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Two New Taxa (Caviomorpha, Rodentia) from the Early Oligocene Tinguiririca Fauna (Chile)

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ABSTRACT

Here we describe two new caviomorphs from the early Oligocene Tinguiririca Fauna of the Andean Main Range of central Chile, representing the most ancient rodents known from the mid to high latitudes of South America, and the second-oldest securely dated rodents from the continent. These two new taxa are each documented by single partial mandibles bearing largely complete dentitions. Representing two new taxa, *Andemys termasi,* gen. et sp. nov., and *Eoviscaccia frassinettii,* sp. nov., these caviomorphs are informally referred to the pan-Dasyproctidae and pan-Chinchillidae, respectively. These taxa, together with recent findings in Peru, confirm that caviomorphs were well diversified prior to the Deseadan SALMA, that they likely originated during the middle to late Eocene, but that they did not spread from the tropics until some time after the Mustersan—a well-sampled interval from which rodents are unknown in higher latitudes. Additionally, in documenting the earliest occurrence of hypsodonty among caviomorphs *Eoviscaccia frassinettii,* sp. nov., provides important insights into the acquisition of this common mammalian dental innovation in rodents.

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INTRODUCTION

The early Oligocene Tinguiririca Fauna from the Andean main range of central Chile includes two new rodent taxa, both represented by partial mandibles (Flynn et al., 2003). We describe and name these taxa in this report.

The sudden mid-Cenozoic appearance of caviomorphs in South America's stratigraphic record is perplexing, given the continent's geographic isolation at the time and the "African-Asian" distribution of the group's nearest putative relatives, Phiomyidae and Baluchimyinae (Marivaux et al., 2000, 2002; Jaeger et al., 2010). The venerable notion of caviomorph monophyly (Wood and Patterson, 1959) has been corroborated repeatedly by molecular analyses (Nedbal et al., 1994; Huchon and Douzery, 2001; Opazo, 2005; Farwick et al., 2006; Poux et al., 2006; Huchon et al., 2007; Blanga-Kanfi et al., 2009; Churakov et al., 2010), but morphological evidence has remained more ambiguous. Auditory (Meng, 1990) and dental (Marivaux et al., 2004; Sallam et al., 2009) features have been interpreted as indicative of caviomorph monophyly, as has a recent combined molecular and morphological dataset (Horovitz et al., 2006). Nevertheless, a polyphyletic origin involving two independent colonizations has also been proposed on the basis of carotid arterial patterns and myology (Bugge, 1985; Woods and Hermanson, 1985; Bryant and McKenna, 1995; McKenna and Bell, 1998; Landry, 1999; Jenkins et al., 2005) and incisor enamel (Martin, 1994). With two exceptions (see discussion of the Santa Rosa and Contamana faunas below), rodents do not occur in or prior to the Mustersan (late middle and/or late Eocene) South American Land Mammal "Age" (SALMA). The group's presence in the high latitudes thus almost certainly postdates the Mustersan given the dense sampling of this and earlier SALMAs in the region (Vucetich et al., 1999; Madden et al., 2010), even for small-bodied taxa. Caviomorphs are widely inferred to have reached South America from Africa (Lavocat, 1974, 1976; Jaeger, 1989; Martin, 1994, 2005; Marivaux et al., 2004; Coster et al., 2010; Sallam et al., 2011), via one or more crossings of a ~1000–1500 km wide South Atlantic (Houle, 1999) during the Paleogene. An earlier alternative scenario, invoking dispersal from North America via the proto-Antilles (Wood and Patterson, 1959; Wood, 1968; 1972; 1974), was predicated on the now discredited (Hoffstetter and Lavocat, 1970; Bugge, 1985; Meng, 1990; Martin, 1994) notion of a close relationship between North American franimorphs and Caviomorpha. An Asian origin for caviomorphs has been proposed on molecular and morphological grounds (Hussain et al., 1978; Flynn et al., 1986; Jaeger, 1989; Huchon and Douzery, 2001). Nevertheless, dispersal between Asia and South America via North America or Australia-Antarctica is contradicted by the lack of early Cenozoic hystricognaths in any of these locations (Hartenberger, 1985; Wood, 1985; Houle, 1999; Marivaux et al., 2002).

South America's isolation during most of the Cenozoic produced highly endemic land mammal faunas. Although this endemicity has hampered intercontinental biochronologic correlations, faunal changes have permitted recognition of a finely subdivided sequence of intracontinental biochronologic units. About 20 SALMAs spanning much of the Cenozoic are recognized (e.g., Simpson, 1940, 1950, 1980; Patterson and Pascual, 1968; Marshall et al., 1983; MacFadden, 1985; Marshall, 1985; Pascual and Ortiz Jaureguizar, 1990; Flynn and Swisher, 1995; Pascual et al., 1996; Flynn et al., 2003, 2012) (fig. 1).

Simpson (1940) subdivided the Cenozoic mammalian record into three broad "faunal strata," based largely on the first appearance of various higher-level taxonomic groups. Simpson's earliest subdivision (Stratum 1) is characterized by the first occurrences of "archaic" lineages: Marsupialia, Xenarthra, and endemic ungulates (e.g., certain "condylarths," Litopterna, Notoungulata). Faunal Stratum 2 is marked by immigration of caviomorph rodents and platyrrhine primates, as well as by a "modernization" of the "archaic" lineages of Stratum 1, particularly various notoungulates. Simpson's faunal Stratum 3 corresponds to an interval spanning the late Miocene to Recent, i.e., the "Great American Biotic Interchange."

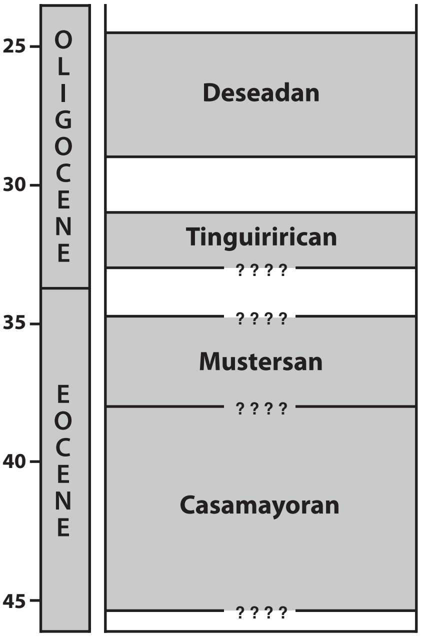

FIG. 1. The transitional Eocene-Oligocene portion of the SALMA sequence (based on Flynn and Swisher, 1995; as modified by Croft et al., 2008).

The base of Simpson's faunal Stratum 2, traditionally the Deseadan SALMA (Simpson, 1948, 1950, 1967, 1980), is marked by the first appearance of numerous clades, including—prior to discovery of the Tinguiririca Fauna—caviomorphs. Deseadan caviomorphs are known from sequences in Patagonian Argentina (Ameghino, 1897, 1902; Loomis, 1914; Wood, 1949; Wood and Patterson, 1959; Vucetich, 1989), Bolivia (Hoffstetter and Lavocat, 1970; Lavocat, 1976; Patterson and Wood, 1982; Vucetich, 1989), Peru (Shockey et al., 2009), Uruguay (Kraglievich, 1932; Mones and Castiglione, 1979), Brazil (Vucetich et al., 1994; Vucetich and Ribeiro, 2003) and Chile (unpublished). In addition to Tinguiririca, pre-Deseadan caviomorphs are also now reported from the Santa Rosa and Contamana faunas of Peru (Frailey and Campbell, 2004; Antoine et al., 2011).

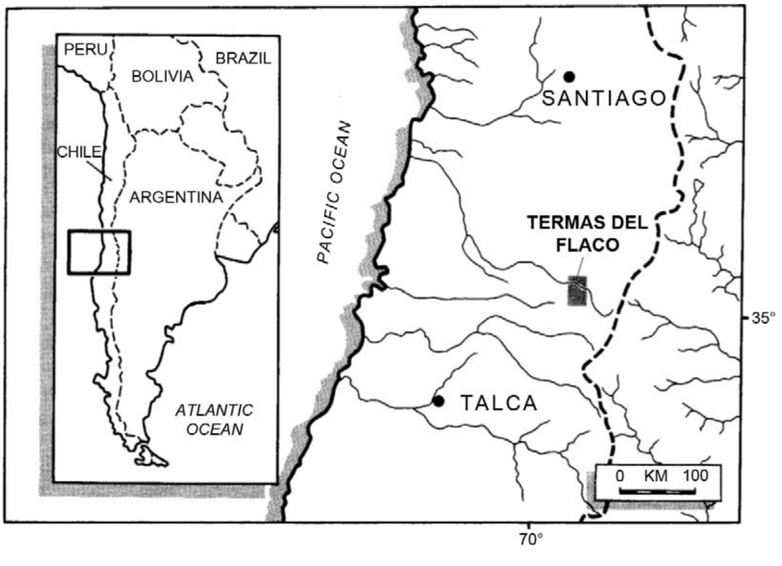

FIG. 2. Location map; Tinguiririca River valley, Termas del Flaco, Chile (modified from Wyss et al., 1994).

TABLE 1. Oligocene and early Miocene caviomorphs used for comparisons in this study, with the proposed taxonomic placement of the two new taxa from the Tinguiririca Fauna (Chile) indicated.

Superfamily	Family	Taxa	Age	Reference number	Locality
	Dinomyidae	*Scleromys quadrangulatus*	Santacrucian	MLP 82-VI-3-2	Santa Cruz Formation, Argentina
Cavioidea	Pan-Dasyproctidae	*Incamys bolivianus*	Deseadan	PU 2093; PU 21952	Salla-Luribay Basin, Bolivia
		Neoreomys australis	Santacrucian - Colloncuran	AMNH 9540; AMNH 9541-3	Santa Cruz Formation, Argentina
		Branisamys luribayensis	Deseadan	PU 21944	Salla-Luribay Basin, Bolivia
		Australoprocta fleaglei	Colhuehuapian	MACN 1781; 1782; 1783; 1784; 1785; 1786; 1788; 1789	Gaiman (Chubut), Argentina
		Dasyprocta punctata	Extant	AMNH 14179; AMNH 40831	Mexico, Ecuador, Venezuela, Colombia, Peru, Bolivia, Brazil, Paraguay, Argentina
		Eoincamys pascuali	?Eocene and/or Oligocene	LACM 143299; 143306; 143308	Santa Rosa, Peru
		Eobranisamys romeropittmanae	?Eocene and/or Oligocene	LACM 143342; 143345; 144293	Santa Rosa, Peru
		Andemys termasi	Tinguirirican	SGOPV 2933	Tinguiririca
	Eocardiidae	*Chubutomys simpsoni*	Deseadan	AMNH 29557	Cabeza Blanca (Chubut), Argentina
Octodontoidea	Undetermined	*Draconomys verai*	Between Deseadan and Tinguirirican	MPEF-PV 7506	Gran Barranca, Argentina
		Paulacoutomys paulista	Deseadan	MNRJ 4082-V	Taubaté Basin, Brazil
		Sallamys pascuali	Deseadan	PU 20907; PU 20909	Salla-Luribay Basin, Bolivia
		Eosallamys simpsoni	?Eocene and/or Oligocene	LACM 143276; 143414	Santa Rosa, Peru
		Eoespina woodi	?Eocene and/or Oligocene	LACM 143281; 143390; 144294	Santa Rosa, Peru
		Eosachacui lavocati	?Eocene and/or Oligocene	LACM 143382; 143393	Santa Rosa, Peru
		Deseadomys arambourgi	Deseadan	MNHN 1903-3-1	Cabeza Blanca (Chubut), Argentina

