

New rodents (Mammalia) from the late Oligocene of Cabeza Blanca (Chubut) and the first rodent radiation in Patagonia

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Caviomorph rodents, the New World Hystricognathi, are one of the most characteristic groups of South American mammals. Although they have been in the continent at least since the middle Eocene, those of the Deseadan Land mammal Age (early–late Oligocene) are the best source to understanding their early history due of their good record, large geographic distribution and good temporal calibration of many of the local faunas. Here, we describe the following new taxa from the classical locality of Cabeza Blanca: Octodontoidea Acaremyidae *Galileomys baios* n. sp., Octodontoidea incertae sedis *Ethelomys loomisi* n. gen., n. comb., *Acarechimys leucotheae* n. sp., *Protacaremys? adilos* n. sp., Chinchilloidea incertae sedis *Loncolicu tretos* n. gen., n. sp., *Incamys menniorum* n. sp., Caviomorpha incertae sedis *Llitun notuca* n. gen., n. sp., *Leucocephalos zeffiae* n. gen., n. sp. and Cephalomyidae *Cephalomys ceciae* n. sp. The DP4 of an ‘eocardiid’, *Asteromys punctus?* is described for the first time. These new taxa allow us to reinterpret the relationships of some of the previously known Deseadan species and genera. They show a great early diversification at least for extra Andean Patagonia, involving at least three of the main caviomorph lineages: octodontoids, chinchilloids and cavioids.

Keywords: Caviomorpha; taxonomy; South America; Deseadan SALMA; Cenozoic

Introduction

Caviomorph rodents, the New World Hystricognathi, are one of the most characteristic groups of South American mammals. Modern representatives are very diverse in dietary and locomotor adaptation, inhabit a broad range of ecosystems and have a great morphological disparity, as well as the broadest range of body size within Rodentia (Mares and Ojeda 1982; Woods 1984; Eisenberg and Redford 2000). They are usually subdivided into four superfamilies: Erethizontoidea (porcupines), Cavoidea (agouties, cavies and capybaras), Chinchilloidea (chinchillas, viscachas and pacaranas) and Octodontoidea (tucutucos, spiny rats, coypus and chinchilla rats) (e.g. Patterson and Wood 1982). New data suggest that caviomorphs have been in the continent at least since the middle Eocene (Contamana, Peru, Figure 1; Antoine et al. 2012), and by the late Eocene–early Oligocene they were already differentiated in these four major clades (Frailey and Campbell 2004; Vucetich, Vieytes, et al. 2010; Arnal et al. in press). They were also widely distributed in the continent at least since the early Oligocene (Figure 1; Wyss et al. 1993; Frailey and Campbell 2004; Vucetich, Vieytes, et al. 2010; Bertrand et al. 2012). However, given the characteristics of the caviomorph record from the interval middle Eocene–early Oligocene – very scarce and/or poorly time-calibrated – the Deseadan South American Land mammal Age (SALMA), referred to the late–early

Oligocene–late Oligocene (Dunn et al. 2013), is still a key moment for the knowledge of the early evolutionary history of the group. It is since this period that the caviomorph fossil record becomes abundant and diverse (Wood and Patterson 1959; Lavocat 1976; Patterson and Wood 1982; Vucetich 1989). Hence, the study of the taxonomic diversity of the Deseadan rodents is essential for the understanding of basic issues concerning the differentiation, early diversification and biogeographic history of the group.

Although Deseadan rodents are geographically widely represented (Figure 1; Kraglievich 1932; Hoffstetter and Lavocat 1970; Lavocat 1976; Gorroño et al. 1979; Mones and Castiglioni 1979; Patterson and Wood 1982; Vucetich 1989; Vucetich, Souza Cunha, et al. 1993; Bond et al. 1998; Vucetich and Ribeiro 2003; Shockey et al. 2009), most of the species and about two-thirds of the genera come from localities in extra-Andean Patagonia (Argentina), especially from the classical localities of Cabeza Blanca and La Flecha (Chubut, Figure 1; Loomis 1914; Wood and Patterson 1959).

About 30 species have been described for the Deseadan (Table 1), but new taxonomic and phylogenetic studies (Arnal 2012; Pérez and Pol 2012; Pérez et al. 2012; Vucetich et al. in press) strongly suggest that the Deseadan diversity has been underestimated, and that Deseadan rodent assemblages were richer and more diverse than currently known.

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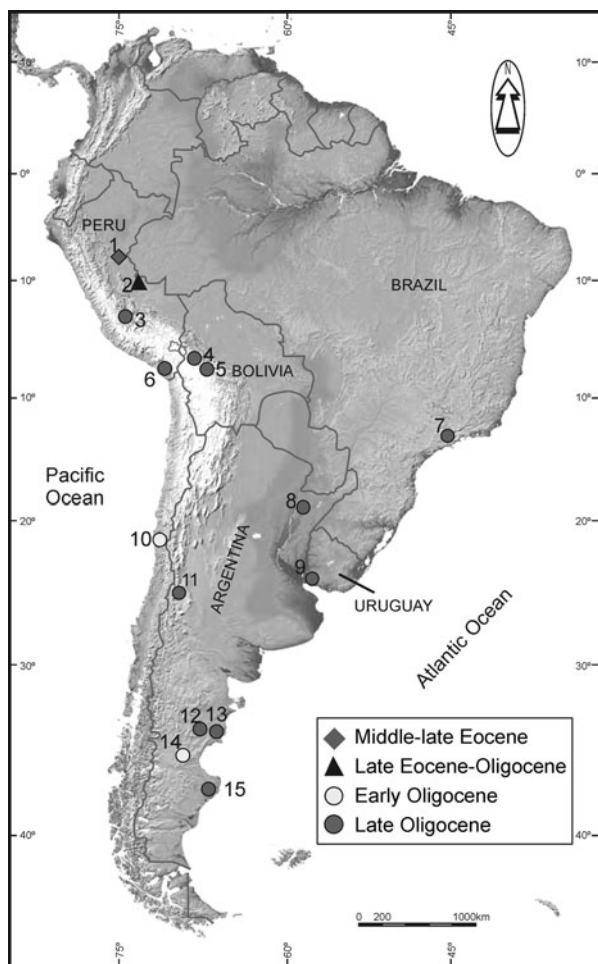


Figure 1. Location map with localities mentioned in the text. 1, Contamana; 2, Santa Rosa; 3, Lircay; 4, Lacayani; 5, Salla-Luribay; 6, Moquegua; 7, Taubate Basin; 8, Arroyo Avalos; 9, Nueva Palmira; 10, Tinguiririca; 11, Quebrada Fiera; 12, Scarritt Pocket; 13, Cabeza Blanca; 14, La Cantera, Gran Barranca; 15, La Flecha.

In this paper, we continue the study of this diversity undertaken some years ago (Vucetich 1989; Vucetich, Souza Cunha, et al. 1993; Vucetich and Ribeiro 2003; Pérez and Vucetich 2011; Pérez et al. 2012; Vucetich et al. *in press*) through the description of new caviomorph taxa from Cabeza Blanca, as well as the addition of new data of poorly known species. Cabeza Blanca has yielded the largest amount of Deseadan caviomorph taxa, and most of the Patagonian representatives have been recorded there. The rodent fauna of this locality, with 12 species (Table 1), was also the richest rodent Paleogene local fauna only surpassed by the fauna of Santa Rosa (Peru, late Eocene–early Oligocene?) for which 17 species have been described (Frailey and Campbell 2004). With this work, we aimed to contribute to the knowledge of caviomorph

taxonomic diversity during the Oligocene, and to make a preliminary assessment of its meaning in the understanding of the early evolutionary history of caviomorph rodents.

