

A New Early Miocene Chinchilloid Hystricognath Rodent; an Approach to the Understanding of the Early Chinchillid Dental Evolution

Alejandro G. Kramarz · María G. Vucetich · Michelle Arnal

© Springer Science+Business Media New York 2012

Abstract Chinchilloidea is an emblematic group of caviomorph rodents characterized by euhipysodont, laminated cheek teeth. Recent molecular analyses proposed that the extant *Dinomys* (and implicitly its fossil allies) is also part of this group. Their relationships with fossil caviomorphs with less derived dental features are still obscured by the deficiency of the fossil record documenting its early dental evolution. The new genus and species *Garridomys curunuquem*, from the early Miocene deposits of the Cerro Bandera Formation, northern Patagonia, is here described. It is represented by numerous mandible and maxillary remains with dentition. This species has protohipysodont cheek teeth with three transverse crests in all ontogenetic stages arranged in a transitory S-shaped pattern, resembling putative early dinomyids. *Garridomys curunuquem* is here interpreted as the sister group of the clade including the living and fossil chinchillids; both chinchillas and viscaccias would have diverged from a *Garridomys*-like ancestor and acquired hipysodonty independently. *Garridomys* and other chinchilloids would have diverged from the lineage leading to chinchillids in pre-Oligocene times, suggesting a very early, still poorly documented chinchilloid radiation.

Electronic supplementary material The online version of this article (doi:10.1007/s10914-012-9215-0) contains supplementary material, which is available to authorized users.

A. G. Kramarz (✉)
CONICET. Sección Paleontología de Vertebrados. Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina
e-mail: agkramarz@macn.gov.ar

M. G. Vucetich · M. Arnal
CONICET. Departamento. Científico Paleontología Vertebrados, Museo de La Plata. Paseo del Bosque s/n (B1900FWA), La Plata, Argentina

Keywords Caviomorpha · Chinchillidae · Early Miocene · Patagonia · Cerro Bandera Formation

Introduction

The Chinchilloidea is the taxonomic unit originally conceived for grouping the extant and fossil viscaccias, chinchillas, and other endemic South American hystricognath rodents with euhipysodont, multilaminated cheek teeth (i.e., neoepiblemids; Kraglievich 1940). Subsequent authors also included other fossil groups of still uncertain affinities (e.g., cephalomyids, perimyids; Loomis 1914; Landry 1957; Vucetich 1985, but see Simpson 1945; Kramarz 2005), and even the cuniculids and abrocomids were proposed as related to chinchillas (Wood and Patterson 1959; Glanz and Anderson 1990). More recently, Huchon and Douzery (2001), based on molecular evidence, concluded that the extant *Dinomys* Peters, 1873 (previously classified in other hystricognath superfamilies) is closely related to chinchillids, suggesting that dinomyids should also be included in the Chinchilloidea. In addition, the West Indian heptaxodontid *Amblyrhiza* Cope, 1868, was recently proposed as related to dinomyids by sharing some apomorphic characters of the enamel microstructure (Vucetich et al. 2005a) and basicranial features (MacPhee 2011), excluding it from the Caviodea or Octodontoidea. This new systematic perspective, as well as the new records, reveals that Chinchilloidea is a more diverse caviomorph clade than supposed, and that their early evolution was more complex than previously thought.

Chinchillids and neoepiblemids first appeared very early in the fossil record (early and late Oligocene, respectively, Loomis 1914; Wood and Patterson 1959; Flynn et al. 2003), already showing very advanced dental characters in terms of hipysodonty and occlusal simplification. In turn, unquestionable,

highly derived dinomyids first appeared during the latest middle Miocene (Kraglievich 1930; Fields 1957; Walton 1997). Some late Oligocene–early Miocene species with less derived dental characters, as *Branisamys* Hoffstetter and Lavocat, 1970, and *Scleromys* Ameghino, 1887, were regarded as Dinomyidae (the attribution of *Branisamys* to Agoutidae by Frailey and Campbell 2004 is unfounded). Nevertheless, the homologies between most of the occlusal structures of these putative primitive chinchilloids and those of the derived species are still uncertain, because the record of both ontogenetic and phylogenetic trajectories, leading to the occlusal pattern of the modern groups, is very incomplete. These facts greatly complicate the understanding of their origins and early diversification.

In this contribution we describe a new genus and species of a hystricognath rodent from early Miocene sediments of the Cerro Bandera Formation at Neuquén Province, northern Patagonia (Leanza and Hugo 1997; Kramarz et al. 2005, 2011). This new taxon is represented by many maxillary and mandible remains with dentition. The materials provide significant support for the confident assignment of this new taxon to the Chinchilloidea, and for a preliminary discussion of its affinities within a cladistic context, as well as dental evolution and probable homologies of the occlusal structures in chinchillids.

Institutional Abbreviations:

MPEF-PV Paleovertebrate Collection, Museo Paleontológico Egidio Feruglio (Trelew, Chubut); MOZ-PV Paleovertebrate Collection, Museo Prof. Juan Olsacher (Zapala, Neuquén).

Systematic Paleontology

Order Rodentia Bowdich, 1821

Suborder Hystricognathi Tullberg, 1899

Superfamily Chinchilloidea Kraglievich, 1940

Garridomys, gen. nov.

Type species: Garridomys curunuquem, sp. nov.

Etymology: In honor of the geologist Alberto Garrido, for his studies on the geology and biostratigraphy of the Neuquén Basin.

Chronological and geographic distribution: Colhuehuapian? South American Land Mammal Age (SALMA; early Miocene, Flynn and Swisher 1995); Neuquén Province, Argentina.

Diagnosis: Small chinchillid, similar in size to *Eoviscaccia* Vucetich, 1989, or the smallest species of *Prologostomus* Ameghino, 1887. Protodysodont cheek teeth, lower crowned than in the species of *Eoviscaccia*, with cement in adult stages. Hypoflexus/id connected with the parafofossette/metafofossettid during juvenile stages. P4-M3

and m1-3 with two very persistent labial (in the uppers) and lingual (in the lowers) fossettes/ids. Mandibular masseteric crest slightly everted, as in *Scleromys* and unlike all known chinchillids.

Garridomys curunuquem, sp. nov.

(Figures 2, 3, 4, and 5)

Holotype: MOZ-PV-920, left mandible fragment with p4-m3 and incomplete incisor.

Hypodigm: The holotype and the following specimens: MOZ-PV-856, left maxillary fragment with P4-M2; MOZ-PV-857, right maxillary fragment with P4-M3; MOZ-PV-858, right maxillary fragment with P4-M2; MOZ-PV-859, left maxillary fragment with P4-M2; MOZ-PV-860, right maxillary fragment with P4-M2; MOZ-PV-861, left maxillary fragment with P4-M2; MOZ-PV-862, right maxillary fragment with P4-M1; MOZ-PV-863, right mandible fragment with p4-m1; MOZ-PV-864, left mandible fragment with p4; MOZ-PV-921, right mandible fragment with p4-m3 and incomplete incisor; MOZ-PV-922, right mandible fragment with p4-m2 and incomplete incisor; MOZ-PV-923, left mandible fragment with p4-m2; MOZ-PV-928, left mandible fragment with p4-m2; MOZ-PV-929, right mandible fragment with p4-m3; MOZ-PV-930, left mandible fragment with p4-m3; MOZ-PV-931, left mandible fragment with p4-m2; MOZ-PV-932, right mandible fragment with p4-m2 y partial incisor; MOZ-PV-933, right mandible fragment with p4-m2; MOZ-PV-934, left mandible fragment with p4-m2; MOZ-PV-935, right mandible fragment with p4-m1 and partial m2; MOZ-PV-936, left mandible fragment with p4-m2; MOZ-PV-937, right mandible fragment with dp4-m1 and incomplete incisor; MOZ-PV-938, right mandible fragment with erupting p4, m1, and partial incisor; MOZ-PV-939, right mandible fragment with p4 and incomplete incisor; MOZ-PV-940, right mandible fragment with p4 and incomplete incisor; MOZ-PV-941, right mandible fragment with incisor and p4; MOZ-PV-942, right mandible fragment with incomplete p4; MOZ-PV-943, isolated right, little worn m1 or m2 (incomplete); MOZ-PV-944, isolated right, unworn m1 or m2; MOZ-PV-945, isolated left M1 or M2; MOZ-PV-946, isolated left M1 or M2; MOZ-PV-947, isolated left, unworn p4; MOZ-PV-948, isolated right M1 or M2; MOZ-PV-1041, right mandible fragment with m1-m2; MOZ-PV-1045, isolated M1 or M2; MOZ-PV-1070, isolated left lower molar.

