarz, 2006b). Although *Neoreomys* is common in the lmPF, it forms a smaller fraction of the fauna than *N. australis* does at Pampa Castillo and many SCF localities (fig. 11).

Cavioids provide mixed evidence for Pampa Castillo’s broader temporal affinities. The presence of *Luantus* seemingly indicates affinities with lmPF and Colhuehuapian faunas, but the presence of *Eocardia* and the absence of *N. pinturensis* seem to show a closer relationship with SCF faunas.

CHINCHILLOIDS: The chinchilloid community supports the Pampa Castillo fauna’s referral to the Santacrucian SALMA. Four *Perimys* species, including the yet unnamed *Perimys* sp. nov.? originally reported from the lmPF (Kramarz, 2002), are found at Pampa Castillo. If up to five currently recognized *Perimys* species are synonymous with *Per. onustus*, as suggested by Kramarz (2002), then all four *Perimys* species known from Santacrucian faunas are found at Pampa Castillo, the only locality where this occurs. There does not appear to be any stratigraphic pattern to these species’ presence or relative abundance at Pampa Castillo (fig. 2). Two of these species, *Per. intermedius* and *Perimys* sp. nov.?, were previously known only from the lmPF and upper Pinturas Formation, respectively (fig. 11; Kramarz, 2002). *Perimys onustus* (fig. 6F–J) was previously known only from the SCE, whereas *Per. erutus* (figs. 5B, 6A–E) was known from the SCF and Pinturas Formation (Scott, 1905; Kramarz, 2002; Arnal et al., 2019). *Prolagostomus pusillus* is the only chinchillid identified from Pampa Castillo and is common throughout the SCF (fig. 8; Rasia, 2016). Kramarz (2002) recognized a probable new species of *Prolagostomus* from the lmPF and upper Pinturas Formation that we did not recover at Pampa Castillo. *Pliolagostomus*, a chinchillid known from core Santacrucian faunas of the SCF, is absent at Pampa Castillo. *Scleromys* is common throughout Santacrucian assemblages, but the taxon from Pampa Castillo, *Scl. quadrangulatus*, was previously known only from the lmPF (fig. 9A–E; Scott, 1905; Kramarz, 2002; Arnal et al., 2019). A single tooth (SGOPV 2704; fig. 9F–G) may represent a new species of *Scleromys*.

Chinchilloids point to a close association of Pampa Castillo and the lmPF. Three taxa, *Per. intermedius*, *Perimys* sp. nov., and *Scl. quadrangulatus*, are known exclusively from these two faunas. The absence of *Pliolagostomus*, *Scl. angustus*, and *Scl. osbornianus* at both Pampa Cas-

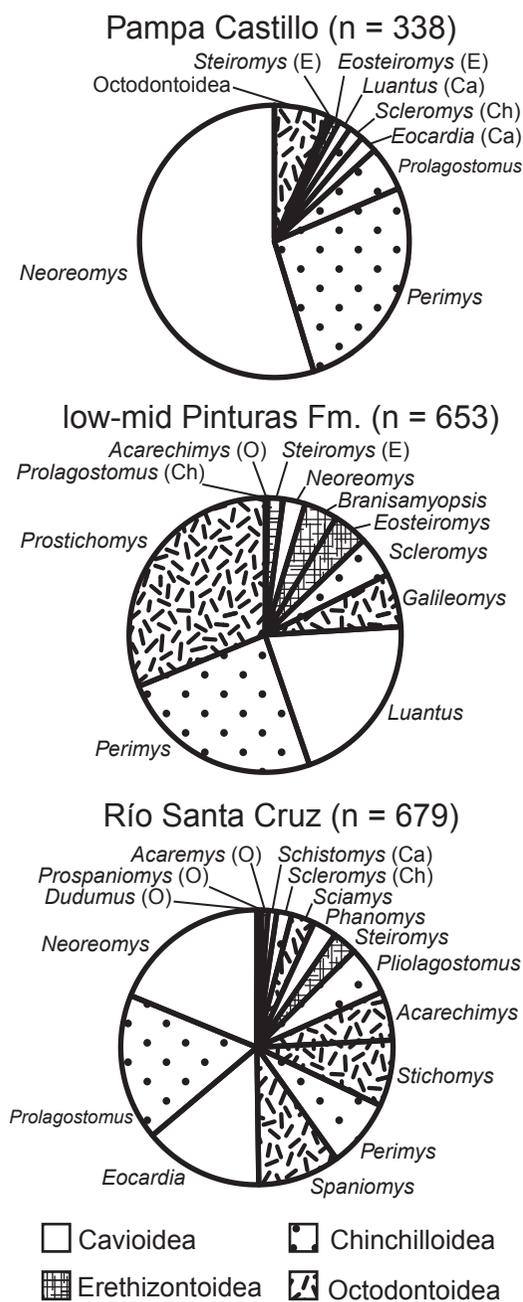


FIG. 11. Relative abundance of rodent genera at Pampa Castillo, lower and middle sequences of the Pinturas Formation, and Río Santa Cruz. Wedges filled according to “superfamily” or labeled with Ca (Caviioidea), Ch (Chinchilloidea), E (Erethizontoidea), and O (Octodontoidea) if too narrow to view fill.