Material and nomenclature

All the material described in this paper comes from the upper levels of the Sarmiento Formation at Cabeza Blanca (Chubut Province, Escalante Department, at 45°13'S and 67°28'W; Feruglio 1949; Sciutto et al. 2000; Figure 1). These levels, also known as the beds with *Pyrotherium*, are grey and yellowish tuffs with grey sandy and conglomerate levels partly stratified, between 24 and 31 m thick. These levels overlay discordantly the beds with *Notostylops* and are topped by marine levels of the Patagoniense (Feruglio 1949). The materials were collected on the surface during several field trips in 1993, 1998 and 2005 by personal of the Laboratory of Paleontology of CENPAT (Puerto Madryn, Chubut), and in 1997 by A. Carlini and M. Reguero (Museo de La Plata).

Due to the scantiness and fragmentary nature of the studied materials, and the controversial results of new phylogenetic analyses, family categories are not used for the taxa described here, with two exceptions, Acaremyiidae, the relationships of which have been recently tested with phylogenetic analyses (Vucetich and Kramarz 2003; Arnal 2012; Arnal and Pérez 2013; Arnal et al. *in press*; Vucetich et al. *in press*), and the peculiar Cephalomyiidae of uncertain affinities within Caviomorpha.

Institutional abbreviations

ACM, Beneski Museum of Natural History, Amherst College (USA); MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Buenos Aires, Argentina); MPEF-PV, Museo Paleontológico Egidio Feruglio, Paleovertebrate Collection (Trelew, Argentina).

Dental nomenclature

Dental nomenclature (Figure 2) follows Marivaux et al. (2004), Candela and Rasia (2012) and Arnal et al. (*in press*).

Dental measurements

AP, anteroposterior length; AW, anterior width; PW, posterior width; ACh, anterior crown height (measured on protocone/id); PCh, posterior crown height (measured on hypocone/id); Hh, hypoflexus/id height; Hi, hypsodont index.

Table 1. Rodent species distribution among main Deseadan localities.

Taxa	Argentina					Bolivia			Brazil	Peru	Uruguay	Ref
	Cabeza Blanca	La Flecha	Scarritt Pockett	Laguna de los Machos	Punta Navas	Arroyo Ávalos	Lacayani	Salla	Taubaté	Moquegua	Nueva Palmira	
<i>Platypitomyys brachyodon</i>			X									1
Gen. et sp. nov.			X									2
<i>Gatileomys batos</i> sp. nov.	X											3
<i>Ethelomys loomisi</i> gen. et comb. nov.	X											3,4
<i>Xylechomys obliquus</i>				X								5
<i>Deseadomys arambourgi</i>	X											4
<i>Protacaremys? adilos</i> sp. nov.	X	X										3
<i>Acarechimys leucotheae</i> sp. nov.	X											3
<i>Sallamys pascuali</i>								X				6
<i>Sallamys quispea</i>										X		7
<i>Sallamys? minutes</i>									X			8
<i>Migraeramus beatus</i>								X				9
<i>Litini notuca</i> gen. et sp. nov.	X											3
<i>Leucocephalos zeffiae</i> gen. et sp. nov.	X											3
<i>Eoiscaccia boliviana</i>	X						X					10
<i>Eoiscaccia australis</i>	X											10
<i>Eoiscaccia</i> sp.	X					X						11
<i>Scotamys antiquus</i>	X	X										12
<i>Incamys bolivianus</i>	X									X		6
<i>Incamys menniorum</i> sp. nov.	X											3
<i>Asteromys punctus</i>	X											13
<i>Chubutomys simpsoni</i>	X	X										4
<i>Chubutomys naraensis</i>	X	X										14
<i>Protosteiromys medianu</i>	X	X			X							4
<i>Protosteiromys asmodeophilus</i>	X	X										4
<i>Paulacoutomys paulista</i>												15
aff. <i>Neoreomys</i>												9
<i>Branisamys luribayensi</i>										X		6
<i>Cephalomyopsis</i> morphotype 2												10,2
* <i>Cephalomyopsis</i> morphotype 3	X								X			10,2
* <i>Cephalomyopsis</i> sp.												11
<i>Cephalomys arcidens</i>	X	X										13
<i>Cephalomys plexus</i>	X	X										13
<i>Cephalomys ceciae</i> sp. nov.	X											3
<i>Cephalomys bolivianus</i>	X									X		16
<i>Litodontomys chubutensis</i>	X											12
<i>Loncolicu tretos</i> gen. et sp. nov.	X											3
<i>Luribayomys masticator</i>								X				16
<i>Palmiramys waltheri</i>											X	17

References: 1. Wood, 1949; 2. Vucetich et al., in press; 3. This paper; 4. Wood and Patterson, 1959; 5. Patterson and Pascual, 1968; 6. Hoffstetter and Lavocat, 1970; 7. Shockey et al., 2009; 8. Vucetich and Ribeiro, 2003; 9. Patterson and Wood, 1982; 10. Vucetich, 1989; 11. Bond et al., 1998; 12. Loomis, 1911; 12. Ameghino, 1897; 14. Perez et al., 2012; 15. Vucetich et al., 1993b; 16. Lavocat, 1976; 17. Kraglievich, 1932.

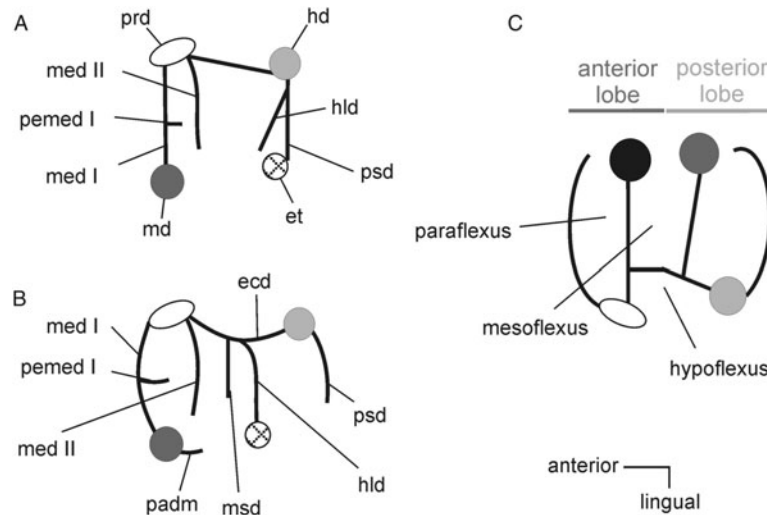


Figure 2. Dental nomenclature. (A) Lower permanent premolar. (B) Lower molar and deciduous premolar. *Abbreviations:* ecd, ectolophid; et, entoconid; hd, hypoconid; hld, hypolophid; md, metaconid; med I, metalophulid I; med II, metalophulid II; msd, mesolophid; padm, posterior arm of the protoconid; pemed I, posterior extension of the metalophulid I; prd, protoconid; psd, posterolophid. (C) Upper molariforms.