Etymology: From Mapuche *curu* = black, and *nüquem* = cliff (*barda* in Spanish), in reference to the type locality Barda Negra.

Geographic provenance: All the specimens come from the NE slope of Barda Negra, Zapala Department, Neuquén Province, Argentina (Fig. 1).

Stratigraphic provenance and age: All the materials come from isolated outcrops of the Cerro Bandera

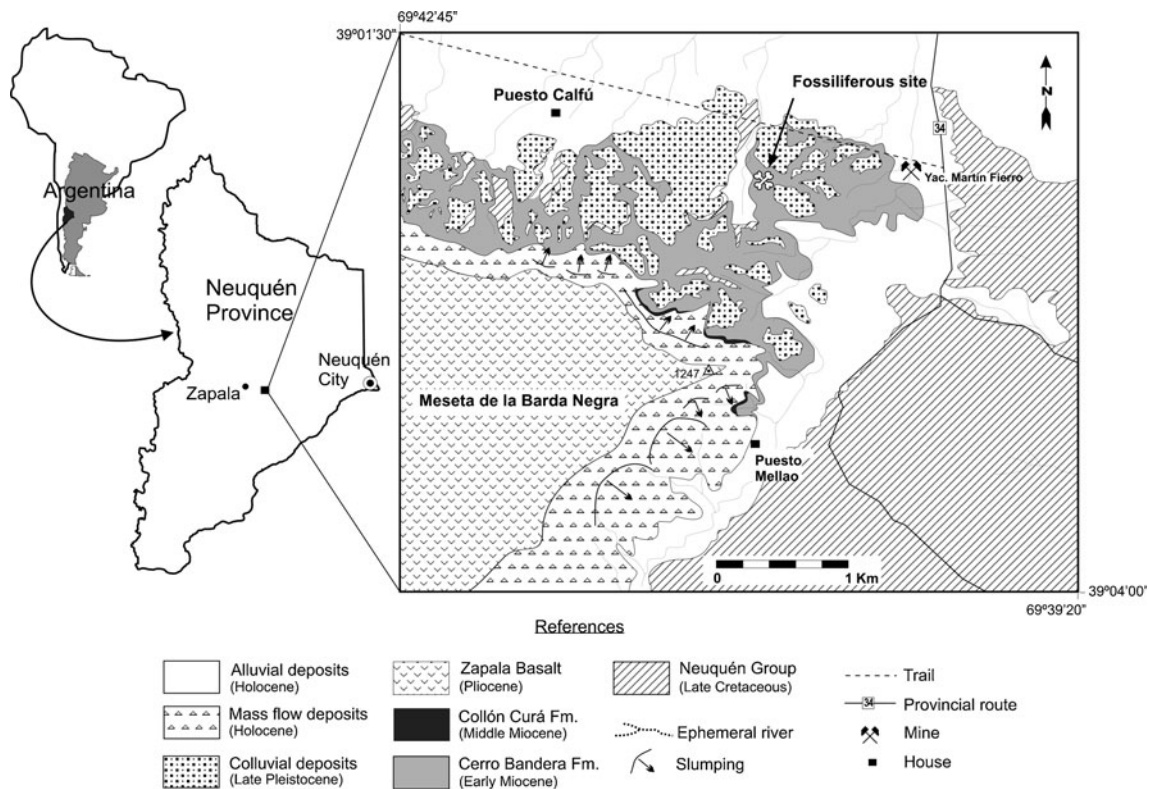


Fig. 1 Geologic map of the northeastern slope of the Barda Negra hill (Neuquén Province, Argentina), showing the exposures of the Cerro Bandera Formation and the location of the site bearing remains of *Garridomys curunuquem*, gen. et sp. nov. Modified from Kramarz et al. (2011)

Formation, in the vicinity of the Puesto Calfú locality (Fig. 1). This unit is a 45 m thick succession of reworked pyroclastic deposits alternating with primary pyroclastic and scant sandstone levels exposed in isolated areas at east central Neuquén Province, northwestern Patagonia. These outcrops represent the relicts of an old alluvial filling developed on small local valleys excavated on Late Cretaceous and Paleocene deposits (Leanza and Hugo 1997; Kramarz et al. 2005). The specimen MOZ-PV-1070 comes from whitish-grayish tuffaceous sediments located about 25 m from the base of the exposed section (S 39°02'26.21"/W 69°40'53.36). The holotype and the remaining specimens come from a level with similar lithology located about 6 m above the base of the stratigraphic section exposed in the area (S 39° 02' 06.3"/W 69° 40' 54.3"). The mammal-bearing deposits of the Cerro Bandera Formation were assigned to the Colhuehuapian SALMA on the basis of a diverse mammalian fauna collected from localities other than Barda Negra (Leanza and Hugo 1997; Kramarz et al. 2005). However, recent findings of some Deseadan (late Oligocene) taxa in the *Garridomys* bearing deposits at Barda Negra could indicate a pre-Colhuehuapian age for these levels (Kramarz et al. 2011).

Diagnosis: As for the genus.

Description and comparisons: Cheek teeth are high crowned and rooted (protohypodont); the crown height (measured on the lingual side of the uppers and the labial one of the lowers) is nearly twice the anteroposterior diameter in unworn teeth; therefore they are lower crowned than in *Eoviscaccia boliviana* Vucetich, 1989, and higher than in *Scleromys osbornianus* Ameghino, 1894. The uppers have marked unilateral hypsodonty.

Unworn or little worn upper molars (Fig. 2a–c) are nearly as long as wide, and have four broad, transverse crests separated by compressed valleys. The anteriormost crest is a combined protocone-antelope. It is somewhat oblique anterolabially-posterolingually, but the labial portion curves backward to contact the paracone; thus, the paraflexus is rapidly closed on the labial side. The second crest runs diagonally from the hypocone to the paracone, probably representing a continuous anterior arm of the hypocone + protoloph. There is not a distinguishable mure; thus, the protocone is isolated from this composite crest and the hypoflexus converges with the paraflexus, resulting in a “taeniodont” pattern. The third crest, probably corresponding to the metaloph, is nearly a semicircle running from the metacone to the central portion of the fourth crest. The valley separating the second from the third crest (mesoflexus?) is long, and

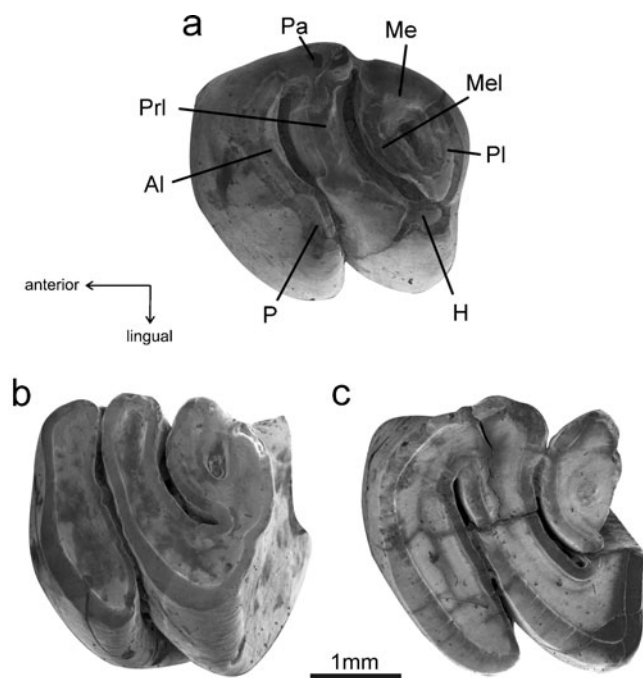


Fig. 2 Unworn and little worn upper molars of *Garridomys curunuquem*, gen. et sp. nov., and terminology used to describe the upper cheek teeth occlusal structures. **a** MOZ-PV-948, right M1 or M2 (shown as left); **b** MOZ-PV-946, left M1 or M2; **c** MOZ-PV-945, left M1 or M2. Abbreviations: **Al**, anteroloph; **H**, hypocone; **Me**, metacone; **Mel**, metaloph; **P**, protocone; **Pa**, paracone; **Pl**, posteroloph; **Prl**, protoloph