Superfamily	Family	Taxa	Age	Reference number	Locality
		Xylechimys obliquus	Deseadan	MLP 59-II-26–81	Cabeza Blanca (Chubut), Argentina
		Platypittamys brachyodon	Deseadan	AMNH 29600	Scarritt Pocket (Chubut), Argentina
		Migraveramus beatus	Deseadan	PU 21948	Salla-Luribay Basin, Bolivia
Chinchilloidea	Pan-Chinchillidae	*Eoviscaccia australis*	Deseadan-Colhuehuapian	MACN CH 1877; 1878; 1882; 1883	Gaiman (Chubut), Argentina
		Eoviscaccia boliviana	Deseadan	MNHN BLV 158 (MNHN(P))	Lacayani, Bolivia
		Eoviscaccia frassinettii	Tinguiririican	SGOPV 2935	Tinguiririca
		Prolagostomus imperialis	Santacrucian–Laventan	AMNH DVP 99300; 9587	Patagonia, Argentina
		Lagostomus maximus	Extant	AMNH 41511	Argentina, Bolivia, Paraguay
	Cephalomiydae	*Litodontomys chubutensis*	Deseadan	ACM 3086	Cabeza Blanca (Chubut), Argentina
		Cephalomys plexus	Deseadan	FAM 111480	La Flecha (Santa Cruz) and Cabeza Blanca (Chubut), Argentina
	Neoepiblemidae	*Scotamys antiquus*	Deseadan	MNHN 1903-3-8; MNHN 1903-3-12	La Flecha (Santa Cruz), Argentina
		Perimys incavatus	Colhuehuapian	FAM 29736	Gran Barranca, Argentina

In his classic treatise Tullberg (1899) subdivided rodents into Sciurognathi and Hystricognathi, based on the angle between the mandibular ramus and the vertical plane of the incisors. Hystricognathous rodents were subsequently shown to form two subdivisions based on morphological (Luckett and Hartenberger, 1993; Marivaux et al., 2002, 2004), molecular (e.g., Huchon et al., 2000, 2002, 2007; Huchon and Douzery, 2001; Murphy et al., 2001; Poux et al., 2006; Blanga-Kanfi et al., 2009), and endoparasitic (Hugot, 1999) evidence. These hystricognath subdivisions include the paraphyletic African Phiomorpha (Old World porcupines, cane rats, dassie rats) and the monophyletic South American Caviomorpha (chinchilla rats, pacas, chinchillas, capybaras, New World porcupines, agoutis, pacarana, spiny rats, tuco-tucos, cavies, hutias), a clade nested deeply within Hystricognathi. (One fossil taxon from Africa was recently assigned to the Caviomorpha; see below.) South American hystricognaths, greater in diversity than their African counterparts, evidently diversified rapidly after their arrival in the New World, contributing to the obscure phylogenetic relationships among the group's major clades, which have been traditionally accorded family or superfamily rank. Moreover, a high degree of parallelism appears to have marked the morphological (Hartenberger, 1985) and molecular (Nedbal et al., 1996) evolution of caviomorphs, further complicating our understanding of their higher-level interrelationships. The phylogenetic placement of many modern and extinct forms thus continue to be debated, sometimes even at high taxonomic levels (Cabrera, 1961; Anderson and Jones, 1984; Corbet and Hills, 1991; Wilson and Reeder, 1993; McKenna and Bell, 1998; Woods and Kilpatrick, 2005). Molecular results indicate that Caviomorpha is divisible into four major clades: Erethizontoidea, Cavioidea, Octodontoidea, and Chinchilloidea (Huchon and Douzery, 2001; Opazo, 2005; Poux et al., 2006; Blanga-Kanfi et al., 2009). Conflicting classificatory schemes have been proposed in numerous morphologically based studies (e.g., Simpson, 1945; Landry, 1957; Patterson and Wood, 1982; McKenna and Bell, 1998; Woods and Kilpatrick, 2005). Here we adopt the classification of Woods and Kikpatrick (2005), which recognizes these four superfamilies (tables 1, 2), in part because of its congruence with molecular evidence.

Over the last two decades the Andean main range of central Chile—once regarded as barren of terrestrial vertebrate fossils—has become recognized as containing one of the continent's most important archives of Cenozoic mammal evolution (Flynn et al., 2003, 2012; Croft et al., 2008). Although the geology of the central Chilean Andes has been intensively studied for decades, and the strata now known to contain fossils are broadly exposed across the region, this rich paleontological resource was not recognized until the late 1900s. The unusually late discovery of these fossils reflects several peculiarities, including the dominance of igneous, metamorphic, and marine sedimentary rocks over terrestrial sedimentary sequences in the country; the dearth of early discoveries of vertebrate fossils; and difficult logistics. Collectively these factors delayed study of terrestrial vertebrate fossils in Chile relative to neighboring Argentina. The Tinguiririca Fauna, discovered in 1988 by a team from the AMNH and collaborating institutions, derives from outcrops north and south of the Tinguiririca River near the summer resort town of Termas del Flaco. This fauna ultimately formed the basis of a novel post-Mustersan, pre-Deseadan SALMA, the Tinguirirican (Flynn et al., 2003).[5]

At least one additional set of localities of Tinguirirican age occurs in the Andean main range of Chile, approximately 100 km north of Termas del Flaco near the Cachapoal River (Flynn and Wyss, 2004). The Cachapoal Fauna includes at least one rodent, and thus promises to shed additional light on the early diversification of caviomorphs once this specimen has been prepared and studied.

Mammal fossils in the central Chilean Andes occur in volcaniclastic sediments of the Abanico (= Coya-Machalí) Formation and its lateral equivalents. Fossiliferous strata were likely produced as distal ignimbrites or debris flows (Croft et al., 2008). In spite of, or perhaps owing to, this unusual mode of deposition, fossils are generally fairly complete and preserve considerable anatomical detail.

MATERIALS, ABBREVIATIONS, AND METHODS

Materials: The impetus for this paper was the recovery of two specimens from the Termas del Flaco area of the central Chilean Andes. Although these specimens for a time represented the oldest rodents known from South America, they have not previously been fully described or named. To be permanently housed in the vertebrate paleontology collections (SGOPV) of the Museo Nacional de Historia Natural (MNHN-S), Santiago, Chile, SGOPV 2933 is designated below as the holotype of *Andemys termasi*, new genus and species, a taxon closely affiliated with dasyproctids. SGOPV 2935, the holotype of *Eoviscaccia frassinettii,* new species, is related to chinchillids. Important comparative taxa, Deseadan and slightly earlier caviomorphs to which the specimens from Termas del Flaco were compared extensively, are listed in table 1.

Dental nomenclature: Nomenclature employed in the following descriptions, detailed in figures 3–6, is based largely on Frailey and Campbell (2004), Marivaux et al. (2004), Jenkins et al. (2005), and Pérez (2010).

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York; **FAM**, Frick Collection, American Museum of Natural History, New York; **LACM**, Los Angeles County Museum of Natural History, Los Angeles, California; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MNHN-S**, Museo Nacional de Historia Natural, Santiago, Chile; **MNHN-P**, Muséum National d'Histoire Naturelle, Paris, France; **MNRJ**, Museo Nacional do Rio de Janeiro, Brazil; **MPEF-PV**, Museo Paleontológico "Egidio Feruglio," paleovertebrate collection, Trelew, Argentina; **MLP**, Museo de la Plata, La Plata, Argentina; **PU**, Princeton University Collection of Yale Peabody Museum, New Haven, Connecticut; **SGOPV**, paleovertebrate collections of the MNHN-S, Santiago, Chile.

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[5] At the time the Tinguirirican SALMA was initially proposed, the "Divisaderan" was also considered to fall within the hiatus between the Mustersan and Deseadan. Fossils recovered from Divisadero Largo (near Mendoza, Argentina) in recent years, and the study of sediments adhering to specimens collected decades ago, have elegantly demonstrated that not all fossils from the region are contemporaneous. Rather, the Divisaderan "fauna" consists of a mixture of taxa that are considerably older *and* younger than previously assumed, invalidating the Divisaderan as a SALMA (Cerdeño et al., 2008; López and Manassero, 2008).

TABLE 2. Higher taxonomic groups of caviomorph rodents recognized in the current work. Superfamilies based in part on the molecular work of Huchon and Douzery (2001), Opazo (2005), Poux et al. (2006), and Blanga-Kanfi et al., (2009). The placement of familes having extant representatives is based on Woods and Kilpatrick (2005), while those for wholly extinct clades (designated by †) are based on Hartenberger (1998) and Vucetich et al. (1999).

	Superfamilies	Extant families	Extinct families
Africa		Bathyergidae	† Phiomyidae
		Hystricidae	† Diamantomyidae
		Petromuridae	† Myophiomyidae
		Thryonomyidae	
South America	Erethizontoidea	Erethizontidae	
	Cavioidea	Caviidae	† Eocardidae
		Dasyproctidae	
		Cuniculidae	
	Octodontoidea	Ctenomyidae	† Acaremyidae
		Octodontidae	
		Abrocomidae	
		Echimyidae	
		Myocastoridae	
		Capromyidae	
		Heptaxodontidae	
	Chinchilloidea	Chinchillidae	† Cephalomyidae
		Dinomyidae	† Neoepiblemidae

SYSTEMATIC PALEONTOLOGY

Rodentia Bowdich, 1821
Entodacrya Landry, 1999 = Ctenohystrica Huchon, Catzelflis and Douzery, 2000
Hystricognathi Tullberg, 1899
Caviomorpha Wood and Patterson, 1955 (in Wood, 1955)
Cavioidea Fischer Von Waldheim, 1817
Pan-Dasyproctidae (see below), Smith, 1842, author of Dasyproctidae

Andemys termasi, gen. et sp. nov.

Figures 3, 4; table 3

Holotype: SGOPV 2933, right mandibular fragment preserving p4–m3 and the incisor root.

Referred specimens: Known only from the holotype.

Etymology: *Ande,* in reference to the cordillera in which this taxon was found. The derivation of *Andes* is uncertain, but for linguistic purposes the root is treated as “Ande-” (Andes representing a Spanish language pluralization of an unknown root, although often argued to be related to the Quechua “andi” referring to mountains; C. Kammerer, personal commun.). The suffix *mys*, Greek for “mouse,” is commonly applied to names of rodents; the species name

TABLE 3. Dental measurements (in millimeters) taken with calipers. Abbreviations: DV, dorsoventral height (crown plus exposed portion of root for *Andemys termasi*, crown above gum line for *Eoviscaccia frassinettii*); LL, labio-lingual width (measured across center of tooth); HI, hypsodonty index = crown height (CH) divided by the mesiodistal length (MD) of the same tooth.