Historical background

The first Deseadan rodents were described by Ameghino (1897) based on materials from his ‘couches à *Pyrotherium*’ cropping out at Cabeza Blanca (Figure 1). Later, Loomis (1914) added two new species to this fauna, and Wood (1949) described the first Deseadan rodent from Scarritt Pocket (Chubut, Figure 1). It was not until 10 years later that Wood and Patterson (1959) published their extensive revision of the Patagonian Deseadan rodents having studied most of the specimens then known, deposited in collections of Europe, USA and Argentina. They described seven new species for Cabeza Blanca, and mentioned for the first time the rodents from La Flecha (Santa Cruz, Figure 1), considered the type locality of the Deseadan SALMA (Palma and Clark 1990). Meanwhile, a few other rodents had been described from Patagonia and Uruguay (Kraglievich 1932; Patterson and Pascual 1968; Mones and Castiglioni 1979). Posteriorly, Deseadan rodents were described from intertropical areas in Bolivia (Salla and Lacayani; Hoffstetter and Lavocat 1970; Hoffstetter et al. 1971; Lavocat 1976; Patterson and Wood 1982; Vucetich 1989) and Brazil (Taubaté; Vucetich, Souza Cunha, et al. 1993; Vucetich and Ribeiro 2003), highlighting important differences in composition between the faunas of Patagonia and those from Salla and Brazil.

For a long time, Deseadan caviomorphs were the oldest South American rodents, although it was clear that, due to their great diversification and disparity, the moment of entrance into the continent had been much earlier: Deseadan rodents display a variety of tooth morphologies

from brachyodont and bunolophodont to euhypsodont with highly simplified occlusal surface. The first caviomorphs older than Deseadan were reported by Wyss et al. (1993) for the latest Eocene–early Oligocene? fauna of Tinguiririca (Chile; Figure 1). Later, Frailey and Campbell (2004) described the rich fauna of Santa Rosa (Peru; Figure 1) late Eocene–early Oligocene? in age, showing an important diversity of taxa within a relatively monotonous brachyodont and bunolophodont tooth morphology. Vucetich, Vieytes, et al. (2010) described the early Oligocene rodent faunule of La Cantera (Figure 1), the oldest rodents in Patagonia, somewhat younger than those of Tinguiririca, but clearly older than the Deseadan rodents (Dunn et al. 2013). Another important contribution to the understanding of the early evolution of caviomorphs was the description of the middle Eocene rodents of Contamana (Peru; Figure 1; Antoine et al. 2012) that allows a refreshing perspective of the early evolution of this group of rodents.

Recently, new Deseadan rodents have been described for Peru (Shockey et al. 2009) and Patagonia (Pérez et al. 2012; Vucetich et al. *in press*), although Cabeza Blanca is still the locality with the highest richness and diversity of caviomorphs for the concerned interval.

Systematic palaeontology

Order **Rodentia** Bowdich, 1821

Infraorder **Caviomorpha** Wood and Patterson, 1955
(in Wood 1955)

Superfamily **Octodontoidea** Waterhouse, 1839

Family ACAREMYIDAE Wood, 1949

Genus *Galileomys* Vucetich and Kramarz, 2003

Type species. *Galileomys antelucanus* Vucetich and Kramarz, 2003.

Species content. The type species, *Galileomys? colloncurensis* Vucetich and Kramarz, 2003 and *Galileomys eurygnathus* Kramarz, 2004.

Horizon and locality. Upper levels of the Sarmiento Formation at Cabeza Blanca, Pinturas and Collón Cura formations (early to middle Miocene) from Patagonia.

Diagnosis. Small-to-medium size Octodontoid, with crowns lower than in *Acaremys*. Cheek teeth terraced; the labial cusps of the upper teeth and the lingual cusps of the lower teeth are bulky, thicker and higher than their corresponding crests. As in *Platypittamys*, mesolophid (= metalophulid II) and posterolophid not reaching the lingual margin of the lower molars. Lower premolars with a flexid on the anterior face that separates the metaconid from the protoconid, as in *Deseadomys* and *Asteromys*. Hypoflexid of the P4 superficial. The fossette for the

insertion of the tendon of the M. Masseter medialis pars infraorbitalis is less marked than in *Sciamys* and *Acaremys*, but much more than in *Platypittamys* (Vucetich and Kramarz 2003).

Galileomys baios n. sp.

(Figure 3, Table 2)

Holotype. MPEF-PV 10676, left mandibular fragment with p4-m2, a root of m3 and the incisor.

Etymology. From the Greek *baios* = small, in reference to the small size of the species.

Diagnosis. Size about 30% smaller than *G. antelucanus*; cheek teeth brachyodont as in *Platypittamys* Wood, 1949 and *G. antelucanus*; p4 with slightly indented anterior wall even with strong wear; m1-m2 with metalophulid II short but separated from the metalophulid I producing a trigonid anteroposteriorly longer and more triangular in shape than in the other acaremyids; lower incisor conspicuously large.

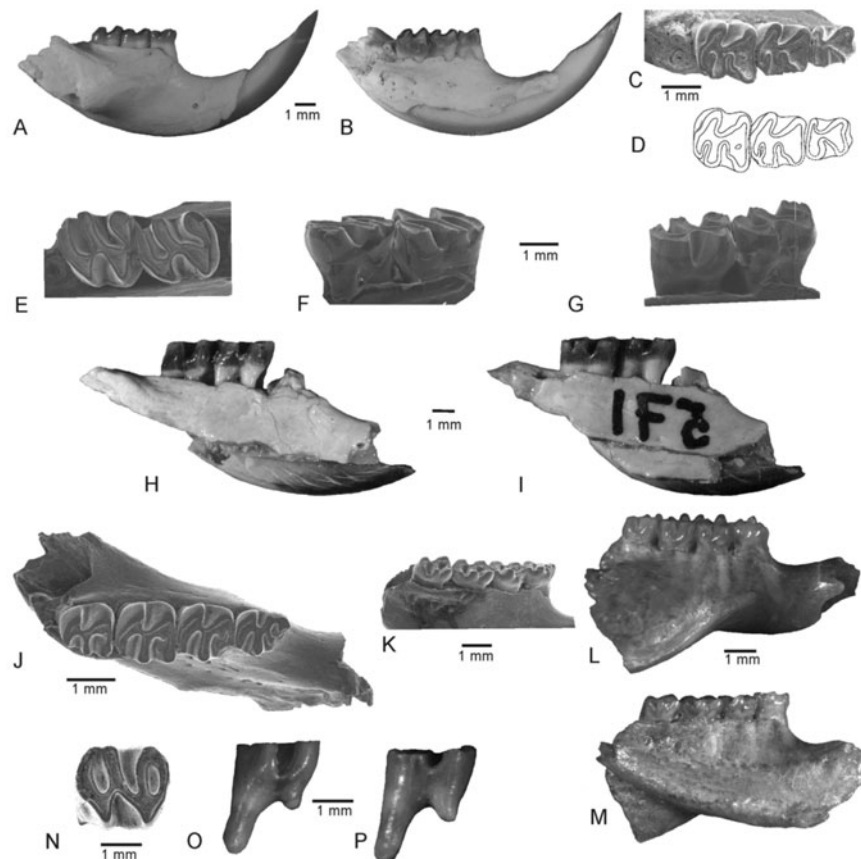


Figure 3. Octodontoids. *G. baios* n. sp. MPEF-PV 10676 holotype left mandible: (A) labial view (reversed); (B) lingual view; (C) p4-m2 occlusal view; (D) scheme of p4-m2. *E. loomisi* n. gen., n. comb. MPEF-PV 571 right mandible: (E) m1-m2 occlusal view; (F) m1-m2 lingual view; (G) m1-m2 labial view; (H) mandible external view; (I) mandible internal view (reversed). *A. leucotheae* n. sp. MPEF-PV 10677 holotype left mandible with p4-m3: (J) occlusal view; (K) p4-m3 labial view; (L) mandible external view (reversed); (M) mandible internal view. *P.? adilos* n. sp. MPEF-PV 10678 holotype right m1 or m2: (N) occlusal view; (O) labial view; (P) lingual view (reversed). Anterior to the right.