tillo and lmPF also support this relationship, as these taxa are common in core Santacrucean coastal SCF and RSC faunas (fig. 11). An important contrast between the rodent faunas from Pampa Castillo and the lmPF is that all *Prolagostomus* specimens from the Pinturas Formation have been assigned to a probable new species (Kramarz, 2002), while all specimens from Pampa Castillo pertain to *Pro. pusillus*, a widespread Santacrucean-Laventan SALMA species.

ERETHIZONTOIDS: Although uncommon, the erethizontoids from Pampa Castillo (fig. 11) are typical of Santacrucean assemblages. *Eosteiomys annectens*, to which we provisionally assign two specimens (fig. 10A–B), was previously known only from the lmPF (Kramarz, 2004). *Eosteiomys* is otherwise known from the Colhuehuapian SALMA, though *Eosteiomys homogenidens* has been provisionally recorded in the lmPF as well (Kramarz et al., 2005; Vucetich et al., 2010b). *Steiromys* is common throughout Santacrucean assemblages. Both *St. detentus* and *St. duplicatus* occur in SCF deposits (Scott, 1905; Candela et al., 2012; Arnal et al., 2019). *Steiromys principalis* is known only from the lmPF, where *St. duplicatus* is also known (Kramarz, 2004). Unfortunately, the two *Steiromys* specimens identified from Pampa Castillo are inadequate for species-level identification (fig. 10C–D). The single erethizontoid genus known from other Santacrucean faunas not represented at Pampa Castillo is *Branisamyopsis*, which is also apparently absent from the SCF. *Branisamyopsis praesigmoides* Kramarz, 2004, is known from the lmPF, but the genus is also known from the Colhuehuapian and Colloncuran SALMAS (Candela, 2003).

The presence of *Eosteiomys* at Pampa Castillo suggests affinities with the lmPF, although

the absence of *Branisamyopsis*, as in the SCF, argues against this. *Steiromys* is common in most Santacrucian assemblages, so its presence at Pampa Castillo is of limited biogeographic significance.

PALEOENVIRONMENTAL IMPLICATIONS

Inferring the predominant vegetational community of Patagonia from the late Paleogene–early Neogene has received much attention because hypsodont and hypselodont herbivores (notoungulates) appear earlier in South America (late Eocene–early Oligocene) and other parts of temperate South America than they do on other continents (e.g., Flynn et al., 2003; López et al., 2010; Reguero et al., 2010; Bellosi et al., 2021). Some authors have taken this as evidence that open habitats and/or grasslands proliferated earlier in those regions. Paleopalynologic and paleopedologic studies have indicated that the semiarid steppe community that dominates modern Patagonia did not arise until the middle to late Miocene (Palazzesi and Barreda, 2012; Bucher et al., 2020; Barreda and Palazzesi, 2021). Bellosi et al. (2021) used various methods (mammalian hypsodonty, paleopedology, ichnology, and phytoliths) to reconstruct a vegetational history that alternated between subhumid savannas and semiarid palm groves and shrublands between ~41 and 15 Ma, resembling the modern South American Chaco or East African wooded savannas. This model contradicts that of Strömberg et al. (2013) who argued for exclusively forested paleoenvironments in their study areas of Gran Barranca and Cañadón Vaca, from the middle Eocene through early Miocene. These alternative models differ primarily in their interpretation of whether certain plant groups and ichnotaxa, such as palms and scarab beetle traces, are indicative of open or closed habitats or are nondiagnostic. The Pampa Castillo fauna is a potentially valuable addition to this debate given that it is further west than and derives from a stratigraphic unit distinct from most localities analyzed in previous studies (Bucher et al., 2020; Barreda and Palazzesi, 2021; Bellosi et al., 2021).