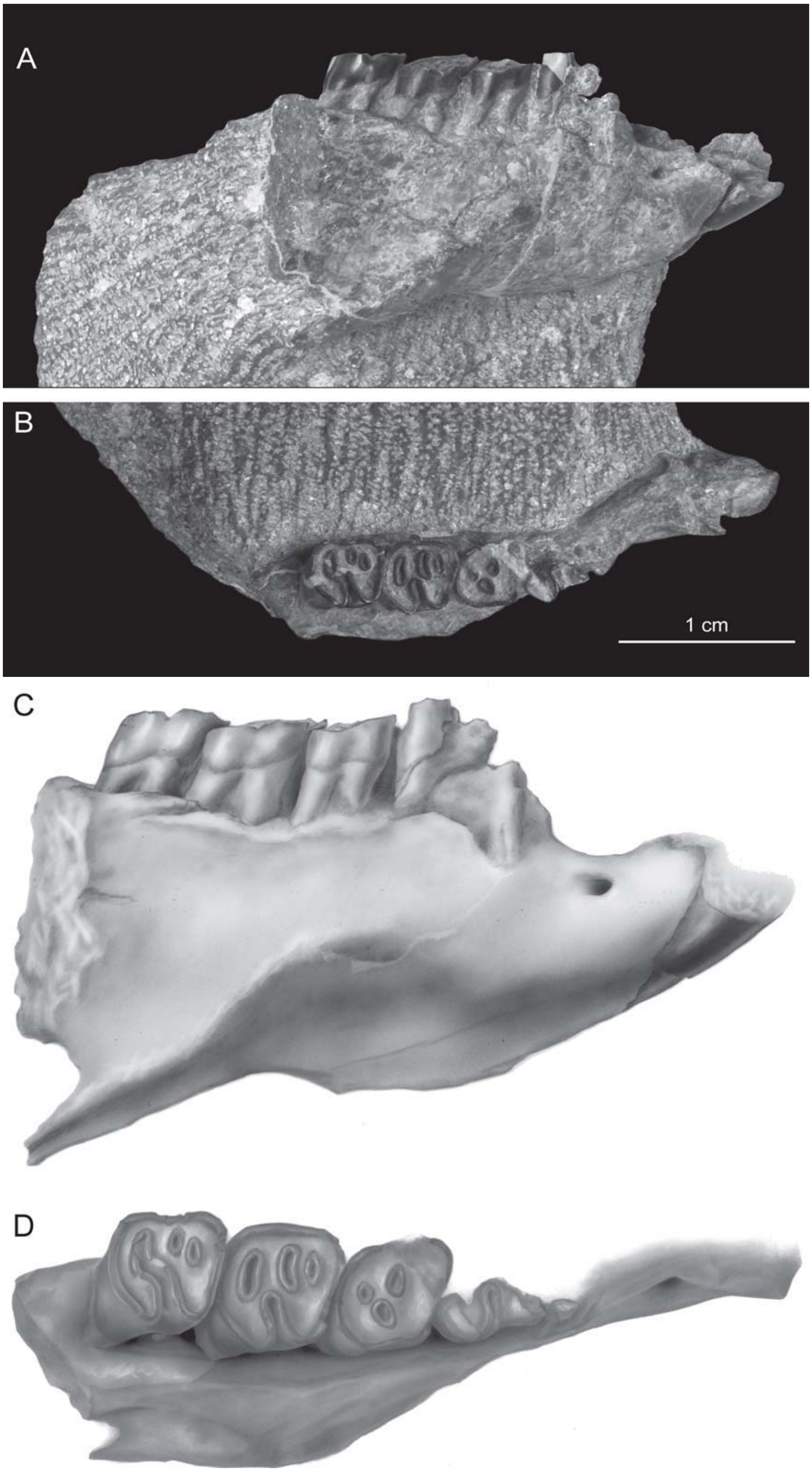
	Andemys termasi	*Eoviscaccia frassinettii*
	SGOPV 2933	SGOPV 2935
p4 MD	—	3.25
LL	—	2.00
DV	—	1.12
m1 MD	4.00	3.37
LL	3.75	3.00
DV	4.00	0.75
CH	1.50	—
HI	0.38	—
m2 MD	4.50	2.75
LL	4.00	3.00
DV	4.25	0.50
CH	2.00	—
HI	0.44	—
m3 MD	4.00	3.25
LL	3.87	3.00
DV	3.75	1.00
CH	2.37	—
HI	0.59	—

termasi derives from Termas del Flaco, the town near which the holotype was recovered and the long-term base of operations for field research in the area.

TYPE LOCALITY: Tinguiririca River valley, Termas del Flaco (34°57′S, 70°27′W), east central Chile (Wyss et al., 1993); Locality Set 3 (Flynn et al., 2003; "Locality C" of Charrier et al., 1996), ~1–2 km north of the Río Tinguiririca (i.e., ~5 km north of the two other Tinguiririca Fauna producing localities in the region, locality sets 1 and 2 of Flynn et al., 2003); see also Wyss et al. (1994: fig. 2), and Charrier et al. (1996).

STRATIGRAPHIC OCCURRENCE: Purplish volcaniclastic sediments representing locally basal levels of the Abanico (= Coya-Machalí) Formation (Wyss et al., 1993, 1994; Flynn et al., 2003).

AGE: ?Late Eocene–early Oligocene, Tinguirirican SALMA. Several whole-rock $^{40}K/^{40}Ar$ dates ranging in mean age from 31.4 to 35.6 Ma (Wyss et al., 1990; Flynn et al., 2003) have been obtained from south of the Tinguiririca River. Dates from the older end of the spectrum


A
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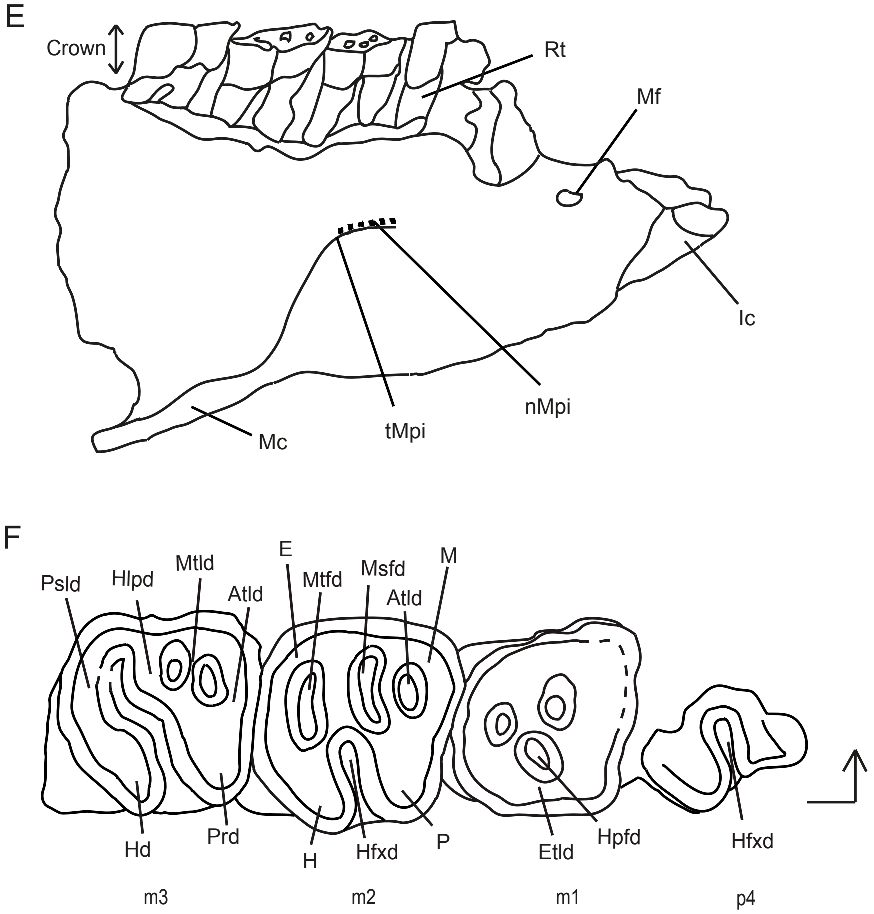

FIG. 3. The holotype of *Andemys termasi*, SGOPV 2933. Photographs (opposite page) in (**A**) lateral, and (**B**) occlusal views, with shaded drawings in (**C**) lateral, and (**D**) occlusal views. Line drawings (above) in (**E**) lateral and (**F**) occlusal views illustrating dental terminology used in text (following in part the nomenclature of Frailey and Campbell, 2004; Marivaux et al., 2004; Jenkins et al. 2005; Pérez, 2010); scale bar applies to A–D. Abbreviations: **Atfd,** anterofossettid; **Atld,** anterolophid; **E,** entoconid; **Etlp,** ectolophid; **Hd,** hypoconid; **Hfxd,** hypoflexid; **Hlpd,** hypolophid; **Hpfd,** hypofossettid; **Ic,** incisor; **M,** metaconid; **Mc,** masseter crest; **Mf,** mental foramen; **Msfd,** mesofossettid; **Mtfd,** metafossettid; **Mtld,** metalophid; **nMpi,** notch for the insertion of the tendon of the pars maxillomandibularis; **Prd,** protoconid; **Psld,** posterolophid; **Rt,** root; **tMpi,** tubercle for the insertion of the tendon of the pars maxillomandibularis. The angled arrow indicates anterior and lingual directions for occlusal views. Mandibular nomenclature follows Pérez (2010).

are from units underlying the fossiliferous unit stratigraphically. In addition, two high-precision ^{40}Ar/^{39}Ar dates, both with means near 31.5 Ma, have been obtained for localities south of the Tinguiririca River (Flynn et al., 2003). Although the most productive localities in the region occur south of the Tinguiririca River, near Paso El Fierro, both rodents described here were collected north of the river. Collecting areas on opposites sides of the river are not directly traceable through a continuous outcrop because of the intervening river valley and alluvial cover, but lithostratigraphic, mapping, and biostratigraphic evidence indicate that all fossiliferous localities in the vicinity of Termas del Flaco fall within the same restricted stratigraphic interval. Perhaps the most convincing basis for regarding the northern and southern collecting areas as contemporaneous is the distinctive taxa they share, including the notoungulates *Protarchaeohyrax gracilis* and *Johnbell hatcheri* (both of which are restricted to the Tinguiririican). Moreover, no obviously Deseadan or younger fossils have been recovered from anywhere in the upper Tinguiririca River valley, all other fossils from this region being Eocene in age. That these two rodents and the associated fauna from north of the Tinguiririca River pertain to anything other than the Tinguiririca Fauna is thus exceedingly unlikely.

Diagnosis (figs. 3, 4; table 4): Tetralophodont lower cheek teeth; m1 rounded to slightly squared as in *Incamys* and *Australoprocta*; m1 fossettids round and centrally positioned; m1 posterolophid roughly half as wide mesiodistally as the anterolophid; metafossettid present on m1–2 as in *Branisamys, Eobranisamys, Neoreomys,* and *Australoprocta*; metafossettid/hypoflexid confluent and "stepped" lingually on m3 as in *Incamys, Eoincamys, Branisamys, Eobranisamys, Dasyprocta, Neoreomys, Australoprocta*; mesofossettid smaller than anterofossettid on m3 as, e.g., in *Incamys, Australoprocta,* and *Neoreomys*; m2 hypoflexid well developed but narrow, reaching the tooth's midline as in *Incamys, Eoincamys,* and *Neoreomys*; brachydont to slightly hypsodont. The combined length of the lower cheektooth row (~12.5 mm) is roughly the same as that of *Australoprocta*, the taxon with which *Andemys* might most easily be confused. In late wear stages (see Kramarz, 1998: fig. 4e and h, for *Australoprocta*), both taxa are characterized by tetralophodont, squared lower molars bearing fossettids that are narrow mesiodistally compared to the lophids. In *Andemys*, however, the lophids and fossettids are transverse, rather than oblique—as in *Australoprocta*. In addition, the labial cusps of *Andemys* are more rounded than in *Australoprocta* (where they are more angular), and the hypoflexid is more anteroposteriorly compressed at its labial end than in *Australoprocta* (wherein the hypoflexid is broadly open).

DESCRIPTION AND COMPARISON

Mensural information is provided in table 3. We have compared *Andemys* to all previously described Deseadan and pre-Deseadan caviomorphs—including those from the Santa Rosa Fauna (Frailey and Campbell, 2004), to several Miocene forms (e.g., *Neoreomys, Scleromys*, and *Australoprocta*), as well as to *Dasyprocta.* Cheektooth enamel is restricted above the gumline. Although there is some question whether this specimen represents a highly worn dentition of a taxon that was considerably more hyposodont early in life, or a moderately worn one of a taxon that was fairly brachydont throughout its ontogeny, for reasons discussed below, the latter possibility appears more likely (fig. 4).

Mandible (fig. 3A, C, E): Only the labial surface of the mandible is exposed. A vertical break immediately behind m3 truncates the specimen posteriorly. The preserved portion of the mandible measures 29 mm anteroposteriorly. Neither the coronoid process nor its base is preserved. The diastema, gently convex along the superior edge of the ramus, is shorter mesiodistally (5 mm) than the combined cheektooth row (12.5 mm). The minimum depth of mandibular ramus within the diastema is 5.6 mm. A small mental foramen (measuring 0.7 mm anteroposteriorly by 0.4 mm dorsoventrally) lies anterior of p4, in the dorsal third of the ramus. The tubercle for insertion of the tendon of the pars maxilomandibularis terminates anterior of m1. The masseteric crest and the tubercle for insertion of the M. masseter medialis pars infraorbitalis are well seen in occlusal view. The anterior end of the incisor root projects slightly lingually.