Table 2. Dental measurements of new taxa of Octodontoidea and Caviomorpha incertae sedis.

	Incisor		p4			m1			m2			m3		
	AP	W	AP	AW	PW	AP	AW	PW	AP	AW	PW	AP	AW	PW
<i>G. baios</i>														
MPEF-PV 10676	2.68	1.46	1.11	0.92	1.11	1.40	1.26	1.48	1.44	1.48	1.48			
<i>E. loomisi</i>														
MPEF-PV 571	1.6	1.34				2.47	2.07	2.07	2.52	2.33	2.29			
<i>A. leucotheae</i>														
MPEF-PV 10677			2.26	1.34	>1.77	2.26	~1.83	1.95	2.32	1.77	1.83	2.07	1.47	1.46
<i>L. notuca</i>														
MPEF-PV 10679	2.44	2.13	1.48	1.04	1.48	1.74	1.29	1.77	1.55	1.52	1.59			
<i>L. zeffiae</i>														
MPEF 585			1.52	1.07	1.41	1.85	1.70	1.74	1.99	1.92	1.88			
MPEF-PV 10680			1.66	1.48	1.74									
MPEF 583	1.85	1.22	1.81	1.55	1.7	1.88	1.66	1.7	2.03	2.15	2.07			
MPEF 584	1.7	0.89	1.48	1.26	1.59	1.85	1.66	1.78						
MPEF 586			1.66	1.41	1.55	1.81	1.66	1.52	1.88	1.96	1.92	1.81	1.78	1.34

Referred material. Only the holotype.

Horizon and locality. Upper levels of the Sarmiento Formation at Cabeza Blanca (late Oligocene).

Description and comparison

This is the smallest acaremyid so far known. A very notorious character is the conspicuously large but very slender lower incisor (Figure 3(A),(B)), larger than in any other acaremyid. Its anteroposterior length is only a little shorter than the p4–m1 length (Table 2). The anterior tip is well above the cheek tooth series, and the posterior end is behind the m3. The mandible is broken at this place but apparently the bottom of the incisor socket could be located above and external to the m3 (Figure 3(B)). The anterior face is very curved, but forms a right angle with the medial wall. The enamel layer is thick. It has little extension on the lateral walls. The occlusal surface is long and very narrow.

The p4 is smaller than m1 and m2 (Table 2). The anterior wall is concave (Figure 1(C),(D)), but the anterior groove is less deep than those of *G. antelucanus* and *G. eurygnathus* in the same stage of wear. The ectolophid is very short. The posterior lophid has a very small and narrow labial end and a much larger lingual portion, suggesting the presence of a hypolophid completely fused to the posterolophid, at least at this stage of wear.

The m1 and m2 have a relatively short metalophulid II which does not reach the lingual side of the tooth, and its lingual end can be seen as a ledge in the posterior face of the anterior wall. At this stage of wear, the metalophulid II is almost completely fused with the metalophulid I in such way that only a minute anterofossettid persists in m2. These characteristics of metalophulid I and II led to a more triangular and long anteroposterior anterior lobe, instead of the oval one present in the other species of *Galileomys*

at the same stage of wear. The posterolophid is short, as in *G. antelucanus*, i.e. shorter than in *Sciamys* Ameghino, 1887 and *Acaremys* Ameghino, 1887; between the hypoconid and the posterolophid, there is a conspicuous constriction. The hypoflexid is slightly more oblique than in the other species.

The mental foramen is, as in other acaremyids, large and near the midpoint of the height of the diastema (Figure 3(A)). The anterior portion of the masseteric fossa is deep, but somewhat shallower than in *G. antelucanus*, *G. eurygnathus* and *Acaremys murinus* Ameghino, 1887; the beginning of the masseteric crest together with the notch for the tendon of the masseter medialis pars infraorbitalis forms a robust structure. The base of the coronoid process is at the posterior portion of m2. There is a wide retromolar fossa, laterally to m2–m3.

Comments. *Galileomys baios* differs from *Platypittamys brachyodon* Wood, 1949, a Deseadan putative acaremyid, in the comparatively shorter p4 (probably with a well-developed hypolophid), a shorter metalophulid II in m1–m2, larger incisor and smaller size. It differs from all other Deseadan acaremyids (Vucetich et al. in press) by its smaller size and evident lower crown height.

The acaremyids are a monophyletic group with controversial relationships within the Octodontoidea. We consider them as a basal lineage of Octodontoidea not closely related to modern Octodontidae and Echimyidae (Vucetich and Kramarz 2003; Arnal and Pérez 2013; Vucetich et al. in press; Arnal and Vucetich 2013; but see Verzi et al. in press). Acaremyids are represented from the Deseadan to post-Colloncuran of Patagonia, and are considered an austral radiation of octodontoids with protohypsodont eight-shaped cheek tooth morphology, which is homoplastic with Octodontidae (Arnal and Vucetich 2013).

Octodontoidea incertae sedis***Ethelomys* n. gen.**

Deseadomys Wood and Patterson, 1959, pp. 310–312, in part.

Type and only species. *Ethelomys loomisi* n. comb.

Etymology. From the Greek ethelos = wished, and mys = rodent, a Greek version of ‘Deseadomys’.

Horizon and locality. Upper levels of the Sarmiento Formation (late Oligocene), at Cabeza Blanca.

Diagnosis. As for the type and only species of the genus.

***Ethelomys loomisi* (Wood and Patterson, 1959) n. comb.**
(Figure 3, Table 2)

Deseadomys loomisi Wood and Patterson, 1959:310–312.

Holotype. ACM 3087, right mandibular fragment with m1–m2.

Emended diagnosis. Small caviomorph, with slightly hypsodont and trilophodont m1–m2; moderately oblique hypolophid; metalophulid I drop-shaped with a feeble connection with the protoconid; anterior-most lingual flexid wide; posterior-most lingual flexid shallower and narrower than the anterior-most lingual flexid, and closing before the anterior-most flexid; hypoflexid long extending almost to the middle of the occlusal surface width; protoconid, ectolophid and hypolophid not completely aligned; lower incisor short with the posterior end of the alveolus below m2; mental foramen well ahead of the first tooth and in the upper half of the diastema height; diastema shallow.

Referred material. MPEF-PV 571, right mandibular fragment with m1–m2 and the incisor.

Horizon and locality. As for the genus.

Description and comparisons. The material here described is very similar to the holotype and only specimen of the new combination *E. loomisi*, and differs from *Deseadomys arambourgi* by the absence of metalophulid II, the presence of thicker lophids and a shorter incisor, as well as a larger size. It is the second-known specimen of this species and is also a fragmentary jaw with m1–m2 (Wood and Patterson 1959), but from an older individual (Figure 3(E)–(G)). The m1–m2 are slightly hypsodont, and trilophodont. A slight thickening on the ectolophid of m1 marks the place of the metalophulid II (or the mesolophid). This thickening is less evident in the holotype; it is absent in the m2 of both specimens. The lingual portion of the metalophulid I is drop-shaped especially in the new specimen. MPEF-PV 571, the new specimen, has some differences with the holotype. In m1, the hypolophid is longer, as long as the metalophulid I, whereas the posterolophid is shorter than the metalophulid I and the hypolophid in both m1 and m2. These differences are probably due to differences in the

ontogenetic age of the specimens and/or individual variation.