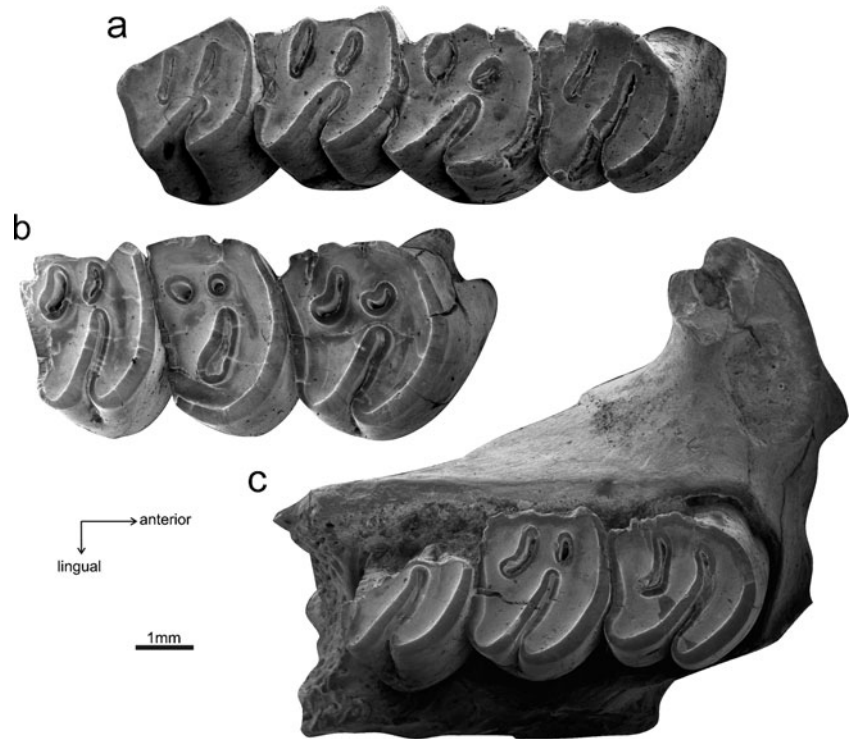
opens on the labial side of the tooth. The fourth crest forms the labial two-thirds of the posterior wall; its lingual end is weakly connected to the hypocone, closing the mesoflexus? on the posterior wall. A small, subcircular fossette is delimited on the posterolabial corner by the last two crests. At this stage of wear the occlusal surface insinuates an S-shaped pattern, strongly resembling that of unworn molars of *Eoviscaccia boliviana* and *Scleromys quadrangulatus* Kramarz, 2006a, and in a lesser degree to *Incamys bolivianus* Hoffstetter and Lavocat, 1970. It also resembles a primitive chinchilloid upper molar (MPEF-PV 5421) from Colhuehuapian levels at Gran Barranca, Patagonia, Argentina, described by Vucetich et al. (2010: fig. 14.3I). This tooth is similar to *Garridomys curunuquem*, gen. et sp. nov., in size and crown height. Nevertheless, it differs in that the enamel thickness is homogeneous, the hypoflexus is funnel-like, wider in its lingual portion, and the occlusal pattern is three-crested, without evidence of metaloph, at least in this stage of wear.

With a little more wear the central valley of the molars of *Garridomys* becomes an elongated, somewhat posteriorly curved enamel lake. Later, the molar becomes wider than long and the posterolabial fossette is worn away, forming a metacone-metaloph-posteroloph complex on the posterolabial corner of the tooth (Fig. 3). At this stage the occlusal surface resembles that of little worn molars of *Eoviscaccia*

boliviana, moderately worn molars of *Scleromys quadrangulatus*, and much worn molars of *Incamys bolivianus*. The enamel layer is continuous, but thicker on the leading edges. As wear progresses, the surface of the metacone-metaloph-posteroloph complex is gradually reduced, and a small septum isolates the parafoesette from the hypoflexus, as in moderately worn molars of *Eoviscaccia boliviana*. A layer of cement fills the lingual portion of the hypoflexus. With increasing wear the hypoflexus becomes more penetrating, reaching nearly two-thirds of the transverse width of the crown, in detriment to the transverse extension of the parafoesette, which gradually changes to a small, oval enamel lake. The mesofossette is a little larger but also becomes a small enamel lake, half moon-shaped in some specimens. In this stage of wear a bilobed occlusal pattern is barely insinuated (see M2 of Fig. 3b and M1-M2 of Fig. 3c). In deeply worn molars the hypoflexus loses its connection with the lingual face of the crown, becoming an elongated hypofossette, and the labial fossettes persist as minute subcircular enamel lakes (see M1 in Fig. 3b). Little worn and much worn P4s (Fig. 3) are similar to the molars in equivalent stages of wear, and probably have similar ontogenetic trajectories. The crown only differs from that of the molars in having a more rounded anterolabial corner, and the base is implanted, curving forward. The M3 differs from M1 and M2 by being wider anteriorly than posteriorly, and in having a small posterior projection of the posterolabial corner (see Fig. 3a).

Unworn and little worn lower molars (Fig. 4a and b) have three main crests. The anterior one (metalophulid I) narrows labially near its contact with the protoconid, and lingually, close to its union with the metaconid. The protoconid has a robust, long, and nearly transverse posterior arm. A short accessory crest (vestigial metalophulid II) runs labially from the posterior arm of the metaconid and its free labial end is opposed to the lingual end of the posterior arm of the protoconid, producing a Y-shaped anterior valley. The hypolophid is broad and transverse, slightly oblique to the posterior arm of the protoconid. In some individuals (Fig. 4b) the hypolophid and the posterior arm of the protoconid are hardly joined, probably involving a short ectolophid, whereas in others they are united even without wear (Fig. 4a). The hypolophid is isolated from the hypoconid; consequently, the metaflexid merges with the hypoflexid and the resulting occlusal pattern is taeniodont, as in the upper molars. The posterior most crest is a combined hypoconid-posterolophid. The lingual portion curves forward, but does not contact the entoconid. Consequently, the posterior valley opens lingually, as well as does the posterior arm of the anterior lingual valley. As for the upper molars, this occlusal pattern strongly resembles that of unworn molars of *Eoviscaccia* (at least *E. australis* Vucetich, 1989) and little worn molars of *Scleromys* and *Incamys*.

Fig. 3 Upper cheek teeth of *Garridomys curunuquem*, gen. et sp. nov. **a** MOZ-PV-857, right P4-M3; **b** MOZ-PV-858, right P4-M2; **c** MOZ-PV-860, right maxillary fragment with P4-M1 and partial M2 in ventral view



With little wear the anterior arm of the Y-shaped valley is worn away (see m1 of Fig. 4c), forming a fused metaconid-

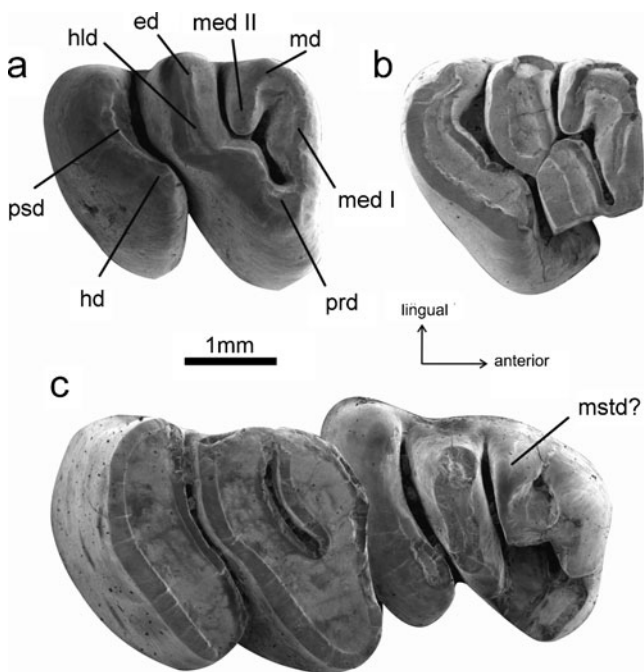


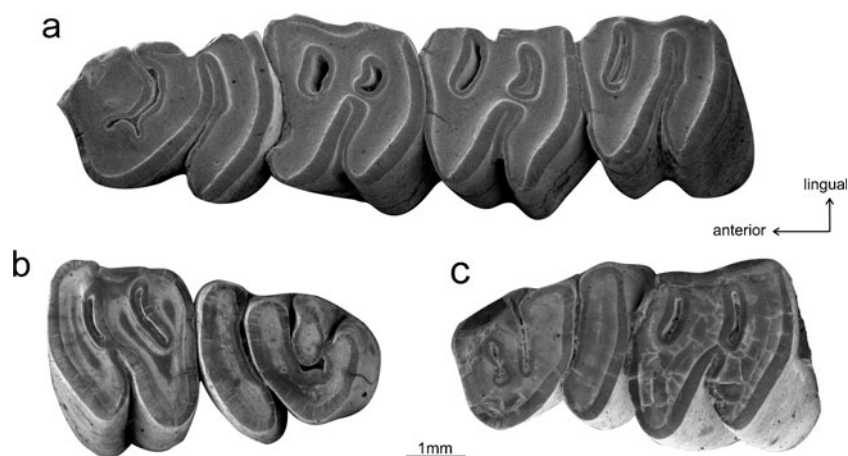
Fig. 4 Unworn and little worn lower cheek teeth of *Garridomys curunuquem*, gen. et sp. nov., and terminology used to describe the lower cheek teeth occlusal structures. **a** MOZ-PV-944, right m1 or m2; **b** MOZ-PV-943, partial right m1 or m2; **c** MOZ-PV-938, right p4 (erupting)-m1. Abbreviations: **ed**, entoconid; **hd**, hypoconid; **hld**, hypolophid; **md**, metaconid; **med I**, metalophulid I; **med II**, metalophulid II; **mstd?**, mesostylid; **prd**, protoconid; **psd**, posterolophid