Most of the anterior part of the tubercle for insertion of the tendon of the pars maxilomandibularis lies anterior of m1 in *Andemys*, *Neoreomys, Incamys, Branisamys,* and *Dasyprocta*; in *Cephalomys* it lies below m1 while in *Platypittamys* it is anterior of p4. The notch for insertion of the tendon of the M. masseter medialis pars infraorbitalis in *Andemys* is connected to the masseteric crest as in *Neoreomys, Incamys, Branisamys,* and *Dasyprocta,* whereas in *Lagostomus* the notch is isolated between the masseteric and horizontal crests. The masseteric crest and the tubercle for insertion of the M. masseter medialis pars infraorbitalis are continuous, as in *Cephalomys, Platypittamys, Dasyprocta*, and *Neoreomys.* The diastema is shorter than the combined cheektooth row as in *Neoreomys, Chubutomys,* and *Dasyprocta;* it is slighty convex as in *Incamys* and *Chubutomys*. The mental foramen is positioned high on the mandible within the diastema, anterior of p4 as in *Incamys*, *Neoreomys, Chubutomys,* and *Dasyprocta.*

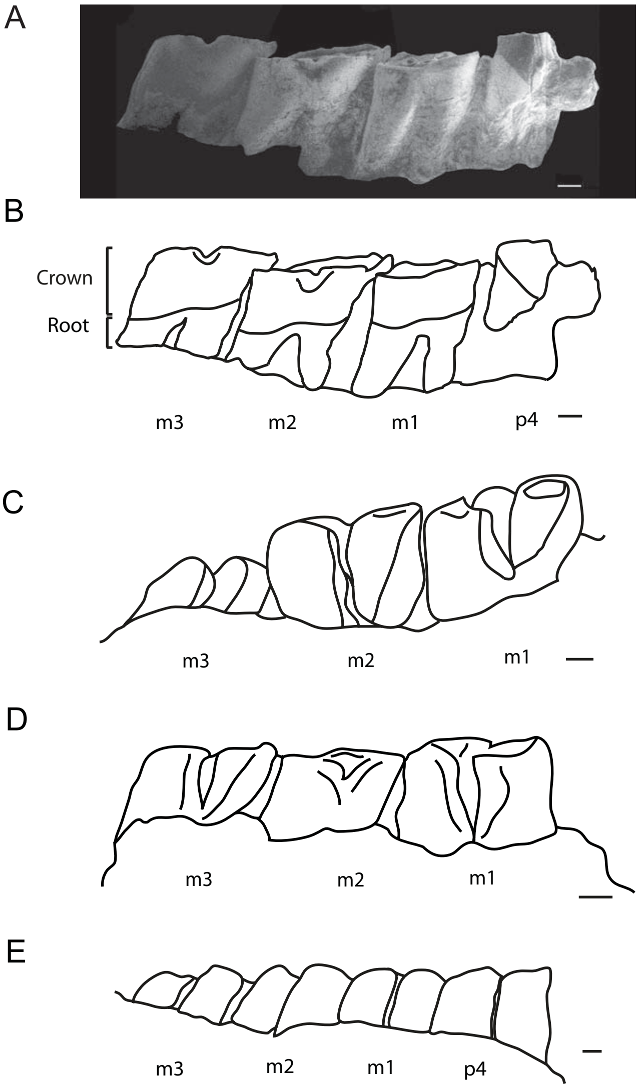

FIG. 4. (**A**) Scanning electron micrograph and (**B**) drawing of the holotype of *Andemys termasi*, SGOPV 2933 in lateral view illustrating the level of hypsodonty. Labial views of the lower dentitions of (**C**) *Branisamys luribayensis* PU 21944; (**D**) *Incamys bolivianus* PU 2093; and (**E**) *Neoreomys australis* AMNH 9542.

Premolar (fig. 3B, D, F): Only the hypoconid and the hypoflexid regions of p4 are preserved. The hypoflexid is shorter labiolingually than on m2–3 (hypoflexid of m1 too worn to judge). The hypoconid region is broad mesiodistally and rounded lingually; it is larger on p4 than on m2–3 (not visible on the heavily worn m1).

The p4 hypoconid region of *Andemys* is proportionally longer mesiodistally than in the molars, as is also the case in *Draconomys, Palaucoutomys, Migraveramus, Scotamys*, *Incamys,* and *Branisamys*. This contrasts with the chinchilloids *Eoviscaccia*, *Cephalomys,* and *Litodontomys*, the dinomyid *Scleromys,* and such pan-dasyproctids as *Dasyprocta, Neoreomys,* and *Australoprocta,* wherein the p4 hypoconid region has roughly the same proportions as on the molars. The p4 hypoflexid of these taxa is compressed anteroposteriorly as in *Andemys*.

First lower molar (fig. 3B, D, F): This tooth has three centrally positioned fossettids, the labial one (hypofossettid) being largest. The hypo-, meso-, and metafossettids were likely longer labiolingually in a less worn state, and the hypofossettid probably opened lingually originally (forming a hypoflexid). The unworn m1 would have borne four lophids (antero-, meta-, hypo-, and posterolophids). The three fossettids are ovoid, but the hypo- and anterofossettids are broader transversely than the metafossettid.

The m1 hypoconid region is highly worn, making it difficult to compare to other taxa. It seems to have been slightly triangular as in *Incamys, Eoincamys, Neoreomys, Australoprocta, Branisamys, Eobranisamys, Plattypitamys,* and *Migraveramus*, rather than rounded as in *Dasyprocta, Scleromys, Cephalomys*, and *Eoviscaccia*. Although the m1 of SGOPV 2933 was undoubtedly more hypsodont earlier in wear, its original crown height was probably no more than twice what is preserved, judging from comparisons to little-worn specimens of *Incamys* and *Branisamys* (in which, for example, the hypoflexid is roughly as deep ventrally seen in labial view, as in SGOPV 2933). In short, SGOPV 2933 appears to preserve a large fraction of its original crown height.

Second lower molar (fig. 3B, D, F): This molar, squared in outline, preserves four well-developed lophids (antero-, meta-, hypo-, and posterolophids). The anterolophid is wider labially than lingually. The metalophid is short transversely, owing to lingual expansion of the protoconid. The meso- and metafossettids are comma shaped (elongate labiolingually) and the anterofossettid is ovoid. The mesofossettid, metafossettid, and hypoflexid are similar in size, while the anterofossettid is considerably smaller. The hypoflexid is centrally positioned and open labially. The hypo- and protoconid regions are rounded, with the former shorter mesiodistally than the latter. The lingual cusps (meta- and entoconid) are completely subsumed within in the hypo- and anterolophids respectively (see Patterson and Wood, 1982: fig. 2; Frailey and Campbell, 2004: fig. 1).

The m2 of *Andemys* is similar in its squaring to its counterparts in *Incamys, Eoincamys, Australoprocta* (pan-Dasyproctidae), *Cephalomys* (Cephalomyidae), *Eoviscaccia* (pan-Chinchillidae), and *Scleromys* (Dinomyidae). The hypolophid is the widest lophid (mesiodistally) on m2, as in *Branisamys* and *Eobranisamys*, but contrary to *Incamys*, *Eoincamys, Australoprocta, Neoreomys,* and *Dasyprocta* whose postero- and hypolophids are equally wide. The postero- and anterolophids are equally deep mesiodistally, as in *Eobranisamys, Sallamys,* and *Eoespina*, but contrary to *Dasyprocta, Australoprocta,* and *Eoincamys* where the anterolophid is narrower. Earlier in wear the hypoflexid and metafossettid of m2 would have been confluent, resulting in the "stepped" arrangement of these structures seen in *Incamys, Eoincamys, Branisamys, Eobranisamys, Dasyprocta, Neoreomys, Australoprocta*, and on the m3 of SGOPV 2933. The metafossettid and hypoflexid of m2 in SGOPV 2933 are no longer joined; in this respect the tooth is comparable to specimens of *Branisamys, Eobranisamys, Australoprocta, Neoreomys,* and some octodontoids

(*Platypittamys, Xylechimys*, *Sallamys*, and *Draconomys*) at comparable stages of wear. The m2 fossettids of *Andemys* are transversely elongate, as in *Dasyprocta, Incamys, Neoreomys, Australoprocta,* and *Branisamys* (all pan-dasyproctids), *Sallamys,* and *Migraveramus*, *Deseadomys*, *Xylechimys*, *Draconomys* (Octodontoidea), *Scleromys* (Dinomyidae), and all rodents from Santa Rosa. The hypoflexid in *Andemys* is narrower than in *Australoprocta*, terminating lingually between the meso- and metafossettids as in a variety of taxa including *Australoprocta* and *Eosallamys*. The anterofossettid is smaller than the mesofossettid as in some octodontoids and *Australoprocta*; in *Branisamys* these fossettids are similar in size, whereas in *Dasyprocta* and *Incamys* the anterofossettid is larger. On the contrary, in *Incamys* the anterofossettid frequently fuses to the mesofossettid through reduction of the metalophid. A conspicuous difference between *Andemys* and *Incamys* is that in the latter the metalophid is reduced to a short crest connecting to the metaconid region (sometimes becoming isolated from the protoconid region), whereas in *Andemys* (as well as *Neoreomys* and *Dasyprocta*), the metalophid consistently joins the protoconid and metaconid regions. *Dasyprocta* differs from *Andemys* and other pan-dasyproctids in having a fifth lophid (metalolophulide II, Marivaux et al., 2004; or mesolophid, Pérez, 2010) between the metalophid and the anterolophid (= metalophulide I, Marivaux et al., 2004). The anterofossettid is located more lingually in *Andemys* than in *Dasyprocta* and *Australoprocta*. Finally, the lingual fossettids likely opened lingually early in wear as is typical in mesodont-protohypsodont caviomorphs (e.g., *Eosachacui*, *Eoespina, Sallamys*, *Eosallamys, Draconomys,* and *Dasyprocta*), but the tooth is too worn to establish this with certainty.

Third lower molar (fig. 3B, D, F): The m3 of *Andemys* is trapezoidal in outline, the labial side being shorter than the lingual. The lingual side is concave centrally. As on m2, there are four lophids (antero-, meta-, hypo-, and posterolophid), with the metalophid the narrowest and the hypolophid the broadest anteroposteriorly. The antero-, meta-, and hypolophids are parallel. The hypolophid is the shortest lophid transversely. The mesofossettid is more lingually positioned and slightly smaller than the anterofossettid. The metafossettid is continuous with the hypoflexid, forming a substantial flexid slanting across the tooth posterolingually. The protoconid region is broader mesiodistally than the hypoconid region. The protoconid region is rounded while the hypoconid region is more angled.

The m3 is longer and wider than m1, unlike in *Eobranisamys, Branisamys,* and *Dasyprocta* (where the reverse is true). The shortest face of m3 is labial as in many pre-Miocene cavioids, *Neoreomys,* and *Dasyprocta*, but contrasting with many octodontoids (e.g., *Eoespina, Sallamys, Xylechimys*, and *Platypittamys*) in which the distal face is the shortest. The m3 of SGOPV 2933 displays the long-persisting union of the metafossettid and hypoflexid, seen also in *Neoreomys*, *Dasyprocta, Incamys, Eoincamys,* and *Australoprocta* (pan-Dasyproctidae), *Protadelphomys* (Octodontoidea), and *Scleromys* (Dinomyidae)—but not in *Eobranisamys.* The joined metafossettid/hypoflexid is "stepped" lingually, the metafossettid portion offset posteriorly relative to the hypoflexid, as in *Dasyprocta, Neoreomys*, *Incamys, Eoincamys, Australoprocta, Branisamys,* and *Eobranisamys.*

When ultimately formed, the m3 metafossettid would have been more transverse than the hypoflexid, the latter of which is more oblique (slanting posterolingually) as in *Dasyprocta, Incamys, Branisamys, Eoviscaccia, Plattypitamys*, and *Cephalomys,* but contrasting with *Chubu-*

tomys where the hypoflexid is transverse. The m3 hypoflexid of *Andemys* is well developed but narrow, reaching the midline of the tooth (excluding the soon to be formed metafossettid), as in *Dasyprocta, Branisamys, Eobranisamys, Australoprocta, Sallamys, Xylechimys, Neoreomys, Eoincamys,* and *Incamys*.