The incisor is short, being its posterior end below m2 as in the Santacrucian (early Miocene) octodontoid *Stichomys* Ameghino, 1887. The lower incisor is also short in several fossil octodontoids: in *Maruchito* Vucetich et al., 1993a reaches up to the anterior part of m2, in *Spaniomys* Ameghino, 1887 (an abrocomid *sensu* Verzi et al. *in press*) and *Stichomys* Ameghino, 1887 up to the posterior part of m2, in *Xylechimys* Patterson and Pascual, 1968 up to m2, whereas in *Adelphomys* Ameghino, 1887 it is long, extending up to a point external and posterior to the m3. The enamel layer is very thin.

MPEF-PV 571 has an ‘essentially plane’ (Wood and Patterson 1959:312) diastema resembling that of the holotype; the mental foramen is large and well ahead of the alveolus of the first cheek tooth (Figure 3(H),(I)). Although the notch for the tendon of the masseter medialis pars infraorbitalis is not preserved in MPEF-PV 571, the holotype shows that it is oblique and continuous with the masseteric crest. The masseteric fossa is shallow. The sulcus between the notch and the base of the coronoid process (lateral crest *sensu* Woods 1972) is evident. The base of the coronoid process begins at the level of the anterior portion of m3.

E. loomisi shares trilophodont lower molars with oblique lophids with other fossil octodontoids grouped in the subfamily Adelphomyinae (*sensu* Patterson and Pascual 1968) (although for some phylogenetic analyses (Arnal 2012) this subfamily is paraphyletic). It differs from *Xylechimys* in the absence of metalophulid II and less sinuous lophids; from *Eodelphomys* Frailey and Campbell, 2004 in its smaller size and less oblique lophids; from *Paradelphomys* Patterson and Pascual, 1968 in the presence of ectolophid and more curve lophids; from *Ricardomys* Walton, 1997 in the less anteroposteriorly enlarged m1–m2 and the transversely longer hypoflexid; from *Quebradahondomys* Croft et al., 2011 in its thicker metalophulid I, more slender posterolophid, different morphology of the anterior flexid in m1–m2, protoconid, ectolophid and hypolophid not aligned, deeper hypoflexid and a very shallow diastema; from *Stichomys* and *Adelphomys*, by the lower crowned cheek teeth, less oblique lophids with rounded ends, hypoflexid posteriorly directed and smaller size; from *Prostichomys* Kramarz, 2001a by the absence of metalophulid II.

Comments. *E. loomisi* was originally described as the second species of the genus *Deseadomys*, but it differs from *D. arambourgi* – the type and single species of *Deseadomys* in our opinion – in several characters (see Description and comparisons) that indicate it represents a different lineage. *Deseadomys* was originally described as an echimyid and the same result was obtained by Verzi et al. (*in press*). Alternatively, Arnal (2012) proposed that ‘*D. loomisi* is not closely related to *D. arambourgi*, which

instead resulted as the basal-most octodontoid in her analyses (see also Arnal et al. [in press](#)); in the same analyses '*D. loomisi*' resulted as more closely related to *Stichomys*, *Spaniomys*, *Xylechimys* and *Prostichomys* (adelphomyines *sensu* Patterson and Pascual, 1968), hypothesis that we follow here.

Genus *Acarechimys* Patterson in Patterson and Wood, 1982

Type species. Acarechimys minutus (Ameghino, 1887).

Species content. The type species and *Acarechimys minutissimus* (Ameghino, 1887), *Acarechimys constans* (Ameghino, 1887), *Acarechimys pulchellus* (Ameghino, 1902), plus several mentions of the genus without species assignment (Vucetich, Mazzoni, et al. 1993; Walton 1997; Flynn, Novacek, et al. 2002, 2008; Kramarz et al. 2004; Croft et al. 2011).

Horizon and locality. Sarmiento, Pinturas, Santa Cruz, Collón Cura and Chichinales formations (early to middle Miocene), Patagonia; Chucal, unnamed formation of Pampa Castillo, Curá-Mallín formations (early to middle Miocene), Chile; Villavieja Formation (middle Miocene), Colombia; unnamed formation of Quebrada Honda (middle Miocene), Bolivia.

Emended diagnosis. Small-to-very small octodontoids. Higher crown molariforms than in *Protacaremys*. Evidenced cusps and thin crests separated by wide flexi. Retention of the deciduous premolars. Upper molars with four straight crests; the antero- and posteroloph fused labially in juveniles with proto- and metaloph delimiting the para- and the posterofossette respectively. Lower molars with accessory cusp behind metalophulid I; metalophulid II variably developed: interrupted or absent on m1–m2, absent or interrupted on m3. Lower deciduous premolar with variably developed metalophulid II and mesolophid fused with the metaconid. Well-developed masseteric crest in the mandible and masseteric fossa anteriorly deep or very deep (Arnal 2012).

Acarechimys leucotheae n. sp.

(Figure 3, Table 2)

Holotype and only specimen. MPEF-PV 10677, left mandibular fragment with the incisor and dp4–m3.

Etymology. From the Greek *Leucothea*, the white goddess who gave Ulysses her peplos to help him to arrive to Ithaca, also making reference to the name of the locality, Cabeza Blanca (White Head in Spanish).

Diagnosis. Small species, within the size range of *A. minutissimus*. Cheek teeth brachyodont and terraced more evident than in the other species of the genus; m1–m3 with posterolophid more transverse than in the other species, with the consequent greater opening of the

posteroflexid; dp4 with the ectolophid conspicuously separated from the protoconid, very oblique, more transverse to the anteroposterior axis of the tooth than in the other species of the genus, metalophulid II very short; m1–m3 with three crests plus a very short metalophulid II unlike the other species of the genus; the notch for the insertion of tendon of the masseter medialis pars infraorbitalis is more oblique than in the remaining species; mental foramen absent, unlike *A. constans* and *A. minutus*.

Description and comparisons

Species smaller than *A. minutus*, *A. constans* and *A. pulchellus*. Cheek teeth brachyodont and terraced, with the metaconid and entoconid higher than the other cusps and crests, this character being more evident than in the other species of the genus (Figure 3(K)).

The dp4 is as long as m1 but slightly narrower (Table 2). Although damaged in its anterior portion, it can be seen it is formed by five lophids (Figure 3(J)). The labial extension of the metalophulid I cannot be determined due to the breakage of the anterior part. The metalophulid II is very short unlike *A. constans* and *A. pulchellus*, and has a posterolingual extension that connects with the mesolophid lower than the rest of the crest, unlike the other species of the genus. The mesolophid is well developed, although its labial end is not preserved. The hypolophid is longer than the posterolophid and transverse to the anteroposterior axis. One interesting character is the very oblique ectolophid conspicuously separated from the protoconid. A similar condition is insinuated, although less evident, in some specimens of *Acarechimys* from 'Pinturan' and Santacrucean SALMAs (e.g. Kramarz 2004, Fig. 4A; Arnal 2012).

In m1–m3, the metalophulid I is straight and transverse to the anteroposterior axis of the tooth (Figure 3(J)). The metalophulid II is reduced, represented by a short spur on the ectolophid on m1–m3, unlike the remaining species of the genus (see Arnal 2012); characteristically for the genus there is a knob on the posterior wall of the metalophulid I; these two features are larger in m1 and decrease in size from m2 to m3. The posterolophid is more transverse than in the other species, with the consequent greater opening of the posteroflexid. The m3 is the smallest cheek tooth (Table 2).

Only part of the intra-alveolar portion of the anterior wall of the incisor is preserved showing a very thin enamel layer. The posterior portion of the alveolus ends external to the m3. The incisor is long, with the posterior end behind and external to the m3 (Figure 3(L),(M)).