metalophulid complex on the anterolingual corner of the tooth. The hypolophid and the posterior arm of the protoconid form a continuous and oblique crest. The anterior valley rapidly becomes a long, anteriorly concave enamel lake (see m1 in Fig. 4b); almost simultaneously or a little later the posterior valley loses its connection with the lingual wall of the tooth (see m3 of Fig. 5a). In this ontogenetic stage the occlusal pattern resembles little worn molars of *Eoviscaccia* (at least *E. australis*) and moderately worn molars of *Scleromys* and *Incamys*. In some specimens the closure sequence of the lingual flexids is reversed, being with the posterior flexid somewhat more ephemeral than the anterior one; thus, a transitory S-shaped configuration is barely insinuated.

With more wear a small wall separates the hypoflexid from the metafossettid (see m1-m2 in Fig. 5a; m1 in Fig. 5b and c). Both lingual fossettids gradually become small, rounded enamel lakes. The hypoflexid penetrates nearly halfway across the crown, opposed to the posterior, smallest fossettid. The hypoflexid is compressed in the lingual portion, but it widens labially. As in the upper molars, in this stage of wear a bilobed pattern is hardly insinuated. In senile stages the hypoflexid becomes isolated from the external face of the tooth.

The p4 is longer than the molars (Table 1), becoming even longer at the base, and the trigonid is narrower than the talonid (Figs. 4c and 5). When unworn (Fig. 4c), the trigonid shows an anterolingual cusp (metaconid?), an anterolabial cusp (protoconid), and an accessory lingual cusp (mesostylid?) between the metaconid and the entoconid. The two anterior cusps are superficially separated by a minute,

Fig. 5 Lower cheek teeth of *Garridomys curunuquem*, gen. et sp. nov. **a** MOZ-PV-920, left p4-m3 (Holotype); **b** MOZ-PV-863, right p4-m1; **c** MOZ-PV-936, left p4-m1



anterior notch. With wear these cusps merge to form a complete anterolophid. The relationships of the accessory lingual cusp with the main cusps vary among the specimens and according to the stage of wear. In some specimens this cusp is robust and initially isolated (Fig. 5b). In other specimens the cusp has a short labial projection connected to a small posterior projection of the metaconid, enclosing a small anterolingual flexid (see Fig. 4c), as seen in some specimens of *Scleromys*. In others, the labial projection of the mesostylid? is longer and connected with a lingual projection of the protoconid, forming a complete transverse crest, which delimits a small anterofossetid (see Fig. 5c). Some specimens have both features combined. With wear all these elements are worn away, and the mesostylid? fuses with the anterolophid (Fig. 5a). The occlusal structures of the talonid are essentially as in the molars, and the entire premolar also has a transitory S-shaped occlusal pattern.

The lower incisors are proportionally more slender than in *Scleromys*, but more robust than in *Prolagostomus*. The cross section is D-shaped, somewhat longer than wide. The enameled face is slightly convex. The incisor does not pass beneath the cheek teeth but ends beneath and internal to the posterior margin of m3.

The mandibular diastema is high, slightly concave in front the p4 (Fig. 6a), as in *Incamys* and *Scleromys*. The mental foramen is large, ovoid, located relatively high on the mandible and slightly anterior to the premolar. The scar for the tendon of the *M. masseter medialis pars infraorbitalis* is located beneath p4-m1 (Fig. 6a). It is very shallow, markedly oblique, and entirely continuous with the masseteric crest. The crest is moderately prominent, but more developed than in all chinchillids. A set of small vascular pits are arranged along the anterodorsal portion of the masseteric crest and the masseteric fossa (Fig. 6a). There is not a differentiated lateral fossa at least at the level of m3. The anterior margin of the base of the coronoid process is located at the level of the middle of m3.

In the available maxillary fragments the ventral root of the zygoma is high and antero-posteriorly short, located at the level of the anterior portion of the P4 (Figs. 3c and 6b). The fossa for the origin of the superficial masseter muscle (sensu Woods and Howland 1979) is conspicuous, subcircular, and well defined by a prominent anterior ridge (Fig. 3b). There is no trace of the groove for nerve and blood vessels on the dorsal aspect of the ventral root of the zygoma (i.e., the floor of the infraorbital foramen) in MOZ-PV-859 and 860, but a very shallow one is present in MOZ-PV-958 and 861 (Fig. 6b), as in *Prolagostomus*. In *Lagostomus* Brookes, 1828, *Scleromys*, *Tetrastylus* Ameghino, 1886, and other dinomyids (but not in *Dinomys*), this groove is much deeper and limited laterally by a high bony wall. The intra-orbital portion of the maxillary is faintly vaulted behind the ventral zygomatic root, nearly above the P4-M1, probably lodging the bases of these teeth (Fig. 6b). No available specimen allows for observation of other relevant features.

Relationships of *Garridomys*

Although Chinchilloidea has not been formally diagnosed yet, *Garridomys* is herein classified as a chinchilloid by having the following, presumably derived characters shared with most of the taxa classified within this group:

- Hypsodont cheek teeth with appressed crests insinuating laminated lobes (rudimentary elasmodonty)
 - Cheek teeth of all chinchillids, dinomyids (but not the lower crowned putative dinomyids *Branisamys* and *Scleromys*), neoepiblemids, and heptaxodontids are composed of laminated and almost isolated prisms. An advanced degree of elasmodonty was attained secondarily in the hydrochoerid cavioids, but not in other hypsodont caviomorphs.
 - Heterogeneous thickness of the enamel layer
- The enamel layer is typically thicker on the leading

Table 1 Dental measurements (mm) for *Garridomys curunuquem*, gen. et sp. nov. APL, anteroposterior length; TRW, transverse width

Specimen			P4		M1		M2		M1 or M2		M3		P4-M3 lenght		
			APL	TRW	APL	TRW	APL	TRW	APL	TRW	APL	TRW			
MOZ-PV 857			2.72	3.14	2.74	3.20	2.92	3.16	—	—	2.88	2.92	11.26		
MOZ-PV 858			3.06	3.62	2.56	3.72	2.54	3.32	—	—	—	—	—		
MOZ-PV 859			2.88	—	2.94	3.40	3.00	3.22	—	—	—	—	—		
MOZ-PV 945			—	—	—	—	—	—	—	3.46	—	—	—		
MOZ-PV 946			—	—	—	—	—	—	2.90	2.46	—	—	—		
MOZ-PV 948			—	—	—	—	—	—	2.64	2.72	—	—	—		
MOZ-PV 958			2.86	3.38	2.82	3.30	2.98	3.50	—	—	—	—	—		
	i1		p4		m1		m2		m1 or m2		m3		p4-m3 lenght		
			APL	TRW	APL	TRW	APL	TRW	APL	TRW	APL	TRW			
MOZ-PV 869			—	—	3.32	3.42	3.16	3.38	—	—	—	—	—		
MOZ-PV 920			2.68	2.16	4.00	3.20	2.76	3.34	3.14	3.42	—	—	3.02	2.98	12.92
MOZ-PV 921			2.46	1.88	3.70	3.22	2.98	3.26	2.76	3.76	—	—	2.18	3.10	11.62
MOZ-PV 922			2.08	1.94	3.62	—	3.12	3.40	3.18	3.30	—	—	—	—	—
MOZ-PV 928			—	—	3.06	3.32	2.88	3.40	3.16	3.46	—	—	—	—	—
MOZ-PV 929			—	—	4.00	3.36	2.78	3.42	3.00	3.46	—	—	3.06	2.84	12.84
MOZ-PV 930			—	—	3.98	3.40	3.10	3.72	3.04	3.46	—	—	3.04	2.86	13.16
MOZ-PV 932			—	1.98	3.92	3.22	2.92	3.70	3.00	3.44	—	—	—	—	—
MOZ-PV 936			—	—	3.18	3.24	2.98	3.42	3.12	3.48	—	—	—	—	—
MOZ-PV 938			2.36	1.98	2.78	2.96	3.20	3.34	—	—	—	—	—	—	—
MOZ-PV 943			—	—	—	—	—	—	—	2.86	—	—	—	—	—
MOZ-PV 944			—	—	—	—	—	—	—	2.86	2.82	—	—	—	—

edges than on the trailing edges in cheek teeth of all chinchillids and hypsodont dinomyids (not in *Branisamys*