Andemys, along with *Neoreomys, Australoprocta*, and *Dasyprocta,* differ from *Incamys* and *Eoincamys* in their labially extended metalophids on m2–3. In *Andemys* the anterofossettid is smaller than the mesofossettid on m2, while this size relationship is reversed on m3, perhaps reflecting differences in wear. These fossettids are similar in size on m2–3 in *Eobranisamys* and *Branisamys*. In *Dasyprocta* and *Neoreomys* the anterofossettid is more transversely elongate than the mesofossettid, but both fossettids are thinner mesiodistally than the lophids (in *Andemys* the fossettids and lophids are equally broad mesiodistally). The latter of these features varies little with wear. The generally low level of hypsodonty in *Andemys* is exhibited particularly well on the labial side of the least worn tooth, m3 (fig. 3A, 4A, B).

Chinchilloidea Bennett, 1833

Pan-Chinchillidae (see below), Bennett, 1833, author of Chinchillidae

Eoviscaccia Vucetich, 1989

Eoviscaccia frassinettii, new species

Figure 5; table 3

HOLOTYPE: SGOPV 2935, partial right mandible bearing p4–m3 and incisor.

REFERRED SPECIMENS: Known only from the holotype.

ETYMOLOGY: Species named in honor of our esteemed colleague and friend, Daniel Frassinetti, who recently passed away. Daniel, a collaborator on our earliest paleontological projects in the Chilean Andes, was responsible for greatly enhancing the MNHN-S fossil vertebrate collections while chief of the paleontology section, and was an unwavering supporter of international scientific collaborations.

DIAGNOSIS (modified from Vucetich, 1989): *Eoviscaccia* is characterized by bilobed hypsodont cheek teeth, with fossettes/ids persisting relatively late in wear; hypoflexus/id disappearing only after extreme wear; lobes triangular in occlusal outline in young and moderately worn individuals rather than rectangular as in the other pan-chinchillids; roots may incipiently close in older individuals.

We amend the diagnosis of *Eoviscaccia* with the following observations concerning the lower dentition: in advanced wear the mesial margin of the anterior lobe becomes concave; a narrow isthmus of dentine connects the lobe pairs lingually; and the anterior lobes are thicker mesiodistally than their posterior counterparts. Enamel covers all faces of the cheek teeth but is thin on the anterior faces of both lobes on the molars, on the anterior face of the posterior lobe on the premolar, and on the labial faces of the posterior lobes of all four cheek teeth. Cementum fills the hypoflexid. The hypoflexid hooks posteriorly at its medial terminus, failing to reach the lingual side of the tooth as in most other pan-chinchillids.

Diagnosis of *E. frassinettii,* n. sp. (figs. 5, 6; table 5): The largest lower cheek tooth in *E. frassinettii* is m1, whereas in *E. boliviana* it is m2 (*E. australis* is known only from isolated

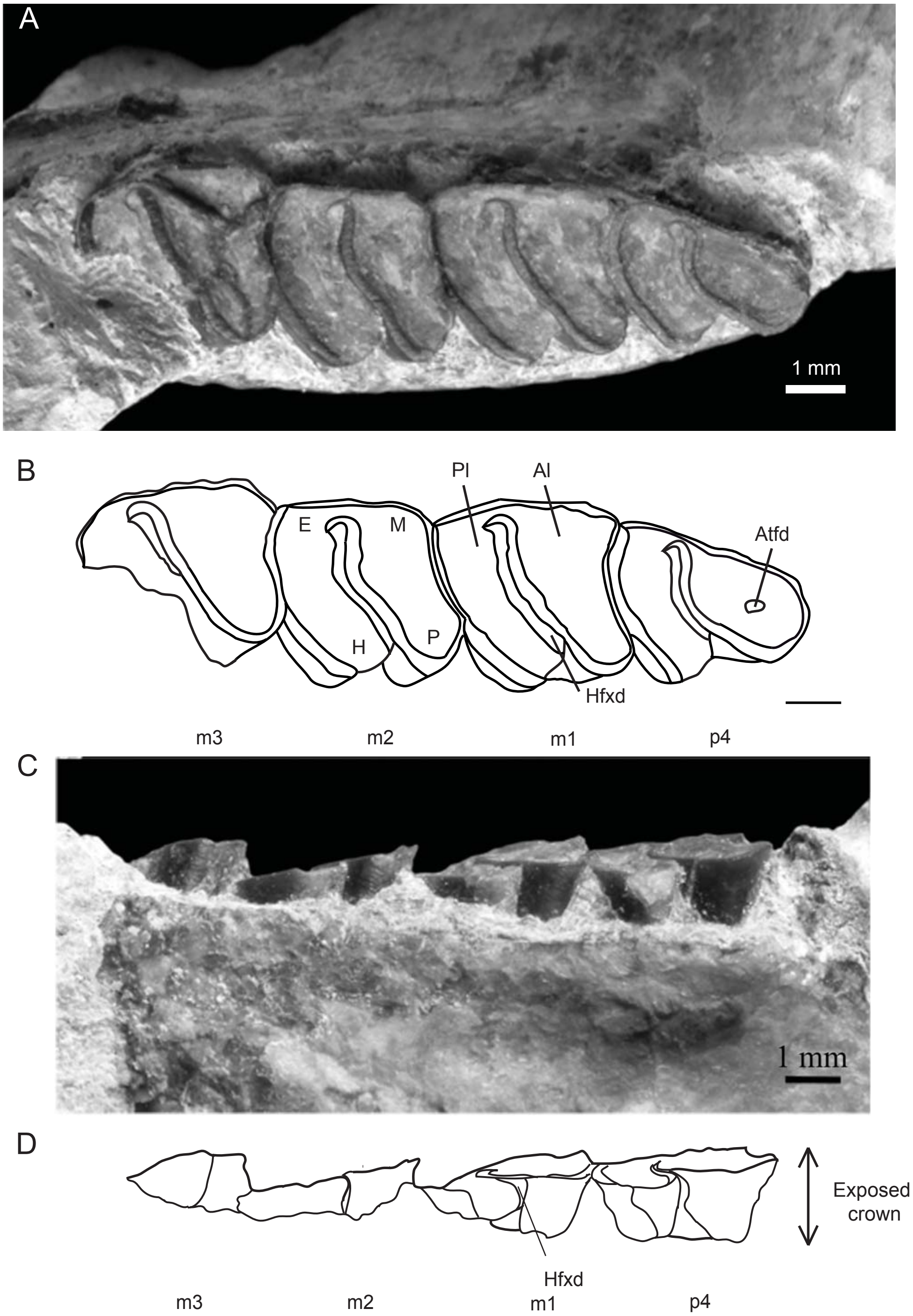

FIG. 5. Holotype of *Eoviscaccia frassinettii* (SGOPV 2935): (**A**) photograph and (**B**) line drawing of right p4–m3 in occlusal view; (**C**) photograph and (**D**) line drawing in labial view. Abbreviations: **Al,** anterior lobe; **Atfd,** anterofossettid, **E,** entoconid; **H,** hypoconid; **Hfxd,** hypoflexid; **M,** metaconid; **P,** protoconid; **Pl,** posterior lobe.

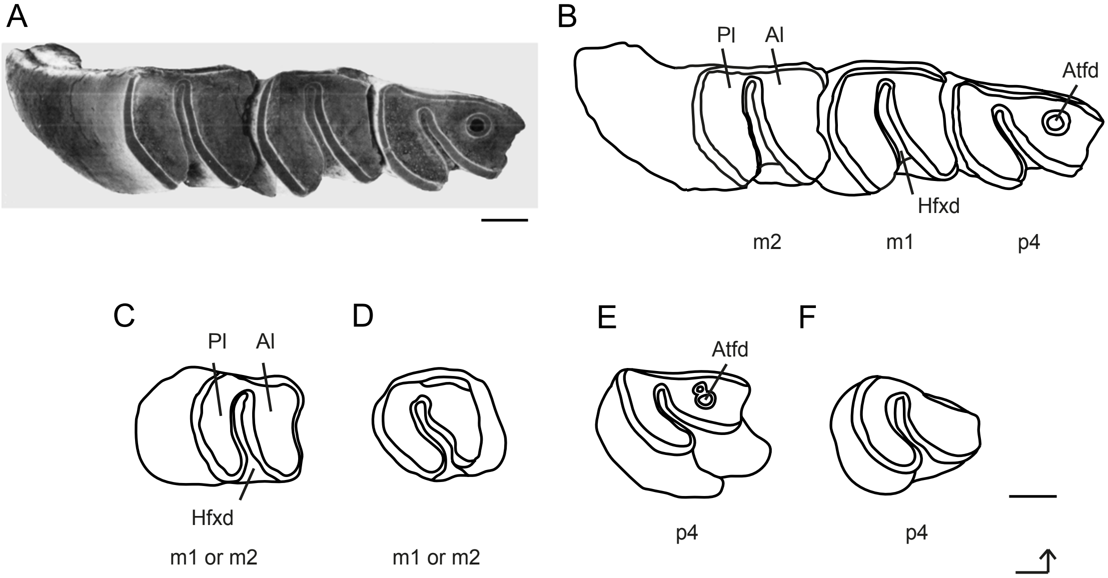

FIG. 6. (**A**) Scanning electron micrograph (from Vucetich, 1989), and (**B**) line drawing of right p4–m2 of *Eoviscaccia boliviana* MNHN BLV 158 (MNHN(P)). (**C–F**) Line drawings of the lower dentition of *Eoviscaccia australis*, (**C**) MACN CH 1883 (left m1 or m2); (**D**) MCN CH 1883 (left m1 or m2); (**E**) MACN CH 1877 (left p4); and (**F**) MACN CH 1878 (right p4) (after Kramarz, 2001). Multiple teeth of *Eoviscaccia australis* are shown to illustrate the variable presence of anterofossettids on p4 and shape variability of teeth presumably from the same locus. Abbreviations: **Al,** anterior lobe; **Atfd,** anterofossettid; **Hfxd,** hypoflexid; **Pl,** posterior lobe. The angled arrow indicates anterior and lingual directions. Scale bars = 1 mm.

teeth). The hypoconid region is more rectangular labially in *E. frassinettii* than in *E. boliviana* and *E. australis*. The m1–2 protoconid region is oblique in *E. frassinettii* and *E. boliviana* (slightly less so in the latter), but transverse in *E. australis*. The anterior face of p4 is sheathed in enamel in *E. frassinettii* whereas this region is bare (or the enamel is greatly reduced) in *E. australis* and *E. boliviana*. As in *E. boliviana* and *E. australis,* enamel occurs on the lingual faces of the anterior lobes of the lower molars in *E. frassinettii* (although this enamel thins in late wear at least in the former two taxa). Furthermore, in SGOPV 2935, whatever its precise stage of wear, the lophids are oblique rather than transverse (compared to *E. boliviana* and *E. australis*), and the p4 anterofossettid appears to persist later in wear, filling with cement.

DESCRIPTION AND COMPARISON

The holotype of *E. frassinettii* preserves the incisor and p4–m3, but the posterior extremity of m3 is missing. Much of the slender incisor (visible in occlusal and lateral view) and the diastema remain covered in sediment, but the latter appears to be roughly as long as the cheektooth row.

PREMOLAR (figs. 5, 6): This tooth is bilobed, as are the molars. The anterior lobe is roughly pear shaped in outline, while the mesiodistally broader and more transverse posterior lobe is reniform. The posterior margin of the anterior lobe is oblique labially but becomes transverse lingually; a posteriorly directed hook marks its lingual terminus. The hypoflexid of p4 is less oblique than that of the other cheek teeth.

The pear- and reniform-shaped outlines of the two lobes on p4 in *E. frassinettii* are similar to those of *E. boliviana*, *E. australis,* and *Perimys*. An anterofossettid occurs on p4 of *E. frassinettii,* as in little to moderately worn specimens of *E. boliviana, E. australis,* and *Scotamys*; in *E. frassinettii,* however, the anterofossettid is filled with cementum. Enamel is reduced on the anterior and labial faces of the posterior lobe as in *E. boliviana* and *E. australis*; enamel is reduced, however, on the anterior face of the anterior lobe of p4 in *E. boliviana* and *E. australis,* whereas in *E. frassinettii* a continuous sheet of enamel is present. The hypoflexid nearly reaches the lingual face of enamel—in the other two species the separation between these structures is greater.