The mandible is very similar to that of *A. minutissimus*, so far the smallest species of the genus. It has no mental foramen (Figure 3(L)), unlike *A. constans* and *A. minutus*. The diastema is robust with a small chin, and dorsally

gently excavated. The notch for the tendon of the masseter medialis pars infraorbitalis is well developed, between the middle of the dp4 and the anterior root of the m1; it is more oblique than in the remaining species of the genus and is continuous with the robust masseteric crest. The masseteric crest is moderately deep as in *A. minutissimus*. The base of the coronoid process is located at the level of m2.

Comments. *Acarechimys* is one of the few caviomorph genera with a large geographic distribution – from southern Patagonia to Colombia – and a long biochron from early to middle Miocene. *A. leucotheae* represents the oldest record of this lineage and extends its biochron in about three million years, to the late Oligocene. Although its phylogenetic position is controversial, we accept *Acarechimys* as a sister taxon of the lineage Echimyidae + Octodontidae as proposed by Arnal et al. (in press).

Genus *Protacaremys* Ameghino, 1902

Type species. *Protacaremys prior* Ameghino, 1902.

Species content. The type species and *Protacaremys avunculus* Ameghino, 1902, *Protacaremys denisae* Vucetich, Mazzoni, and Pardiñas, 1993a, plus a mention of a new species (Vucetich, Vieytes, et al. 2010).

Horizon and locality. Sarmiento and Collón Cura formations (early to middle Miocene), Patagonia.

Emended diagnosis. Smaller octodontoid than *Prospaniomys* Ameghino, 1902. Tetralophodont molars, except m3 which can be trilophodont; slightly oblique crests. Cheek teeth lower crowned than *Acarechimys* and *Sciamys*, and higher crowned than *Prospaniomys* Ameghino, 1902. Only the parafochette of upper molariforms close in juveniles, unlike *Acarechimys* and *Prospaniomys*. Lower premolars with well-developed metalophulid II, unlike *Prospaniomys*. Similar size of m3 and m2. Mandible with a shallow masseteric fossa whose anterior limit lies below m1 (Arnal 2012).

Protacaremys? adilos n. sp.

(Figure 3)

Holotype. MPEF-PV 10678, an isolated right m2.

Etymology. From the Greek *adilos* = dubious, referring to the uncertainty of the genus assignment.

Diagnosis. Size larger than in *P. avunculus* and similar to *P. prior*; tooth somewhat narrower than in both species, thicker lophids and slightly more hypsodont; metalophulid II long extending from the protoconid and reaching the metaconid; anterofossettid formed before the posterofossettid and smaller than in the other two species; anterior lobe oval; hypolophid straight and posteriorly directed, unlike the remaining species of the genus;

ectolophid straight and strongly oblique; hypoflexid long surpassing the labial end of the mesoflexid and triangular in outline, unlike the other species.

Referred material. Only the holotype.

Description and comparisons

This specimen, an isolated m1 or m2, is low crowned but slightly more hypsodont than in the remaining species of the genus. It is tetralophodont and more rectangular in occlusal outline than in the other species of the genus (AP = 2.13 mm; AW = 1.76 mm; PW = 1.83 mm). The four crests have a similar length (Figure 3(N)), unlike *P. avunculus* and *P. prior* in which the metalophulid II is shorter. The lingual end of the posterolophid contacts the hypolophid forming a posterofossettid smaller than in *P. prior*, *P. avunculus* and *P. denisae* in which the posterofossettid is larger.

The lophids are thicker than in *P. prior* and *P. avunculus* in the same stage of wear, and similar to that present in *Protacaremys* sp. nov. from Gran Barranca (Vucetich, Kramarz, et al. 2010). The metalophulid I is posteriorly concave and unites protoconid and metaconid. The metalophulid II extends from the protoconid, unlike the remaining species of the genus in which it extends from the ectolophid; the metalophulid II is long and contacts the metaconid in early stages of wear, forming an anterofossettid smaller than in *P. prior*, *P. avunculus* and *Protacaremys* sp. nov. The anterofossettid forms prior to the posterofossettid, unlike in *P. prior* and *P. avunculus*, and the shape of metalophulid I and II defines an oval anterior lobe. The ectolophid is straight and strongly oblique, and with the anterior arm of the hypoconid it delimits a penetrating and triangular hypoflexid, unlike *P. prior*, *P. avunculus*, *P. denisae* and *Protacaremys* sp. nov. in which this flexid is broader and less penetrating. The hypolophid is straight and posteriorly oblique, unlike *Protacaremys* sp. nov. The posterolophid is long and posteriorly convex. All the lingual flexids are equal in length, traversing about two-thirds of the occlusal surface, unlike the other species in which the mesoflexid is shorter than the other two. The hypoflexid is deeper than the lingual flexi (Figure 3(O),(P)).

Comments. Because the described material is an isolated tooth, its assignation to *Protacaremys* is tentative, pending on the recovery of more material. If this generic assignation is confirmed, it would extend the biochron of the genus in about 3 million years. Arnal et al. (in press) consider *Protacaremys* as the sister taxon of the lineage formed by *Acarechimys* + (Echimyidae + Octodontidae).

Superfamily **Cavioidea** Fischer de Waldheim, 1817

Genus ***Asteromys*** Ameghino, 1897

Type and only species. *Asteromys punctus* Ameghino, 1897.

Horizon and locality. Deseadan levels of the Sarmiento Formation, Cabeza Blanca and Laguna de los Machos (late Oligocene).

Emended diagnosis. Small 'eocardiid' (similar in size to *Chubutomys navaensis*) with mesodont molars and crowns slightly lower than those of *Luantus initialis* Ameghino, 1902; enamel homogeneous and continuous all around the crown, no cement, persistent fossettids, antero- and metafossettids narrow and long, anterofossettids disappearing before the metafossettids, lingual wall of lower molars straight, hypoflexid wide with round apex opposite the metafossettids, metalophulid II present; p4 with deep vertical furrow on the anterior side; anteroposterior length of p4–m1 approximately equal to that of m2–m3; similar sized lower molariforms (Pérez and Vucetich 2011).

Asteromys punctus?

(Figure 4)

Material. MPEF-PV 595 isolated right DP4; MPEF-PV 597 isolated left DP4 with damaged lingual wall.

Description

The specimens are deeply worn deciduous upper fourth premolars [MPEF-PV 595 (AP = 2.81 mm AW = 2.22 mm; PW = 1.95 mm), MPEF-PV 597 (AP = 2.77 mm; PW = 1.96 mm)]. They are very low crowned (probably because of wear), bilobed and lack cement, and the enamel is continuous in the entire crown (Figure 3(A),(B)). In occlusal view, the lobes are triangular with the labial margin straight. The anterior lobe has a straight anterior border, and the anterolingual margin is straight, anterolabial–posterolingually oblique and has an anteriorly concave notch that becomes shallower with wear. The posterior lobe has straight anterior and posterior margins, and the apex is transversally oriented. The hypoflexus is narrow and transversally extended up to half of the crown. The DP4 has a parafofsette in the anterior lobe, a metafofsette in the posterior lobe that is transversally elongated and narrow, and lacks mesofossette in advanced ontogenetic stages.