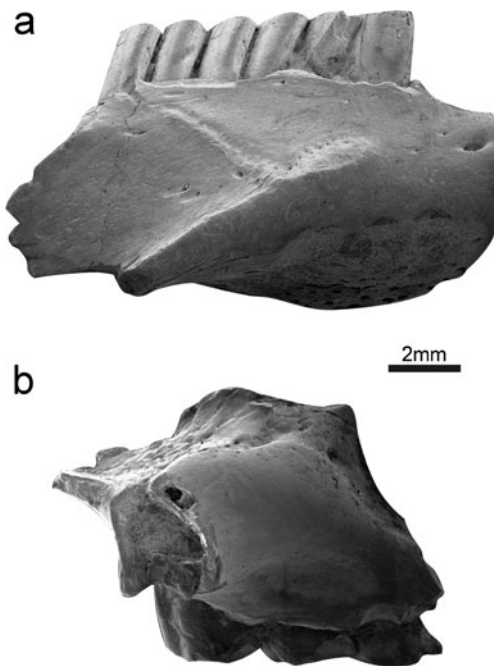


Fig. 6 *Garridomys curunuquem*, gen. et sp. nov. **a** MOZ-PV-922, right mandibular fragment in lateral view; **b** MOZ-PV-861, left maxillary fragment with P4-M2 in lateral view showing the cross section of the ventral root of the zygoma and the floor of the infraorbital foramen

and only insinuated in *Scleromys*). This condition is related to the fact that laminae become very close to each other and the interlaminae cement is extremely reduced. Thus, the enamel layers of the leading and trailing edges are almost in contact; keeping both layers the same width would result in an excessively thick enamel layer. In those taxa in which the laminae are separated by a thick interlaminae layer of cement (as in neopiblemids), the enamel has a homogeneous thickness.

– P4 completely molarized

All known chinchillids, dinomyids (including *Branisamys* and *Scleromys*), and neopiblemids (but not in the putative neopiblemids *Scotamys* Loomis, 1914 and *Perimys* Ameghino, 1887) have fully molarized P4. Basal Caviodea *sensu stricto* (i.e., “eocardiids,” see Pérez 2010) and Patagonian dasypodids have simple, unilobed P4, which gradually evolved during the early Miocene to a molar-like (bilobed) tooth in some taxa (e.g., *Luantus* Ameghino, 1899, *Schistomys* Ameghino, 1887, variable in *Neoreomys* Ameghino, 1887). All octodontoids with normal dental replacement have simple, non-molarized P4 (e.g., acaremyids, *Sallamys* Hoffstetter and Lavocat, 1970, and its allies). Only erethizontids and modern cavioids also have molarized P4.

Assuming that *Garridomys* is correctly located within Chinchilloidea, it shows some characters that appear to be

primitive for most chinchilloids (e.g., rooted cheek teeth). However, *Garridomys* shares with *Eoviscaccia* the early fusion of the metaloph and posteroloph in the upper molars and the reduction of the metalophulid II in the lowers, resulting in a three-crested occlusal design. No dinomyid (including *Branisamys*) exhibits these conditions. Such occlusal design of *Garridomys*, especially in moderately worn cheek teeth, strongly resembles the trilaminar pattern of modern chinchillas, suggesting that it could be a basal member of the Chinchillinae. On the other hand, it lacks many presumably derived characters shared by later diverging chinchillines and lagostomines (e.g., ephemeral fossettes/fossetids, transversally deep hypoflexus/id, reduced masseteric crest). *Garridomys* thus appears to be a basal member of the chinchillid radiation, and it could not be classified within chinchillines neither lagostomines.

To test these alternative hypotheses, we performed a cladistic analysis focused on resolving the relationships of *Garridomys* with the main caviomorph groups belonging to the Chinchilloidea clade (i.e., Chinchillidae, Dinomyidae, and Neoepiblemidae). Among dinomyids, we selected *Dinomys* and *Tetrastylus* as representing the Dinomyidae crown group, and *Branisamys* and *Scleromys*, considered as basal dinomyids (Fields 1957; Patterson and Wood 1982; Walton 1997), since they are lower crowned and retain occlusal structures that can be certainly compared with those in *Garridomys*. Other taxa presumably belonging to Chinchilloidea, as *Perimys*, cephalomyids, and heptaxodontids, are not included in the analysis because it would require a much more comprehensive systematic framework, which is beyond the scope of the present study.

Previous studies (Huchon and Douzery 2001) proposed that Octodontoidea is the sister group of Chinchilloidea. We selected the early Miocene octodontoid *Prospaniomys* Ameghino, 1902, as the outgroup because this is the oldest, and probably the basal most octodontoid of which cranial, mandibular, and dental characters are well known (Arnal and Kramarz 2011).

The available materials of *Garridomys* are maxillary and mandible fragments with dentition and isolated teeth. These elements provide very few characters other than dental ones to analyze the phylogenetic relationships within a cladistic framework. Moreover, most of the dental characters cannot be compared with those of other probably related caviomorphs because the homologies of many occlusal structures of the euhypsodont chinchilloids are still unclear. Accordingly, our cladistic analyses using strictly those characters that can be scored in *Garridomys* have failed in determining unequivocally the position of this taxon. Therefore, we included cranial and mandibular characters that could not be scored in *Garridomys*, mostly modified from

previous studies dealing with chinchilloids systematics: Fields (1957: 322–323), Patterson and Wood (1982: table 7), Kramarz (2001a: table 4), and Rinderknecht et al. (2011). Some of the characters from these bibliographic sources were not included, because they did not show significant variations among the analyzed taxa, they could not be scored in the majority of the analyzed taxa, and/or they could not be defined by unambiguous character states.

The resulting data matrix contains 39 characters scored in 12 ingroup taxa (online Appendixes 1, 2 and 3). An equally weighted parsimony analysis was conducted using NONA 2.0 (Goloboff 1993), performing a heuristic search of 100 Wagner tree replicates followed by TBR. The analysis produced three most parsimonious trees of 79 steps. The strict consensus tree is shown in Fig. 7a. All the obtained trees show *Garridomys* as the sister group of the clade including all extant and fossil chinchillids. This position is supported in all trees by three unambiguous synapomorphies: hypoflexus/id penetrating more than halfway across the crown [character 3(1)], presence of cement [character 5(1)] (convergent in *Neoepiblema* Ameghino, 1889, and late diverging dinomyids), and enamel on leading edges thicker than on trailing edges [character 8(1)] (convergent in late diverging dinomyids). Within the Chinchillidae clade, *Chinchilla* Bennett, 1829, and *Lagidium* Meyen, 1833, cluster in all the obtained trees, supporting the monophyly of Chinchillinae, but the taxa traditionally included within Lagostominae (i.e., *Eoviscaccia*, *Prolagostomus*, and *Lagostomus*) appear in three alternative, equally parsimonious arrangements: the three grouped as the monophyletic sister group of the Chinchillinae clade (Fig. 7b), only *Prolagostomus* and *Lagostomus* grouped (*Eoviscaccia* excluded) (Fig. 7c.), and the three as successive stems of Chinchillinae (Fig. 7d).

Beside the affinities of *Garridomys* with the chinchillids, the relationships of the remaining chinchilloids here analyzed deserve some comments. Our results support the claimed affinities of *Scleromys osbornianus* and “*Scleromys*” *shurmanni* Stehlin, 1940, with the late diverging dinomyids. However, in all the obtained trees *Neoepiblema* is nested within the Dinomyidae clade as the sister group of the late diverging dinomyids *Dinomys* and *Tetrastylus*. Although this previously unexpected position of *Neoepiblema* probably could be the consequence of the large amount of missing data in this taxa (all the mandibular characters and many dental characters are unknown), the affinities of the neoepiblemids with the dinomyids rather than with chinchillids is essentially in accordance with the proposal by Sánchez-Villagra et al. (2003) based on postcranial characters combined with molecular data. Concerning *Branisamys*, our results do not support its dinomyid affinities alleged by previous studies (Fields 1957; Patterson and Wood 1982).