The fossil rodents of Pampa Castillo are indicative of a forested paleoenvironment with some open areas. Erethizontoids are considered forest dwellers due to their brachydont dentition, an inference based on extant species and, at least for *Steiromys*, scansorial-arboreal specializations of their skeleton (Kramarz and Bellosi, 2005; Candela et al., 2012; Muñoz et al., 2019). Erethizontoids are not abundant at Pampa Castillo. High-crowned (hypsodont) and ever-growing (hypselodont or euhypsodont) cheekteeth in rodents and ungulates are widely considered indicative of grazing habits and/or open environments (Williams and Kay, 2001; Mendoza and Palmqvist, 2008; Kaiser et al., 2013; Ma et al., 2017). Alternatively, some authors contend that this dental feature may be more closely related to levels of grit consumption (Janis, 1988; Jardine et al., 2012). Several hypselodont rodents (*Prolagostomus*, *Perimys*, and *Eocardia*) occur at Pampa Castillo. *Perimys*, the most common hypselodont genus (fig. 11), has been interpreted as a digger based on its forelimb anatomy (Muñoz et al., 2019), and thus its hypselodonty may reflect abrasive subterranean food sources like roots and tubers rather than open habitats. *Eocardia*, however, has a cursorially adapted skeleton, likely reflecting the presence of some open paleohabitats at Pampa Castillo (Candela et al., 2012; Muñoz et al., 2019). Modern

chinchillids favor open habitats, but the locomotory and dietary preferences of *Prolagostomus* have never been analyzed in their own right. The most abundant rodent at Pampa Castillo, *Neoreomys australis*, has been interpreted as ambulatory with running and possibly swimming capabilities and a diet similar to, but slightly harder and more abrasive than, modern dasyproctids (agoutis), again suggesting a closed or somewhat closed forest habitat (Candela et al., 2012; Muñoz et al., 2019). The octodontoid caviomorphs of Pampa Castillo are not described here, but the majority of specimens are brachydont suggesting a closed habitat.

Pampa Castillo appears to record a paleoenvironment intermediate between those of fossiliferous localities of the core Santacrucian localities, and those of the lower to middle sequences of the Pinturas Formation (ImPF). Fossil vertebrate-based, sedimentological, and paleobotanical studies focusing on core Santacrucian localities have reconstructed the paleoenvironment as a mosaic of open and closed habitats on a coastal floodplain with a seasonal subtropical paleoclimate (Brea et al., 2012; Kay et al., 2012; Raigemborn et al., 2015, 2018a, 2018b; Cuitiño et al., 2019a, 2019b; Catena and Croft, 2020; Kay et al., 2021). Arnal et al. (2019) summarized the taxonomic composition and abundance of rodents at different RSC sites, where *Neoreomys australis* is the most abundant rodent. However, it is not as dominant there as at Pampa Castillo, given the nearly equal abundance of *Neoreomys*, *Eocardia*, and *Prolagostomus* in RSC faunas versus the clear dominance of *Neoreomys* at Pampa Castillo (fig. 11). The most abundant octodontoids at RSC sites (*Spaniomys*, *Stichomys*) are hypsodont, unlike those present at Pampa Castillo. As mentioned, the cursorial *Eocardia* is very abundant at RSC, and the morphologically similar *Schistomys* is also present. Erethizontoids are represented solely by *Steiromys* spp. in RSC faunas (and throughout the SCF).

The fossil fauna of the ImPF suggests that it records a more humid paleoenvironment than at Pampa Castillo (Kramarz and Bellosi, 2005; Novo and Fleagle, 2015). The paleopedological, sedimentological, and ichnofossil record suggest semiarid conditions (Bown and Lariestra, 1990; Genise and Bown, 1994). Kramarz and Bellosi (2005) reconciled this contradiction by suggesting that while the fossil fauna was composed primarily of taxa that inhabited the area during relatively humid times, the sedimentological record is dominated by processes operating during drier intervals. Accordingly, the ImPF rodent community may be seen as having inhabited a relatively humid paleoenvironment, despite seemingly conflicting lithological indicators. Erethizontoids are generally considered indicators of forested paleohabitats due to their brachydont dentitions, arboreal adaptations, and the habits of extant taxa (Candela and Picasso, 2008; Candela et al., 2012; Kay et al., 2012). Erethizontoids are more diverse (three genera; five species) and abundant in the ImPF than at Pampa Castillo (Kramarz, 2004). Additionally, no hypselodont “eocardiids” are present in the ImPF (Kramarz, 2006a), unlike at Pampa Castillo. *Neoreomys australis*, the most abundant rodent at Pampa Castillo, is found in the ImPF, but a lower-crowned species, *Neoreomys pinturensis*, is also present in the ImPF, suggesting a more closed habitat there than at Pampa Castillo (Kramarz, 2006b). Chinchilloids of the ImPF (*Per. intermedius*, *Sci. quadrangulatus*, and *Pro-*

lagostomus sp. nov.) are not paleoenvironmentally informative, as these taxa have not been linked to any particular habitat type through their dietary or locomotory adaptations (Kramarz, 2002; Kramarz and Bellosi, 2005).