Comments. These two DP4s are very similar morphologically to the right DP4 described as 'Eocardiidae gen. et sp. indet.' (MACN 52-87) by Wood and Patterson (1959, p. 376) from Cabeza Blanca. MACN 52-87 has the large anterior root, but the posterior roots are broken. MACN 52-87 is higher crowned than MPEF-PV 595 and 597, it has a

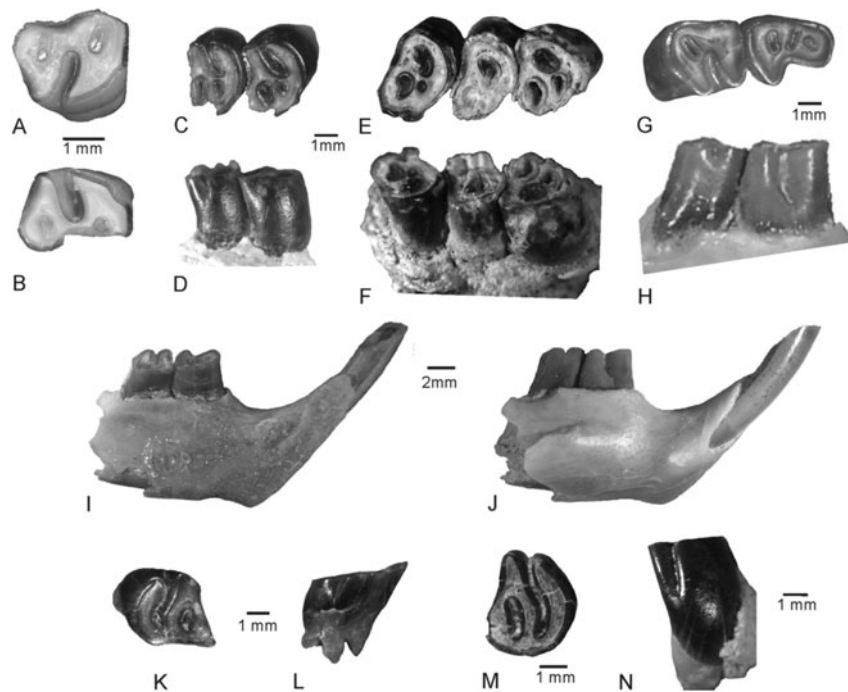


Figure 4. Cavioids and chinchilloids. *A. punctus?* (A) MPEF-PV 595 right DP4 occlusal view; (B) MPEF-PV 597 left DP4 occlusal view. *L. tretos* n. gen., n. sp. MPEF-PV 10682 holotype left M1-M2: (C) occlusal view; (D) lingual view. MPEF-PV 10683 left P4–M2: (E) occlusal view; (F) lingual view. MPEF-PV 10681 right mandible with p4–m1: (G) occlusal view; (H) labial view; (I) mandible internal view (reversed); (J) mandible external view. *I. menniorum* n. sp. MPEF-PV 10685 holotype left m3: (K) occlusal view; (L) posterolabial view (reversed); MPEF-PV 10686 left M1 or M2: (M) occlusal view; (N) lingual view (reversed). Anterior to the right.

wide and transversally long parafossette and a wide mesoflexus, and the posterior lobe is broken but has a large metaflexus. These characters indicate that this tooth is less worn than the DP4s from Cabeza Blanca. Wood and Patterson (1959) considered that MACN 52–87 and ACM 3054 (right M3?) could be referred to *A. punctus* because the enamel is distributed in the entire crown. We agree that these specimens may tentatively be referred as *A. punctus* because the enamel is continuous and they lack cement in all wear stages, the mesofossette is ephemeral, the parafossette and metafossette are persistent, and the dental measurements match with the range size of this species. Although *A. punctus* and *C. navaensis* Pérez, Vucetich and Krause, 2012 are the smallest species within eocardiids (stem group of Caviioidea *sensu stricto* – Caviidae, Hydrochoeridae and the parafiletic ‘Eocardiidae’ – Pérez, 2010a), *C. navaensis* has higher crowns. Other DP4s known within eocardiids correspond to *Luantus propheticus* Ameghino, 1902, *Phanomys mixtus* Ameghino, 1887 and *Eocardia montana* Ameghino, 1887. The DP4s of Cabeza Blanca assigned here tentatively to *A. punctus* differ from those of the mentioned species in the smaller size and very low crowns. Moreover, *L. propheticus* has longer fossettes, and in *P. mixtus* and *E. montana*, the prisms are lobe-shaped, the fossettes are much more ephemeral and the enamel is not continuous around the entire crown.

Superfamily **Chinchilloidea** Bennet, 1833

Genus ***Loncolicu* n. gen.**

Type and only species. *Loncolicu tretos* n. sp.

Etymology. From the Mapuche lonco = head, and licu = white, in reference to the name of the locality.

Horizon and locality. Upper levels of the Sarmiento Formation (late Oligocene), at Cabeza Blanca.

Diagnosis. As for the type and only species of the genus.

***Loncolicu tretos* n. sp.**

(Figure 4, Table 3)

Holotype. MPEF-PV 10682, left M1–M2.

Etymology. From the Greek tretos = perforated, in reference to the large and persistent fossettes/ids on the cheek teeth.

Diagnosis. Small caviomorph similar in size to *Garridomys curunuquem* Kramarz et al., 2013, and *Eoviscaccia* Vucetich, 1989. Cheek teeth protohypsodont, but with crowns lower than in *Garridomys* and *Eoviscaccia*; two persistent labial fossettes in upper teeth, different from *Eoviscaccia*; posterior labial fossette as large as the hypofossette, different from *G. curunuquem*; hypoflexus/id closing well above the base of the tooth forming a hypofossette/id; enamel thick and homogeneously distributed becoming thinner only on the posterior wall with age, different from *G. curunuquem* and *Eoviscaccia*; p4 with the trigonid much narrower than the talonid different from *G. curunuquem* and *Eoviscaccia*; cement absent as in *Incamys* Hoffstetter and Lavocat, 1970; mental foramen absent, different from *G. curunuquem* and *Eoviscaccia boliviana* Vucetich, 1998, diastema more excavated than in *G. curunuquem*; lower incisor more robust than in *G. curunuquem*.

Referred material. MPEF-PV 10683, left P4–M2 of an old individual; MPEF-PV 10681, right mandible fragment with p4–m1.

Description and comparisons

The cheek teeth are high crowned, but with roots and with unilateral hypsodonty, less hypsodont than *G. curunuquem* (Figure 4(C)–(H)). In moderate stages of wear, the enamel layer is homogeneous and continuous (Figure 4(C)) as far as it can be seen in the holotype, while it thins on the posterior wall in senile individuals (Figure 4(E)).

Although there are not very young individuals in the sample as to see the unworn structure, a tetralophodont pattern for the upper cheek teeth is inferred because the labial end of the posterior loph is enlarged suggesting the fusion of two lophs as in *G. curunuquem*, *Incamys* and *Scleromys* Ameghino, 1887. All the upper cheek teeth bear, with moderate wear, two labial fossettes, whereas the hypoflexus crosses the occlusal surface up to half the transverse diameter. With wear the hypoflexus becomes a

Table 3. Dental measurements of *L. tretos*.

	P4			M1			M2		
	AP	AW	PW	AP	AW	PW	AP	AW	PW
MPEF-PV 10682				2.01	~3.54	3.35	~2.56	3.42	3.35
MPEF-PV 10683	3.16		3.98	2.75		4.08	2.96	4.08	4.18
	p4			m1					
	AP	AW	PW	AP	AW	PW			
MPEF-PV 10681	3.88	2.24	3.16	3.57	3.06	3.47			

hypofossette (Figure 4(E)). All the fossettes are large being the hypofossette and the posterior-most labial fossette similar in size, unlike *G. curunuquem* in which the labial fossette is smaller than the hypofossette/flexus. The hypoflexus is shorter than in *Incamys* more similar to *G. curunuquem* and closes well above the tooth base forming a sub-cylindrical crown (Figure 4(D)). The hypoflexus is irregular in width, wider at its labial end unlike *G. curunuquem* and *Incamys bolivianus* Hoffstetter and Lavocat, 1970. The P4 has the anterior wall strongly curved with an anterior projection, whereas in *Garridomys* it is more gently curved.