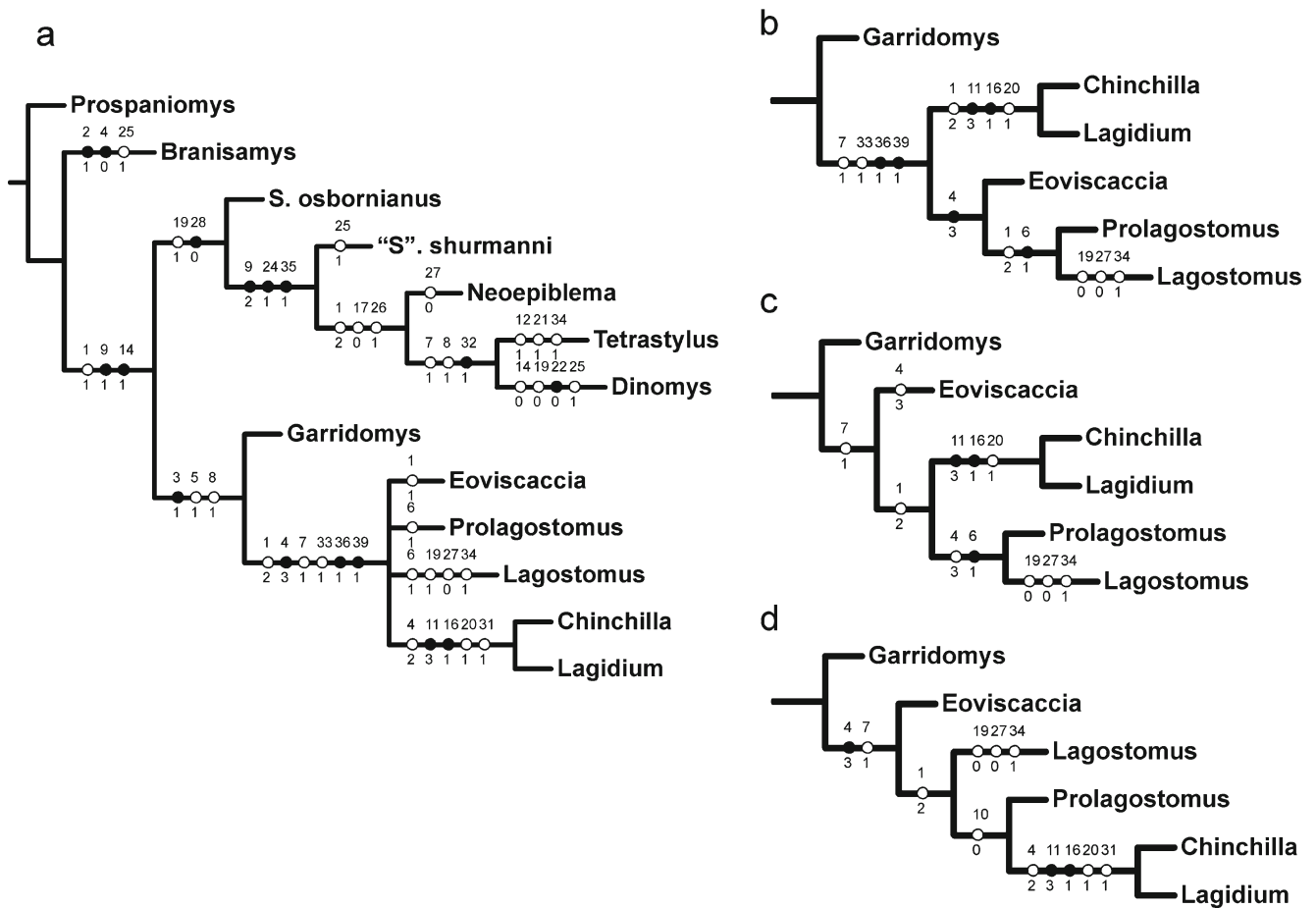


Fig. 7 Phylogenetic relationships of *Garridomys curunuquem*, gen. et sp. nov., with selected chinchilloid rodents. **a** strict consensus from three most parsimonious trees (length = 79, ci = 58, ri = 67) generated by an exhaustive search in NONA (Goloboff 1993) employing 39 dental, cranial, and mandibular characters (online Appendix 1) coded

for 12 chinchilloid genera (using *Prospaniomys* as the outgroup). Data matrix is shown in online Appendix 2; **b–d** details of the three most parsimonious trees showing the alternative hypotheses of chinchillid phylogeny. Characters indicated with black circles are synapomorphies; characters indicated with white circles indicate homoplasies

Cheek Teeth Evolution in Chinchillidae. Alternative Evolutionary Pathways and Occlusal Homologies

Chinchillines chinchillids are characterized by having trilaminar cheek teeth [character 4(2)]. Lagostomines instead have typically bilaminar cheek teeth [character 4(3)], except M3. Even though *Eoviscaccia* has a complex occlusal pattern during very juvenile stages, with wear the cheek teeth become bilaminar, markedly simplified. A similar process occurs in *Prolagostomus* (Vucetich 1984). These facts led Vucetich (1989) and Vucetich and Verzi (1993) to interpret that *Eoviscaccia* is more closely related to lagostomines than to chinchillines, and that the loss of some occlusal structures (by reduction or fusion with others) is irreversible once euhypsodonty is achieved because of ontogenetic restrictions associated with hypsodonty. Therefore, a trilaminar pattern cannot be derived from a euhypsodont bilaminar one.

According to the results of the cladistic analysis presented above, *Garridomys*, with protohypsodont [character

1(1)] three-crested pattern [character 4(2)], is the closest sister group of all taxa previously classified within Chinchillidae. Thus, all chinchillids would have diverged from a hypothetical ancestor with non-euhypsodont cheek teeth in which three transverse occlusal elements remained independent during ontogeny, and would potentially have evolved into transverse laminae. Nevertheless, our analysis did not resolve entirely the relationships among the studied chinchillids, providing three alternative hypotheses of the sequences of cheek teeth evolution.

In the hypothesis represented by the cladogram shown in Fig. 7b, the bilaminar pattern [character 4(3)] typifying the lagostomines is the derived condition within Chinchillidae, and supports the monophyly of Lagostominae (including *Eoviscaccia*). The homologies of this bilaminar pattern can be deduced analyzing the dental ontogenetic transformations in *Eoviscaccia*. In the upper cheek teeth, the anterior lamina derives from the protocone-anteroloph crest; the posterior lamina derives from the hypocone-protoloph crest

prematurely merged with the metacone and related structures (the metacone-metaloph-posteroloph complex). In the lower cheek teeth, the posterior lamina belongs to the hypoconid-posterolophid crest; the anterior derives from a combined protoconid-hypolophid crest fused early with the metaconid-metalophulid complex. The compressed valley separating the laminae is not derived from the confluent hypoflexus-paraflexus/hypoflexid-metaflexid, but from an extremely extended hypoflexus/hypoflexid. Based on the evolutionary context represented in Fig. 7b, the homologies of the laminae in *Eoviscaccia* are very likely as in the euhypsodont lagostomines. *Eoviscaccia boliviensis* and *E. australis* document a gradual transition from a protohypsodont to an almost euhypsodont bilaminar pattern (Kramarz 2001b). In *Prolagostomus* the latter pattern is definitively consolidated, but still retained a somewhat complex occlusal design during very juvenile stages. *Lagostomus* represents the extreme expression of this gradient, in which the occlusal surface of the cheek teeth is entirely simplified, even when unworn.

The homologies of the three laminae of the chinchillines cheek teeth cannot be deduced by comparisons with more basal chinchillines, because the paleontological record of the chinchillines is extremely poor and the cheek teeth of the oldest known chinchillas (i.e., from the early Miocene Chucal Formation, northern Chile, Flynn et al. 2002) are essentially as in the extant species. Nevertheless, in this

evolutionary context the chinchilline occlusal pattern is the plesiomorphic condition directly derived from that of *Garridomys* (Fig. 8a). Therefore, the additional laminae of chinchillines cheek teeth would be homologous to the metacone-metaloph-posteroloph complex in the upper teeth and to the metaconid-metalophulid complex in the lower teeth of *Garridomys*. The lagostomines would have acquired the euhypsodont condition independently from chinchillines and after the reduction of one of the ancestral crests, as schematized in Fig. 8a.

This evolutionary scenario agrees with that proposed by Vucetich and Verzi (1993), and implies that lagostomines and chinchillines would have diverged very early in the evolution of the group. The gradual occlusal simplification associated with increasing hypsodonty inferred in lagostomines parallels that documented in early-middle Miocene cavioids (Kramarz 2006a; Pérez and Vucetich 2011). The persistence and rearrangement of ancestral occlusal structures associated with increasing hypsodonty interpreted in chinchillines is also recognized in middle-late Miocene dinomyids (Kramarz 2006b; Nasif 2011). This general evolutionary dental pathway strongly resembles the one known for the late Miocene Octodontidae evolution (Verzi et al. 2011 and literature therein).