BIOCHRONOLOGICAL IMPLICATIONS OF PAMPA CASTILLO CAVIOIDS, CHINCHILLOIDS, AND ERETHIZONTOIDS

Together, cavioids, chinchilloids, and erethizontoids support temporal correlation of the Pampa Castillo fauna to other assemblages from the Santacrucian SALMA, but a more precise assignment is challenging. There are resemblances to, but also differences from, the rodent faunas from both core Santacrucian and “Pinturan” (the lower to middle Pinturas Formation [ImPF] and UFZ at the Gran Barranca) faunal assemblages. The Pinturas Formation was first recognized as bearing a fauna distinct from and more “primitive” than Santacrucian assemblages by Ameghino (1906) which he termed the Astrapothericulense after the astrapothere *Astrapothericulus* Ameghino, 1902. This distinction was endorsed by Frenguelli (1931) and Castellanos (1937), who referred to the fauna as the “Pinturense,” but was subsequently disregarded by most researchers (e.g., Wood and Patterson, 1959; Marshall et al., 1983; Flynn and Swisher, 1995). Thorough description of Pinturas Formation rodents more recently (e.g., Kramarz, 2001b, 2002, 2004) led Kramarz and Bellosi (2005) to refer to the rodent community of the lower and middle sequences of the Pinturas Formation (ImPF) as the “Pinturan” association. Since then, various authors have used the term “Pinturan” to refer to this fauna from the ImPF as a whole as well as to the hypothesized biochronologic interval that would be typified by it (e.g., Flynn et al., 2008; Kramarz et al., 2010; Dunn et al., 2013; Solórzano et al., 2020). Though “Pinturan” and Astrapothericulense (or Astrapothericulan) refer to similar assemblages, the former name is preferable. Ameghino (1906) coined Astrapothericulense based on fossil collections made without precise stratigraphic control, likely including fossils from all levels of the Pinturas Formation, whereas “Pinturan” is restricted to faunas from the lower and middle sequences (Kramarz and Bellosi, 2005).

It may be that taxonomic differences between core Santacrucian and “Pinturan” faunas are more reflective of differences in paleoenvironment than age distinctions. The Pampa Castillo rodent fauna represents an assemblage that appears to be taxonomically and paleoenvironmentally intermediate between the ImPF and core Santacrucian faunas. More detailed analyses of the taxonomic composition and geochronological age of other elements of the Pampa Castillo fauna may shed additional light on its correlation with and affinities to other faunas within the Santacrucian SALMA. Better characterizing faunal similarities between the Pinturas Formation of Argentina and the Galera Formation/Pampa Castillo fauna would help justify formally recognizing “Pinturan” as a distinct SALMA or a “subage” of the Santacrucian, if it can be clearly determined to be temporally and faunally distinct from core Santacrucian faunas.

CONCLUSIONS

Each of the three major clades (“superfamilies”) of caviomorphs described in this article is represented by multiple taxa. Cavioids are represented by three genera and three species (figs. 3–4, 5A), including the most abundant taxon in the Pampa Castillo fauna, *Neoreomys australis* (fig. 11). Chinchilloids are represented by three genera and six or seven species. Pampa Castillo is the only fauna where four species of *Perimys* co-occur (figs. 5B, 6–7). Erethizontoids, although rare, are represented by two genera (fig. 10).

Caviomorphs of the Pampa Castillo fauna suggest a paleoenvironment intermediate between the open and closed mosaic habitat of the core Santacrucian faunas of the Santa Cruz Formation along the Río Santa Cruz and Atlantic coast and the closed forest of the lower and middle sequences of the Pinturas Formation (ImPF). Hypselodont, cursorial rodents such as *Eocardia*, indicators of open habitats in modern ecosystems, are present in the Pampa Castillo fauna but are less diverse and abundant than in core Santacrucian faunas (fig. 11). Erethizontoids, presumed to have been somewhat arboreal and therefore indicative of closed paleohabitats, are more diverse and abundant in the ImPF than at Pampa Castillo.

The cavioid, chinchilloid, and erethizontoid rodents of Pampa Castillo support its assignment to the Santacrucian SALMA, in agreement with previous work (Flynn et al., 2002a; McGrath et al., 2020). We also agree with the earlier observation by Chick et al. (2010) that the Pampa Castillo rodent community shares certain similarities to that of the ImPF which some authors recognize as the characteristic fauna of a distinct but as yet not formalized biochronologic interval, the “Pinturan.” Additional taxonomic and geochronologic work is needed, however, to more clearly assess whether the Pampa Castillo fauna supports or refutes the existence of a distinct “Pinturan” biochron.

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