First and second lower molars (figs. 5, 6): The first two molars are similar in morphology, m1 being slightly larger. They are rhomboidal in occlusal outline, contrasting with the more triangular p4. They are nearly identical in width, both being slightly broader than p4. The lingual margins of m1–2 are straight. The posterior margins of both lophids are parallel. The anterior lophid of m1 forms a rough isosceles triangle, its vertex directed labially, while on m2 it is reniform. The anterior margins of the anterior lobes of m1–2 are mildly concave, somewhat more so on m1. The posterior margins of the anterior lobes are transverse lingually, becoming more oblique labially. The posterior lophids of m1–2 are reniform and convex posteriorly, more strongly on m2 than m1. The protoconid regions of both teeth are roughly triangular while the hypoconid regions are more quadrate. Lingually m1 is more squared and longer anteroposteriorly than labially; m2 is equally long lingually and labially. As on the other cheek teeth, a distinctive enamel hook projects posteriorly from the lingual end of the hypoflexid. Enamel is discontinuous across the anterior face of both lobes and the labial face of the posterior lobe on all molars; it is roughly twice as thick on the posterior margins of the cheek teeth as elsewhere.

The hypoconid region is more rectangular in *E. frassinettii* than in *E. boliviana* and *E. australis*. The anterior lobes are slightly to substantially longer mesiodistally than the posterior ones, as in other members of the genus. The protoconid regions of m1–2 are slightly more oblique in *E. frassinettii* than in *E. boliviana*; in *E. australis* this region is transverse. In SGOPV 2935 enamel occurs on the lingual faces of both lobes, whereas this covering is reduced in *E. boliviana* and *E. australis* in advanced wear. The hypoflexids of SGOPV 2935 do not reach the lingual sides of the teeth, being isolated from the latter by a thin isthmus of dentine after minimal wear, as in *E. australis* and *E. boliviana*.

Third lower molar (figs. 5, 6): Only the anterior part m3 of SGPV 2935 is preserved. The anterior lobe is oriented obliquely (as on m1–2), is triangular in outline (as on m1), and bears a thicker enamel rim lingually than labially. Lingually, the anterior lobe is broader mesiodistally than its counterparts on m1–2.

The posterior rim of the anterior lobe fails to reach the tooth's lingual margin, becoming incorporated in a posteriorly directed enamel hook (as on the preceding teeth), a primary distinction between *Eoviscaccia* other pan-chinchillids. The hypoflexid nearly reaches the lingual wall of enamel after wear, terminating slightly more lingually than on m1 and m2 (m3 is unknown for *E. australis* and *E. boliviana*).

TABLE 4. Diagnostic characters of *Andemys* and their absence (-) /presence (+) in compared taxa.

	Characters	*Andemys*	*Australoprocta*	*Incamys*	*Branisamys*	*Eobranisamys*
1	Tetralophodonty	+	+	+	+	+
2	m1, all fossettids rounded	+	-	-	-	-
3	m1 fossettids centrally positioned	+	-	-	-	-
4	m1 posterolophid half the width of the anterolophid	+	-	-	-	-
5	m1-m2 metafossettid present	+	+	+	+	+
6	m3 metafossettid/hypoflexid confluent	+	+	+	+	+
7	m3 mesofossettid smaller than anterofossettid	+	+	+	+	+
8	m2 hypoflexid well-developed but narrow, reaching the tooth's midline	+	+	+	-	-
9	Fossettids narrow mesiodistally compared to the lophids	+	+	-	-	-
10	Squared lower molars	+	+	-	-	-
11	Slightly hypsodont	+	-	-	-	+
12	Lophids and fossettids transverse	+	-	-	+	-
13	Labial cusps rounded	+	-	-	-	-
14	Hypoflexid compressed labially	+	-	-	-	-

TABLE 5. Diagnostic characters of *Eoviscaccia frassinettii* and their absence (-) /presence (+) in the two other other species of the genus.

	Characters	*E. frassinettii*	*E. boliviana*	*E. australis*
1	Hypoconid region rectangular labially	+	-	-
2	m1 the largest lower cheek tooth	+	-	
3	Protoconid region on m1-2 oblique	+	+	-
4	Anterior face of p4 sheathed in enamel	+	-	-
5	Enamel on lingual faces of the anterior lobes remains thick into late wear	+	-	-
6	Lophids oblique	+	-	-
7	p4 anterofossettid persists late in wear filling with cement	+	-	-

DISCUSSION

Andemys termasi: Among pre-Pliocene and living caviomorphs, *Andemys* most closely resembles *Dasyprocta, Australoprocta, Neoreomys, Eoincamys*, *Incamys, Branisamys,* and *Eobranisamys*.

A mental foramen, when present in caviomorphs, is positioned either high on the mandible within the diastema, well anterior of p4, as in *Incamys, Dasyprocta, Neoreomys,* and *Eobranisa-*

mys (pan-Dasyproctidae), *Chubutomys* (Eocardiidae), and *Scleromys* (Dinomyidae), or below the roots of p4, as in *Draconomys, Platypittamys*, *Eoespina, Migraveramus,* and *Sallamys* (Octodontoidea). *Andemys* is characterized by the former condition (fig. 3), arguing against the echimyid affinities suggested for it by Frailey and Campbell (2004).

In *Andemys* the anterior arm of the hypoconid (cristid obliqua) does not separate the hypoflexid and the metafossettid until late wear, as is also the case in *Dasyprocta, Incamys*, *Eoincamys,* and *Australoprocta.* In *Neoreomys, Branisamys,* and *Eobranisamys*, this separation occurs earlier in wear. The lingual part of the hypoflexid lies between the meso- and metafossettid in *Andemys*, as in *Incamys*, *Eoincamys, Neoreomys, Australoprocta, Branisamys,* and *Eobranisamys*. A hypoconid arm occurs consistently on the molars of pre-Miocene octodontoids such as *Sallamys, Eosachacui, Eoespina*, and *Eosallamys* (in all stages of wear). This arm occurs on m1–2 of *Andemys,* but it is absent on m3 (the least worn tooth) (fig. 3B, D, E).

The lower molars of *Andemys* maintain four lophids fairly late into wear (as do those of *Branisamys, Eobranisamys, Neoreomys,* and *Australoprocta*) and bear long hypoflexids (as do *Incamys*, *Dasyprocta, Neoreomys*, and *Australoprocta*). *Andemys* resembles *Australoprocta* in several respects. The lower molars of both taxa become squared and narrow transversely in advanced wear, the fossettids are narrow mesiodistally compared to the lophids, and the labial cusp regions become enlarged. In contrast to *Australoprocta*, however, the lophids and fossettids of *Andemys* are transverse (they are oblique in *Australoprocta*), the labial cusps are rounded (rather than angular as in *Australoprocta*), and the hypoflexid is anteroposteriorly compressed labially (it is broadly open in *Australoprocta*). Finally, *Andemys* is substantially less hypsodont than *Australoprocta* (see figs. 3, 4; table 4).

Higher-level taxonomic assignment of *Andemys:* Fitting *Andemys* into existing caviomorph taxonomies poses a number of challenges, some stemming from uncertainties about phylogenetic relationships, and some from a previous lack of attention to the definitions of supraspecific taxon names. Although *Andemys* is obviously a member of the Caviomorpha, it is not immediately apparent to which of the four currently recognized "superfamily" or 12+ "family"-level groups it belongs or is most closely affiliated. As mentioned, the poorly resolved interrelationships of many of these groups poses one difficulty; of particular relevance here are the debated affinities of many early diverging extinct taxa to the various crown clades. A second problem of assigning *Andemys* to a recognized "family" stems from the scant attention that has been paid historically to the definitions of the names themselves.

Andemys resembles a variety of Oligocene, Miocene, and evidently late Eocene taxa, including, *Australoprocta*, *Branisamys*, *Eobranisamys*, *Scleromys*, *Neoreomys*, *Eoincamys,* and *Incamys,* all of which have been referred to the Dasyproctidae at least on occasion. Nevertheless, assignment of most of these taxa to the Dasyproctidae has been questioned for a variety of reasons, including issues related to the proper conception of the name Dasyproctidae. (We follow Patterson and Wood, 1982, and most of the recent literature on fossil caviomorphs in using the name Dasyproctidae rather than Agoutidae; see also Woods and Kilpatrick, 2005.)

The higher-level placements of many of the taxa with which we have compared *Andemys* closely are controversial. *Scleromys* exemplifies the highly unstable phylogenetic position of many fossil caviomorphs. Fields (1957) considered *Scleromys* a dinomyid, the latter of which had long been generally regarded as cavioids. Other researchers considered *Scleromys* a dasyproctid—and hence still a cavioid (Miller and Gidley, 1918; Wood and Patterson, 1959). Thus, although the familial assignment of *Scleromys* was disputed, there was general agreement about its suprafamilial placement (Cavioidea). More recently, however, molecular evidence points to membership of *Dinomys,* the sole extant dinomyid, within the Chinchilloidea rather than Cavioidea (Huchon and Douzery, 2001). This poses the question of whether extinct taxa such as *Scleromys* should be transferred to Chinchilloidea along with *Dinomys,* assuming the dinomyid affiliation of *Scleromys* is accepted. Kramarz (2006) followed Fields (1957) in assigning *Scleromys* to the Dinomyidae, but he maintained the traditional placement of the Dinomyidae within Cavioidea rather than Chinchilloidea, in conflict with molecular evidence. In short, the familial (Dinomyidae or Dasyproctidae) and superfamilial (Chinchilloidea or Cavioidea) affinities of *Scleromys* may thus be seen as highly uncertain. The fluctuating familial and superfamilial assignments of *Branisamys* illustrate a similar problem: this taxon has been considered, in turn, a dasyproctid (Hoffstetter and Lavocat, 1970), a dinomyid (Patterson and Wood, 1982), and an "agoutid" (Frailey and Campbell, 2004). (The placement of *Incamys, Eoincamys,* and *Neoreomys* are plagued with similar uncertainties.) Resolution of these and myriad other classificatory questions awaits comprehensive phylogenetic analyses of the taxa involved.

As noted above, at the center of many of these problems are several early putative dasyproctids. A strong case can be made that the name Dasyproctidae should apply to the least-inclusive clade of which the extant *Dasyprocta* and *Myoprocta* are members (consistent with the usage of Simpson, 1945; Landry, 1957). (This conception of the name, incidentally, agrees with recent recommendations that well-known taxonomic names apply to crown clades; see below.) Miller and Gidley (1918) and Wood and Patterson (1959) referred the Miocene *Neoreomys* and its apparent close relatives, *Scleromys* and *Olenopsis,* to the Dasyproctidae and, given that such matters were not considered important at the time, they did so without concern for whether extinct forms nested within the crown clade.

For the sake of argument we may assume that *Neoreomys* is a proximal outgroup to (*Dasyprocta* + *Myoprocta*), as supposed by Wood and Patterson (1959) though not articulated as such (since their work took place prior to the invention of cladistic methods and terminology). We may also assume a similar phylogenetic placement for *Andemys*. Whether these extinct taxa are termed "dasyproctids" thus hinges simply on the question of how the name "Dasyproctidae" is defined. There is growing consensus that widely used taxonomic names are most appropriately applied to crown clades, rather than to crown clades plus their stems or portions of their stems (de Queiroz and Gauthier, 1992). Consistent with Simpson (1945) and Landry's (1957) views, Dasyproctidae should therefore be tied to the clade encompassing the most recent common ancestor of *Dasyprocta* and *Myoprocta* plus all its descendants. Numerous tools for defining taxonomic names phylogenetically currently exist (de Queiroz and Cantino, 2001), none of which, to our knowledge, have been applied to caviomorphs. (The name "Caviomorpha" itself is in desperate need of a phylogenetic definition, a task complicated slightly by the poorly resolved branching sequence at the base of the relevant crown clade.) Although it is tempting to propose definitive phylogenetically based names to the groups of organisms discussed here, we feel that doing so would be premature. Our objective here is limited to describing two new fossil caviomorphs, identifying them with the specificity that the preserved material and current taxonomic practices permit, not to provide a comprehensive phylogenetic taxonomy of the major clades of caviomorphs.