Other alternative evolutionary scenarios seem to be less likely to us. In the one represented by the cladogram of Fig. 7d, the trilaminar pattern of chinchillines is the

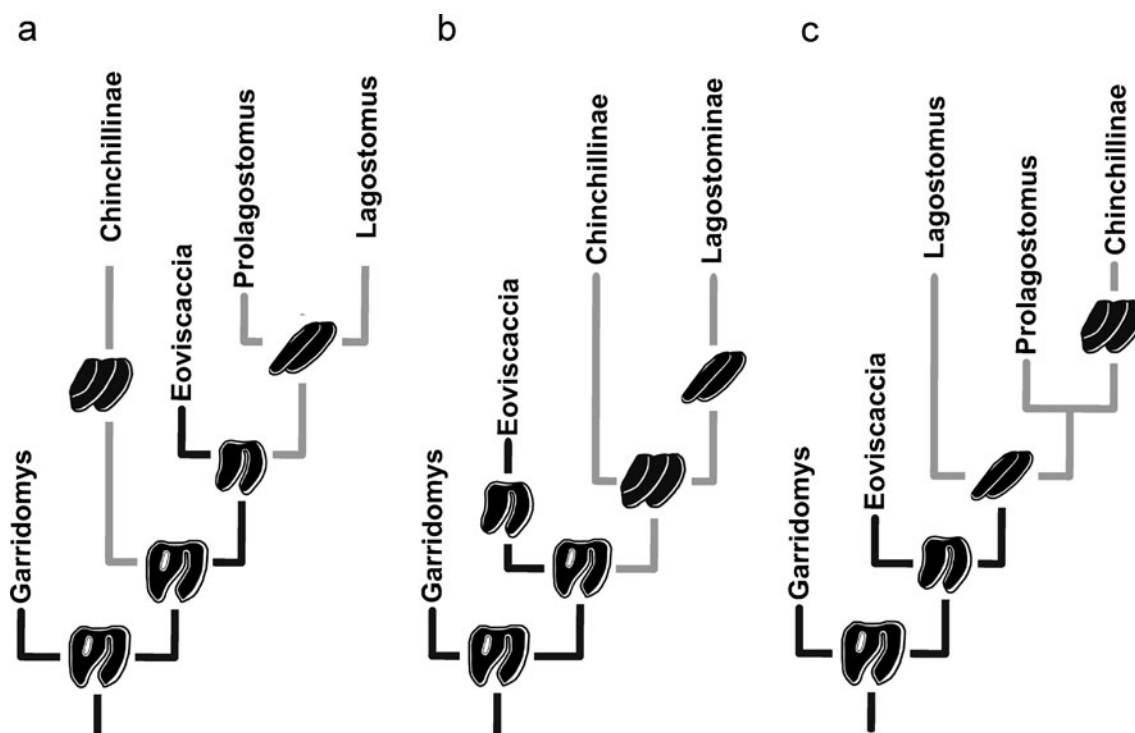


Fig. 8 Schematic trees comparing alternative hypotheses of hypsodonty and occlusal pattern evolution in chinchillids cheek teeth based on the three most parsimonious trees obtained in the cladistic analysis.

a based on cladogram of Fig. 7b; **b** based on cladogram of Fig. 7c with Deltran optimization; **c** based on cladogram of Fig. 7d. Black lines represent protohypsodonty; grey lines represent euhypsodonty

apomorphic condition derived from a lagostomine-like, euhypsodont bilaminar one, as schematized in Fig. 8c. It implies the addition of a new lamina or simple partition of a pre-existing one in a hypothetical chinchilline ancestor with euhypsodont cheek teeth. The concerned process clearly opposes the ontogenetic restrictions proposed by Vucetich and Verzi (1993). However, the development of new structures in euhypsodont intermediate elements (i.e., M1/m1 and M2/m2) was recently demonstrated as occurring in fossil capybaras (Vucetich et al. 2005b), and thus it could be accepted as possible in chinchillids. This alternative evolutionary scenario implies a single acquisition of euhypsodonty among chinchillids, and that the additional lamina of chinchillines is not homologous to any of the three ancestral crests of *Garridomys* (see Fig. 8c). This hypothesis is as parsimonious as the former, although the involved process is apparently an infrequent phenomenon among caviomorphs, and the intermediate stages (i.e., between euhypsodont bilaminar and trilaminar cheek teeth) are still not documented.

In the third most parsimonious phylogenetic hypothesis (Fig. 7c), the optimization of the number of crests (character 4) is ambiguous. According to Acctran optimization, the trilaminar pattern derived from the plesiomorphic bilaminar one, as in the second hypothesis. With Deltran optimization, the euhypsodont bilaminar pattern in *Lagostomus* and *Prolagostomus* is derived from a euhypsodont trilaminar one, whereas in *Eoviscaccia* the protohypsodont bilaminar pattern derives from a protohypsodont trilaminar one, as schematized in Fig. 8b. Therefore, the homologies of these laminae in *Lagostomus* and *Prolagostomus* cannot be interpreted from *Eoviscaccia*. This scenario is incompatible with the tight morphological gradient represented by *Eoviscaccia*–*Prolagostomus* and *Lagostomus*. Alternatively, *Eoviscaccia* would be derived from an ancestor with euhypsodont bilaminar cheek teeth. Nevertheless, this hypothesis is less parsimonious than the former ones, and it would imply a reversion from a euhypsodont to a protohypsodont condition, which is an improbable phenomenon, not documented among caviomorphs.

Concluding Remarks

The new genus and species *Garridomys curunuquem* here described is a small rodent with protohypsodont cheek teeth with rudimentary laminated lobes, heterogeneous thickness of the enamel layer, and P4 fully molarized. These characters are shared with most of the known chinchilloids, supporting the inclusion of the new taxon in this superfamily.

The cladistic analysis based on dental, cranial, and mandibular characters suggests that *Garridomys* represents the

earliest diverging chinchilloid within the clade including modern chinchillas and viscachas and the fossil taxa previously referred to Chinchillidae. All chinchillids would have diverged from a *Garridomys*-like ancestor with three crested, protohypsodont cheek teeth. Additionally, the results provide three equally parsimonious evolutionary hypotheses of Chinchillidae evolution, all supporting the monophyly of Chinchillinae, but only one of them supporting the monophyly of Lagostominae as currently conceived (i.e., *Lagostomus*, *Prolagostomus*, and *Eoviscaccia*). Under this hypothesis, the chinchillines cheek teeth would have evolved from the ancestral condition represented by *Garridomys* directly to a typical euhypsodont trilaminar pattern, whereas lagostomines would have evolved to a more simplified bilaminar one, as interpreted from ontogenetic variations in *Eoviscaccia* (Vucetich 1989). This scenario is here considered as more likely because it agrees with evolutionary patterns documented in other groups of hypsodont caviomorphs. Alternative hypotheses (i.e., chinchillines deriving from a lagostomine-like ancestor or vice versa) are herein considered as less probable, although they should be explored with further evidence.

No chinchilloid is yet known for the Eocene Contamana fauna (Perú, Antoine et al. 2011) and the late Eocene–Oligocene Santa Rosa fauna (Frailey and Campbell 2004), although the affinities of *Eobranisamys* Frailey and Campbell, 2004, should be revised. Similarly, only a partial cheek tooth of a putative chinchilloid is known from the early Oligocene La Cantera fauna (Vucetich et al. 2010). Interesting, *Eoviscaccia*, here interpreted as a lagostomine, occurs in Tinguirirican, Deseadan, and Colhuehuapian levels (Vucetich 1989; Kramarz 2001b; Flynn et al. 2003; Vucetich et al. 2010; Bertrand et al. 2012). These records reveal that chinchillines and lagostomines, if they are correctly interpreted as natural groups, would have diverged in pre-Tinguirirican times. Accordingly, the *Garridomys* and the dinomyid lineages would have diverged even earlier, probably in pre-Oligocene times, although this main chinchilloid radiation is still very scarcely documented in pre-Deseadan faunas.

Acknowledgments We thank A. Garrido (MOZ), A. Forasiepi (Museo de Historia Natural de San Rafael, Mendoza), L. Filippi, S. Saldivia (Museo Carmen Funes, Neuquén), A. Martinelli, and G. Aguirrezabala for their help during the fieldtrips; C. Deschamps for help editing the manuscript; R. Coria (Museo Carmen Funes, Neuquén) and Dirección Provincial de Minería de la Provincia del Neuquén for technical support during fieldworks; and D. Flores (División Mastozoología, MACN) for access to specimens under his care. Special thanks to M. E. Pérez (MEF) for providing electronic photos of UCMP specimens, and F. Tricárico for helping us with the SEM photographs. Two anonymous reviewers improved this work by providing very constructive critical reviews. This work is a contribution to the projects PIP CONICET 6018/05 and 0276/2011, PICT 38112, and UNLP N/568.

References

- Amal M, Kramarz AG (2011) First complete skull of an octodontoid (Rodentia, Caviomorpha) from the Neogene of South America and its bearing in the early evolution of Caviomorpha. *Geobios* 44:235–444
- Bertrand CO, Flynn J, Croft D, Wyss A (2012) Two new taxa (Caviomorpha, Rodentia) from the early Oligocene Tinguiririca Fauna (Chile). *Am Mus Novitates* 3750:1–36
- Bowdich TE (1821) An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers. J. Smith, Paris
- Fields RW (1957) Hystricomorph rodents from the late Miocene of Colombia, South America. *Univ Calif Publ Geol Sci* 32:273–404
- Flynn J, Croft D, Charrier R, Herail G, Wyss A (2002) The first Cenozoic mammal fauna from the Chilean Altiplano. *J Vertebr Palaeontol* 22:200–206
- Flynn J, Swisher CC III (1995) Cenozoic South American Land Mammal Ages: correlation to global geochronologies. In: Berggren WA, Kent DV, Aubry M-P, Hardenbol J (eds) *Geochronology, Time Scales, and Global Stratigraphic Correlation*. SEPM (Society for Sedimentary Geology) Sp Publ No. 54., pp 317–333
- Flynn J, Wyss A, Croft D, Charrier R (2003) The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal 'Age'. *Palaeogeogr Palaeoclimatol Palaeoecol* 195:229–259
- Glanz WE, Anderson S (1990) Notes on Bolivian Mammals. 7. A new species of *Abrocoma* (Rodentia) and relationships of the Abrocomidae. *Am Mus Novitates* 2991:1–32
- Goloboff PA (1993) NONA ver. 2.0. MS-DOS tree-searching program and documentation. Published by the author (<http://www.cladistics.com/aboutnona.htm>).
- Huchon D, Douzery EJ (2001) From the Old to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. *Mol Phylogenet Evol* 20:283–251
- Kraglievich L (1930) La Formación Friasiana del río Frias, río Fénix, laguna Blanca, etcétera, y su fauna de mamíferos. *Physis* 10:127–161
- Kraglievich L (1940) Los roedores extinguidos del grupo Neoepiblemidae. In: Torcelli AJ (ed) *Obras de Geología y Paleontología*, 3. Ministerio de Obras Públicas de la Provincia de Buenos Aires, La Plata, pp 739–764
- Kramarz AG (2001a) Revision of the family Cephalomyidae (Rodentia, Caviomorpha) and new cephalomyids from the early Miocene of Patagonia. *Palaeovertebrata* 30: 51–88
- Kramarz AG (2001b) Registro de *Eoviscaccia* (Rodentia, Chinchillidae) en estratos colhuehuapenses de Patagonia, Argentina. *Ameghiniana* 38:237–242
- Kramarz AG (2005) A primitive cephalomyid hystricognath rodent from the early Miocene of northern Patagonia, Argentina. *Acta Palaeontol Pol* 50:249–258
- Kramarz AG (2006a) Eocardiids (Rodentia, Hystricognathi) from the Pinturas Formation, late early Miocene of Patagonia, Argentina. *J Vertebr Palaeontol* 26:770–778
- Kramarz AG (2006b) *Neoreomys* and *Scleromys* (Rodentia, Hystricognathi) from the Pinturas Formation, late early Miocene of Patagonia, Argentina. *Rev Mus Arg Cien Nat*, NS 8:53–62
- Kramarz A, Garrido A, Forasiepi A, Bond M, Tambussi C (2005) Estratigrafía y vertebrados (Mammalia – Aves) de la Formación Cerro Bandera, Mioceno Temprano de la provincia del Neuquén, Argentina. *Rev Geol Chile* 32:273–291
- Kramarz A, Tejedor M, Forasiepi A, Garrido A (2011) New early Miocene primate fossils from northern Patagonia, Argentina. *J Hum Evol* 62:186–189
- Landry SO (1957) The interrelationships of the New and Old World hystricomorph rodents. *Univ Calif Publ Zool* 56:1–118
- Leanza HA, Hugo CA (1997) Hoja geológica 3969-III Picun Leufú. Boletín N° 218. SEGEMAR, Buenos Aires
- Loomis FB (1914) The Deseado Formation of Patagonia. Rumford Press, Amherst
- MacPhee RDE (2011) Basicranial morphology and relationships of Antillean Heptaxodontidae (Rodentia, Ctenohystrica, Caviomorpha). *Bull Am Mus Nat Hist* 363:1–70
- Nasif NL (2011) Los Dinomyidae (Rodentia, Caviomorpha) del Mioceno superior del Noroeste argentino. Su anatomía craneo-dentaria. Ph.D dissertation. Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán
- Patterson B, Wood AE (1982) Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bull Mus Comp Zool* 149:371–543
- Pérez ME (2010) A new rodent (Cavioidea, Hystricognathi) from the middle Miocene of Patagonia, mandibular homologies, and the origin of the crown group Cavioidea *sensu stricto*. *J Vertebr Palaeontol* 30:1848–1859
- Pérez ME, Vucetich MG (2011) A revision of the fossil genus *Phanomys* Ameghino, 1887 (Rodentia, Hystricognathi, Cavioidea) from the early Miocene of Patagonia (Argentina) and the acquisition of euhypsodonty in Cavioidea *sensu stricto*. *Palaeontol Z*. doi 10.1007/s12542-011-0120-2
- Rinderknecht A, Bostelmann E, Ubilla M (2011) New genus of giant Dinomyidae (Rodentia: Hystricognathi: Caviomorpha) from the late Miocene of Uruguay. *J Mammal* 92:169–178.
- Sánchez-Villagra MR, Aguilera O, Horovitz I 2003. The anatomy of the world's largest extinct rodent. *Science* 301:1708–1710.
- Simpson GG (1945) The principles of classification and a classification of Mammals. *Bull Am Mus Nat Hist* 85:i-xvi +1–350
- Tullberg T (1899) Ueber das System der Nagethiere: eine phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 3:1–514
- Verzi DH, Vieytes EC, Montalvo CI (2011) Dental evolution in *Neophanomys* (Rodentia, Octodontidae) from the late Miocene of central Argentina. *Geobios* 44: 621–633
- Vucetich MG (1984) Los roedores Hystricognathi del Mioceno temprano de Patagonia. Resúmenes I Jornadas Argentina de Paleontología de Vertebrados: 24
- Vucetich MG (1985) *Cephalomyopsis hipselodontus* gen. et sp. nov. (Rodentia, Caviomorpha, Cephalomyidae) de la Edad Colhuehuapense (Oligoceno tardío) de Chubut, Argentina. *Ameghiniana* 22:243–245
- Vucetich MG (1989) Rodents (Mammalia) of the Lacayani fauna revisited (Deseadan, Bolivia). Comparison with new Chinchillidae and Cephalomyidae from Argentina. *Bull Mus Natl Hist Nat* 4C 11:233–247
- Vucetich MG, Verzi DH (1993) Un nuevo Chinchillidae del Colhuehuapense (Mioceno Inferior?) de Gaiman (Chubut): su aporte a la comprensión de la dicotomía vizcachas - chinchillas. Resúmenes IX Jornadas Argentinas de Paleontología de Vertebrados, Ameghiniana 30:115
- Vucetich MG, Deschamps CM, Olivares AI, Dozo MT (2005b) Capybaras, size, shape, and time: a model kit. *Acta Palaeontol Pol* 50:259–272
- Vucetich MG, Kramarz AG, Candela AM (2010) The Colhuehuapian rodents from Gran Barranca and other Patagonian localities: the state of the art. In: Madden R, Carlini A, Vucetich MG, Kay R (eds) *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic*. Cambridge University Press, Cambridge, pp 206–219

- Vucetich MG, Vieytes EC, Verzi D, Noriega J, Tonni EP (2005a) Unexpected primitive rodents in the Quaternary of Argentina. *J S Am Earth Sci* 20:57-64
- Walton AH (1997) Rodents. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C., pp 392-409
- Wood AE, Patterson B (1959). Rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bull Mus Comp Zool* 120:281-428
- Woods CA, Howland EB (1979) Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. *J Mammal* 60:95-116