With regard to the taxonomic placement of *Andemys*, as detailed elsewhere, we contend that it is more closely allied to the minimally inclusive clade of which *Dasyprocta* and *Myoprocta* are members than with any other living caviomorphs. This poses the practical problem of what name should attach to the clade encompassing *Andemys* and the dasyproctid crown, but that excludes most other caviomorphs, a task complicated by the lack of a comprehensive phylogenetic analysis of *Dasyprocta* and *Myoprocta* and their potentially related extinct taxa.

Despite these obstacles, as a provisional measure we propose the term “pan-Dasyproctidae” to informally refer to the dasyproctid total clade, that is, the clade consisting of the dasyproctid crown plus all taxa sharing a more recent common ancestor with that crown than with any other caviomorph crown clade(s) (de Queiroz, 2007). The precise wording of such a definition can be formalized at a later date, but for the moment this convention simplifies the task of referring to this particular clade of caviomorphs succinctly. In a parallel fashion we employ the name pan-Chinchillidae to refer informally to the chinchillid total clade; see above. Besides Chinchillidae and Dasyproctidae, other caviomorph “families” merit having their crown clades and total clades bear different names. Nevertheless, since our immediate objective here is to provide a taxonomy for a chinchillid and a dasyproctid ally, we have treated all other caviomorph “family”-level names in the traditional fashion, not restricting them to their respective crown clades.

It should also be noted that the placement of Dasyproctidae within Caviomorpha has varied historically. Wood and Patterson (1959) transferred the family from the Cavioidea, its traditional placement, to the Chinchilloidea. Patterson and Wood (1982) reversed course, returning Dasyproctidae (along with Dinomyidae) to the Cavioidea, cementing the view that both families represent early cavioid offshoots.

Leaving aside ambiguities about how the name Dasyproctidae has traditionally been employed, the affiliation of *Andemys* to this clade, as originally proposed (Wyss et al., 1993), has been questioned (Frailey and Campbell, 2004). Frailey and Campbell (2004: 99) assigned SGOPV 2933 to the Echimyidae based on (1) “a deep hypoflexid, which is equal in length to the opposing flexids and which terminates at the base of the hypolophid,” and (2) “four slightly oblique lophids, of which the anterior two are the first to fuse and form a single lophid.” It may be noted that the first condition applies only to m2 of SGOPV 2933, not to the other molars (fig. 3B, D, E). More importantly, several early octodontoids lack hypoflexids of this form (e.g., *Sallamys, Eosallamys, Eosachacui*), making it unclear what condition typifies this clade ancestrally. Regarding the second feature, the antero- and metalophids are the first lophids to fuse in a wide variety of early caviomorphs including *Incamys, Australoprocta, Neoreomys, Cephalomys, Eoviscaccia, Scleromys, Sallamys,* and *Platypittamys*. The feature is thus very likely primitive for Caviomorpha and certainly not restricted to Octodontoidea. It should also be emphasized that the two anterior lophids of m2–3 on SGOPV 2933 remain decidedly unfused (m1 is highly worn, so the condition of its anterior lophids cannot be assessed; fig. 3B, D, E). With additional wear the antero- and metalophids would have merged increasingly as the anterofossettid diminished. The antero- and metalophids initially merged labially, increasing the apparent size of the protoconid region. Later in wear the anterofossettid would have been obliterated (shifting lingually in the process), resulting in complete fusion of the two anterior lophids, the lingual limits of the protoconid no longer being discernable. The first significant fusion to take place on m2 would have been between the hypoflexid and the metafossettid. Finally, we note that in *Andemys* the hypoflexid projects ventrally beneath the hypolophid, as is common to *Dasyprocta, Incamys*, *Eoincamys, Neoreomys, Branisamys,* and *Eobranisamys* (all of which are widely considered dasyproctids—or pan-dasyproctids in the terminology preferred here) rather than under the metafossettid as in octodontoids, including *Scleromys* (Kramarz, 2006).

On the least worn tooth of SGOPV 2933, m3, the hypoflexid, and metafossettid are confluent, forming a common trough (fig. 3B, D, E). These structures are confluent during early wear in other pan-dasyproctids, in early dinomyids (e.g., *Potamarchus*), in early pan-chinchillids (e.g., *Eoviscaccia*), and in some (*Protadelplomys*) but not all (e.g, *Eosachacui, Eoespina, Eosallamys, Paradelphomys*) octodontoids. On balance, and as is more fully discussed below, the totality of evidence indicates that *Andemys* shares closer affinities with dasyproctids than with octodontoids.

Eoviscaccia frassinettii: The lower cheek teeth of *Eoviscaccia frassinettii* consist of two large lophids or lobes (fig. 5) as in *Perimys, Scotamys*, the lagostomines (*Lagostomus* and *Prolagostomus*), and worn individuals of *E. boliviana* and *E. australis*, contrasting with the figure eight–shaped arrangement in *Cephalomys* and *Litodontomys*. The largest cheek tooth of *E. frassinettii* is m1 (figs. 5, 6), whereas in *E. boliviana* it is m2 (the condition for *E. australis* is unknown). In *E. frassinettii* enamel is uniformly distributed around the lower cheek teeth, whereas in other species of the genus enamel is thin or discontinuous on the anterior faces of both lobes of m1–3, on the anterior face of the posterior lobe of p4, and on the labial faces of the posterior lobes of all known lower cheek teeth (figs. 5, 6). With wear the two lophids become separated by a hypoflexid as is typical of chinchillids and neoepiblemids. Cementum fills the hypoflexid, as in *E. boliviana, E. australis, Perimys*, *Prolagostomus*, and *Scotamys* (partially). Although the cheek teeth of SGOPV 2935 are moderately worn, enamel extends below the alveolar border, indicating a substantial degree of hypsodonty (figs. 5, 6). Furthermore, the hypoflexid nearly reaches the lingual wall of enamel, another indicator of hypsodonty—seen also in *E. australis* (Vucetich, 1989).

Although similar to the *E. boliviana* and *E. australis, E. frassinettii* is nevertheless distinct from both. In *E. frassinettii* (1) the cheektooth lobes are oblique rather than transverse, (2) a cementum-filled anterofossettid persists late into wear on p4, (3) enamel is thicker lingually on both lobes (than in the other two species), (4) the hypoconid region is rectangular (rather than rounded), (5) the hypoflexid nearly reaches the lingual side of p4 and m3 (on m1–2 it terminates slightly more labially), and (6) enamel occurs on the anterior face of p4 (reduced in the other two species). This combination of features is unique to *E. frassinettii* (see figs. 5, 6; table 5).

Eoviscaccia compares more closely to *Scotamys* and *Perimys* (Neoepiblemidae) than to Cephalomyidae, despite the lophids being substantially thinner in *Scotamys* and *Perimys* than in *Eoviscaccia*. Enamel forming the posterior margins of the anterior and posterior lobes of *Eoviscaccia* is thick (compared to the anterior margins), whereas in *Scotamys* and *Perimys* enamel is uniformly thick. In *Eoviscaccia* the lobes are tightly appressed and the hypoflexid is very thin (the typical "chinchillid" pattern), compared to *Scotamys* and *Perimys* wherein the lobes are separated by a comparatively broad hypoflexid (the neoepiblemid pattern).

Hoffstetter (1971) referred specimens now regarded as pertaining to *E. boliviana* either to the Chinchillidae (resembling *Scotamys*) or the Eocardiidae. Vucetich (1989) assigned *E. boliviana* and *E. australis* to the Chinchillidae. Kramarz (2001), reporting important additional material of *E. australis* (known only from two teeth until that time) affirmed this taxon's placement in the Chinchillidae. Vucetich (1989) regarded *E. boliviana* (Deseadan) as the most "primitive" and *E. australis* (Deseadan-Colhuehuapian) as the most "derived" member of the genus based on levels of hypsodonty (greater in *E. australis)*, the lack of anterofossettids (in *E. australis)*, and a hypoflexid that completely traverses the teeth basally (in *E. boliviana* the hypoflexid fails to reach the lingual wall of enamel in late wear, whereas in *E. australis* it very nearly does). An anterofossettid occurs on p4 in *E. frassinettii* (likely a shared plesimorphy with *E. boliviana*), and the hypoflexid very nearly reaches the lingual part of this tooth in late wear (approaching the condition seen in *E. australis*). This latter feature suggests that the level of hypsodonty in *E. frassinetti* roughly matches that of *E. australis,* whereas that in *E. boliviana* is lower (figs. 5, 6).

HYPSODONTY: Tinguiririacan faunas represent the earliest global occurrence of mammalian communities dominated by highly hypsodont herbivores. High levels of hypsodonty were attained across a diversity of taxa some 15–20 million years earlier in South America than on other continents (Patterson and Pascual, 1968; Simpson, 1980; MacFadden, 1985; Pascual et al., 1996; Flynn et al., 2003; Croft et al., 2008; Zucol et al., 2010). This suggests a correspondingly early paleoenvironmental shift from closed forests to sparse trees and extensive open habitats on this landmass (Croft, 2001; Flynn et al., 2003; Croft et al., 2008), a conclusion supported by notoungulate postcranial evidence (Shockey and Flynn, 2007). The traditionally accepted notion that the development of hypsodonty is tied to the spread of grasslands has recently been called into question on the basis of paleobotanical evidence from Argentina (Strömberg et al., 2010). Phytolith assemblages in the Sarmiento Formation at Gran Barranca indicate that grass-dominated habitats did not occur there until after the late early Miocene (18.5 Ma), implying that other factors must have driven the origin of hypsodonty in the region—perhaps simply the appearance of "open," nongrassy habitats. In sum, the Tinguiririca Fauna demonstrates that levels of hypsodonty in South American native ungulates increased dramatically near the Eocene-Oligocene transition. This coincides roughly with the paleoclimatic and paleoenvironmental changes of the earliest Oligocene "climatic deterioration" event (Prothero and Berggren, 1992).

At least one of the rodents from the Tinguiririan Fauna (*Eoviscaccia*) exhibits a similar tendency toward precocial hypsodonty. The question of the original degree of hypsodonty in *Andemys* (SGOPV 2933; figs. 3, 4) (i.e., whether this specimen was significantly more hypsodont earlier in wear or was conistently brachydont) is best addressed through its two least worn teeth (m2–3). The slightly bulbous crowns are restricted above the gum line, the roots beginning immediately beneath. The floor of the hypoflexid occurs well above the base of the crown. In *Incamys* and *Branisamys*, both minimally hypsodont, the hypoflexid terminates at, or slightly below, the gum line, with the base of the crown extending below the gum line as well. In the vast majority of worn molars of *Incamys* (a fairly hypsodont taxon) we have examined the base of the hypoflexid is positioned below the gumline. Only in rare instances, after extreme wear, does the base of the hypoflexid ultimately emerge above the gum line (figs. 3, 4). This suggests that SGOPV 2933 likely represents a moderately worn example of a brachydont taxon, rather than an extremely worn example of a hypsodont form. The crowns of *Incamys, Australoprocta,* and *Branisamys* are thus deeper (i.e., more hypsodont) than in *Andemys*. In still more hypsodont taxa (e.g., *Neoreomys, Dasyprocta,* and *Eoviscaccia*), the base of the hypoflexid always resides below the gum line, given the tremendous height of the decidedly nonbulbous (but rather straight-sided) crowns (figs. 4, 5). *Andemys* is also apparently significantly less hypsodont than specimens of *Incamys*, *Branisamys,* and *Cephalomys* at presumably similar levels of wear (again with the caveat that determining the degree of wear of SGOPV 2933 is hampered by the limited sample from Chile).

Eoviscaccia frassinettii, by contrast, is substantially more hypsodont than *Andemys* (or any of the rodents from the Santa Rosa or Contamana faunas for that matter), implying that ecological diversification of caviomorphs had already occurred at the latitudes of central Chile by the early Oligocene (Vucetich et al., 2010).

Establishing the ancestral tooth crown height for caviomorphs is not entirely straightforward. Early (and presumably basal) phiomorphs and the earliest caviomorphs exhibit a range of conditions. Asian-African hystricognaths such as *Protophiomys, Phiomys,* and *Hodsahibia* are slightly less hypsodont than the African *Gaudeamus* (Coster et al., 2010; Sallam et al., 2011), but *Gaudeamus* is clearly less hypsodont than early pan-chinchillids. A more fully resolved understanding of higher-level relationships within and between phiomorphs and caviomorphs is required to assess the pattern of character evolution of this feature. Work in progress explores the question of basal caviomorph relationships more fully (Bertrand et al., in prep.). It seems inescapable, however, that high levels of homoplasy are involved, with numerous independent acquisitions of hypsodonty and possibly some instances of character reversal (Candela and Vucetich, 2002; Vucetich et al., 2010).

Chinchilloids and the Deseadan cavioid *Chubutomys* are the only Oligocene hystricognaths exhibiting high degrees of hypsodonty. Given that chinchilloids are unlikely to be basal to all other caviomorphs and that most phiomorphs and early caviomorphs (including those from Santa Rosa and Contamana) are considerably more brachydont than chinchilloids, it seems implausible that hypsodonty typified caviomorphs ancestrally. The early attainment of hypsodonty in chinchilloids (relative to other caviomorphs) is almost certainly autapomorphic, suggesting something unusual about their dietary or habitat preferences. It is noteworthy that many lineages of notoungulates, and even one edentate (McKenna et al., 2006), from the Tinguiririca Fauna, exhibit a similarly precocious attainment of hypsodonty relative to mammalian herbivores on other continents.

PRE-TINGUIRIRICAN RODENT-BEARING LOCALITIES: Although the age of Santa Rosa, a Paleogene rodent-bearing fauna from Peru, is uncertain, it has been argued to be pre-Tinguiririca

(Frailey and Campbell, 2004; Antoine et al., 2011). More recently a middle Eocene (~41 Mya) rodent-containing fauna has been described from Contamana, Peru (Antoine et al., 2011). The Contamana Fauna rodents, the most ancient recorded in South America, are taxonomically distinct from those from Tinguiririca and Santa Rosa. The Santa Rosa Fauna includes diverse octodontoids (*Eoespina, Eosachacui, Eosallamys*), dasyproctids—"agoutids" in the terminology of Frailey and Campbell, 2004—(*Eobranisamys, Eoincamys*), but only a single erethizontoid, *Eopululo* (represented by a single specimen). By contrast, the Contamana Fauna includes *Eobranisamys* and *Eoespina* (each known from a single specimen), but is dominated by erethizontoids.

The Santa Rosa Fauna has been argued to be Eocene (i.e., pre-Tinguiririican) in age based on the "stage of evolution" of endemic marsupials (Goin and Candela, 2004), the apparent morphological primitiveness of the rodents themselves (Frailey and Campbell, 2004) and—more recently—the similarity of some of its rodents (*Eobranisamys* and *Eoespina*) to those from Contamana (Antoine et al., 2011), a fauna having independent age constraints. Dental features of the Santa Rosa rodents that have been argued to be primitive and thus suggestive of an Eocene age (Frailey and Campbell, 2004) include a low level of hypsodonty and the limited degree of fusion of the anterior two lophids of the lower molars of most taxa compared to SGOPV 2933 from the Tinguiririca Fauna (as illustrated in Wyss et al., 1993). Others have advocated, based on sparse evidence from ungulates, an Oligocene age for the Santa Rosa Fauna (Shockey et al., 2004).

Despite uncertainty about its age, the Santa Rosa Fauna is of far-reaching importance in representing one of only two reasonably well-sampled Paleogene assemblages currently known from the Neotropics. The degree to which the Santa Rosa rodent fauna differs from that from Contamana is remarkable given the geographic proximity of these locales, and their apparent similarity in age.

Pentalophodonty vs. tetralophodonty: The number of lophids varies across "family"-level clades of early caviomorphs, complicating attempts to assess the ancestral lophid number in caviomorphs as a whole. Although it is generally argued that the upper molar pattern of phiomorphs and caviomorphs derive from pentalophodont antecedents (Hoffstetter and Lavocat, 1970; Patterson and Wood, 1982; Vucetich and Verzi, 1994; Marivaux et al., 2004; Coster et al., 2010), this notion remains largely untested from a rigorous phylogenetic perspective. Phiomorphs exhibit pentalophodont (*Phiomys:* late Eocene–early Oligocene; *Protophiomys:* late middle Eocene; *Gaudeamus aslius:* late Eocene), tetralophodont (*Talahphiomys:* late middle Eocene; *Gaudeamus hylaeus:* late Eocene) and trilophodont (*Gaudeamus aegyptius:* late Eocene–early Oligocene) arrangements of the upper molars. Early caviomorphs include pentalophodont (most erethizontoids, *Australoprocta, Eobranisamys,* and *Neoreomys*) as well as tetralophodont (*Incamys, Eoincamys, Draconomys*, *Eoespina*, and *Eoviscaccia*—in early wear stages) forms. Tantilizingly, caviomorphs from Contamana are consistently pentalophodont (Antoine et al., 2011). Resolving the question of whether caviomorphs were penta- or tetralophodont ancestrally will require a comprehensive phylogenetic analysis of the group and its nearest kin.

Early caviomorph biogeography: *Gaudeamus,* from Egypt, has recently been interpreted to represent a caviomorph, closely related either to *Incamys* (Coster et al., 2010; Antoine et al., 2011; Sallam et al., 2009, 2011) or to *Branisamys* and *Sallamys* (Bertrand, 2009; Coster et al., 2010; Sallam et al., 2011). If *Gaudeamus* is truly nested within Caviomorpha and is not simply convergent upon isolated caviomorph taxa (such as being "taeniodont," i.e., lacking a connection between the hypoconid and hypolophid and thus having a confluent metafossettid and hypoflexid, with fusion of the hypoflexus and the paraflexus on the upper molars), this would have obvious biogeographic implications. Such a phylogenetic position would imply that caviomorphs immigrated to South America multiple times (Bugge 1971; Wood, 1972; Bryant and McKenna, 1995; Candela, 1999, 2002; Martin, 2005), that some "back-migrated" to Africa (Sallam et al., 2011; Antoine et al., 2011), or both (Sallam et al., 2011).

Paleobiogeography: The Contamana and Santa Rosa faunas of Peru imply that caviomorphs arrived in the low latitudes of South America by the late Eocene (i.e., prior to the Tinguiririca), the group not dispersing southward until sometime later. The occurrence of *Eoviscaccia frassinettii* in the Tinguiririca Fauna, the oldest pan-chinchillid known, clarifies this group's biogeographic history. Apart from SGOPV 2935, Oligocene pan-chinchillids are otherwise known only from the Lacayani locality of Bolivia (Vucetich, 1989) and sparse remains from Patagonia (Vucetich, 1989; Kramarz, 2001), including a possible pre-Deseadan post-Tinguirirican chinchilloid recently reported from the Gran Barranca (Vucetich et al., 2010). The group evidently did not reach the latitudes of southern Argentina in significant numbers before the early Miocene (Colhuehuapian SALMA), a pattern suggesting an origin for the clade outside the high latitudes, perhaps not far from the early Oligocene occurrence of *Eoviscaccia* in central Chile. The curious absence of pan-chinchillids from the heavily sampled locality of Salla, Bolivia, suggests that ecological factors other than latitude influenced the early evolution and distribution of members of this clade.

It is noteworthy that the other rodent clade currently represented at Tinguiririca, pan-Dasyproctidae, is abundant at Salla, Bolivia, but not at classic high-latitude Deseadan localities in Argentina (Patterson and Wood, 1982). At these southern localities, as well as at Lacayani, cephalomyids are the dominant rodent group. Assuming that the two specimens currently known are representative of the Tinguiririca rodent fauna as a whole, it more resembles Deseadan faunas of Bolivia than those of southern Brazil or southern Argentina, sharing faunal elements characteristic of both Salla and Lacayani.

CONCLUSIONS

Andemys termasi and *Eoviscaccia frassinettii* from the earliest Oligocene (Tinguirirican SALMA) represent the oldest caviomorphs known from southern South America; the latter represents the oldest pan-chinchillid (and chinchilloid) known anywhere on the continent. That these taxa are members of two distinct clades (pan-Dasyproctidae and pan-Chinchillidae), indicates that caviomorphs were well diversified at the latitude of central Chile by earliest Oligocene (Tinguirirican SALMA) time. These findings are broadly consistent with the long-held suppostion (e.g. Wood and Patterson, 1959; Patterson and Wood, 1982; Hoffstetter and Lavocat, 1970; Vucetich, 1989; Carvalho and Salles, 2004; Vucetich and al., 2010) that caviomorphs originated and differentiated prior to the Deseadan, given the group's considerable diversity in that SALMA. This view is further corroborated by recent reports of diverse late Eocene rodent-containing faunas from the low latitudes (Frailey and Campbell, 2004; Antoine et al., 2011).

The lower molars of *Andemys*, the Tinguirirican pan-dasyproctid, bear four lophids, three fossettids, and a moderately compressed hypoflexid. The hypoflexid and metafossettid separate only late in wear, as in *Dasyprocta, Australoprocta, Neoreomys,* and *Incamys*; this separation tends to occur earlier in wear in basal octodontoids. The hypoconid region of *Andemys* is oblique (as in *Neoreomys, Incamys, Eoincamys, Australoprocta*, *Branisamys, Eobranisamys,* and *Dasyprocta*) compared to Octodontoidea (*Sallamys, Deseadomys*, *Eosachacui*, *Platypittamys,* and *Migraveramus*)—where the hypoconid regions are transverse. Among early caviomorphs *Andemys* closely resembles *Incamys* and *Eoincamys* (pan-Dasyproctidae), both of which possess four lophids early in wear (antero-, meta-, hypo-, and posterolophid) and a moderately compressed hypoflexid. *Andemys* is also similar to *Neoreomys, Australoprocta*, *Branisamys,* and *Eobranisamys* (pan-Dasyproctidae) in retaining four lophids even after heavy wear.

The transversely narrow lower cheek teeth of *Andemys* and *Australoprocta* are especially similar, including becoming squared in late wear. In addition, the fossettids are narrower mesiodistally than the lophids in both taxa. *Andemys* is marked by several features not seen in *Australoprocta,* however, including: (1) lophids and fossettids transverse (rather than oblique), (2) labial cusps rounded (rather than angular), and (3) a hypoflexid labially compressed (rather than open). Lastly, *Andemys* is less hypsodont than *Australoprocta.* Accordingly we provisionally assign *Andemys* to the pan-Dasyproctidae pending the outcome of ongoing phylogenetic work.

The Tinguirirican-Colhuehuapian pan-chinchillid *Eoviscaccia* is characterized by: bilobed lower cheek teeth; a pear-shaped p4; a long, thin, cementum-filled, and centrally positioned hypoflexid; and thin/discontinuous enamel on the anterior faces of both lobes on the lower molars, on the anterior face and posterior lobe of p4, and on the labial faces of the posterior lobes of p4–m3. In *E. frassinettii* (the sole known specimen of which is fairly advanced in wear), the lophids are oblique, and the anterofossettid persists on p4, filled with cementum. In *E. frassinettii* enamel is thicker on the lingual faces of both lobes of the molars and on the anterior face of the anterior lobe of p4 compared to the two other species. The hypoconid region is rectangular and the hypoflexid (lined by enamel) nearly reaches the lingual side of p4 and m3 (it ends less far lingually on m1–2). Finally, *E. frassinettii* appears to be roughly as hypsodont as *E. australis* and more so than *E. boliviana.*

As best documented by the Contamana Fauna of Peru, caviomorphs arrived in South America prior to the Tinguirirican, no later than the late Eocene. Discovery of two anatomically distinct and distantly related rodents in the Tinguirirican indicates that the group's initial diversification was extremely rapid.

Ongoing phylogenetic work seeks to clarify whether the two rodents from the Tinguiririca Fauna are more closely related to taxa from northern (Peru and Bolivia) or southern (Patagonia) portions of the continent, underscoring how much about the paleobiogeographic patterns of early caviomorphs remains to be learned. Unresolved questions include whether faunal distinctions between the middle and low latitudes existed from early in the group's history, and what influence paleoenvironmental (including altitudinal) differences had on faunal composition at early caviomorph-bearing sites. Our understanding of the direction and timing of latitudinal migrations that undoubtedly occurred during this time will remain clouded until these issues are resolved.

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