The single mandible known is of an old individual. The p4 (Figure 4(G)) has the trigonid much narrower than the talonid not defining the hypoflexid at least in the stage of wear of the single-known mandible; this is different from *Garridomys*, *Eoviscaccia* and *Incamys* in which the trigonid is only slightly narrower than the talonid, and hence the hypoflexid is present. In m1 (the single lower molar known), the hypoflexid closes, as in the upper tooth, far from the base (Figure 4(H)). The m1 (Figure 4(G)) has the anterior wall straight and the posterior wall very curved. At this stage of wear, the hypoflexus is short reaching only half of the occlusal surface. Only the posterofossettid is present at this stage of wear. In one specimen of *G. curunuquem* (MOZ-PV 929) with a stage of wear similar to MPEF-PV 10681 (with the hypoflexus near to close), both lingual fossettes are present, similar in size and more or less round in shape, whereas in *G. curunuquem* the anterior fossettid is not present, and the posterior fossettid is large, long and narrow.

The lower incisor is robust with the anteroposterior diameter (2.86 mm) only a little longer than the labio-lingual diameter (2.8 mm). The anterior wall is gently curved.

The upper border of the lower diastema is well excavated forming a clear result in front of the p4 deeper than in *Garridomys curunuquem*; its anterior end is located higher than the molar alveolous border. There is a conspicuous chin a little ahead the anterior wall of the p4. There is no mental foramen, different from *G. curunuquem* and *E. boliviana* in which there is large mental foramen near the anterior border of the diastema. The notch for the tendon of the masseter medialis pars infraorbitalis is oblique, below the m1, whereas in *G. curunuquem* it is a little anteriorly located, below the posterior root of the p4 and the anterior root of m1.

Comments. *L. tretos* share several dental characters with *G. curunuquem*, especially the persistent fossettes/ids and the formation of a hypofossette in P4/M2. These similarities suggest that they are closely related species. However, they present several differences (e.g. absence of mental foramen, different size, shape and timing of reduction among fossettes/ids) that indicate they could represent different lineages, although somehow related.

Especially suggestive of this is the different morphology of the p4. Differences among dp4 have been considered a key character in caviomorph taxonomy (Candela 2000; Emmons 2005, p. 260). We think that, although yet not fully explored, differences among p4 are important as well; in fact such differences have been used as important characters to differentiate genera among octodontoids (Vucetich and Kramarz 2003; Vucetich and Ribeiro 2003).

Genus *Incamys* Hoffstetter and Lavocat, 1970

Type and only species. *I. bolivianus* Hoffstetter and Lavocat, 1970 (the status of *Incamys pretiosus* Lavocat, 1976 pends on a deep revision).

Horizon and locality. Salla beds of Bolivia (late Oligocene).

Diagnosis. Cheek teeth tetralophate, marked lingual hypsodonty in uppers; anteroloph fully separated in earliest stages of wear, becoming joined with paracone buccally; other lophs united early and converge posterointernally on hypocone; posterolophid isolated in early stages of wear of lower teeth; other lophids united early and converge anteroexternally on protoconid; metalophid short, connected to protoconid (only cheek teeth; Patterson and Wood 1982).

Incamys menniorum n. sp.

(Figure 4)

Holotype. MPEF-PV 10685, left isolated m3.

Etymology. In honour of Roberto C. Menni and Matías Menni, husband and son, respectively, of one the authors (MGV) for their support full of good humour.

Diagnosis. Species within the size range of *I. bolivianus*; protocone/id and hypocone/id closer to each other than in *I. bolivianus*; hypoflexus/id with homogeneous width, not funnel shaped (Pérez 2010a) as in *I. bolivianus*. In moderate stages of wear the posterior fossette of upper teeth larger than in *I. bolivianus*. Lingual portion narrower than the labial portion.

Referred material. MPEF-PV 10686 left isolated M1 or M2.

Description and comparisons

Both teeth have a simplified occlusal pattern with a laminar lobe posterior in the lower tooth (Figure 4(K)) and anterior in the upper (Figure 4(M)), and a larger triangular lobe formed by at least two crests, but possibly by three as in *I. 'pretiosus'*, the chinchillids *Eoviscaccia* and *Prolagostomus* Ameghino, 1887 and the chinchilloid *Garridomys*. The triangular lobe bears a large long-lasting fossettid. The lower tooth (AP = 3.92 mm; AW = 3.42 mm; PW = 3.23 mm) is somewhat larger than the upper with its anteroposterior diameter longer

than the transverse diameters, whereas in the upper tooth the anteroposterior diameter is shorter than both transverse diameters (AP = 2.99 mm; AW = 3.29 mm; PW = 4.48 mm). These differences in size and proportions may result from different degrees of wear, different positions in the tooth row and/or to individual differences. The protocone and the hypocone are closer to each other than in *I. bolivianus*. This character is related to two other differences with the Bolivian species. On the one hand, the lingual portion of the upper tooth is narrower than the labial portion resulting in a subtapezoidal outline, whereas in *I. bolivianus* all upper teeth have a more quadrangular outline. On the other hand, the hypoflexus is homogeneous in width along its length, not widening in its lingual extreme (funnel-shaped, Pérez 2010a) as in *I. bolivianus*. In the lower tooth (Figure 4(M)) the anterior wall is oblique and the posterior one is very convex; the enamel layer thins on the posterior wall of the hypoflexid, and it has almost disappeared from the anterior wall of the tooth. The upper tooth is less worn (Figure 4(L),(N)) and the enamel layer is continuous, although becoming thinner on the posterolabial angle and the anterior wall of the hypoflexus (Figure 4(M)). In this tooth, the anterior and labial walls form a long continuous curved wall, whereas the posterior wall is slightly sinuous.

I. menniorum differs from the species of *Eoviscaccia* (Vucetich 1989; Kramarz 2001b; Bertrand et al. 2012) in its lower crowns, and in the triangular lobe that maintains the shape until advanced stages of wear. In *Eoviscaccia*, the triangular lobe is more laminar even in young individuals, whereas in *Garridomys* and *Incamys* it is wider denoting the presence of a more robust meso- or metaloph/id. In *I. menniorum*, the fossette/id in the triangular lobe is wide and persists until the tooth is almost erased, whereas in *Eoviscaccia* it is small, very narrow and fades with advanced wear. In *Eoviscaccia*, the enamel layer is variable in thickness, whereas in *I. menniorum* the enamel layer thins only slightly in the trailing edges as in *G. curunuquem* (Kramarz et al. 2013).

Comments. *I. bolivianus*, the type species of *Incamys*, has been always considered as a dasyproctid cavioid since the extensive description of Lavocat (1976). However, this assignment is questionable. Some characters as the large incisive foramen with the premaxilla-maxillary suture dividing it at about the middle point of its anteroposterior length suggest that it is not a dasyproctid. In the living *Dasyprocta* Illiger, 1811 and *Myoprocta* Thomas, 1903, the incisive foramen is comparatively shorter and the premaxillary-maxillary suture is behind the foramen. Moreover, some dental features such as the type of reduction of loph/ids and the thinning of the enamel layer on the leading edges suggest chinchilloid, and even chinchillid affinities. Chinchilloids group the living Chinchillidae and Dinomyidae, plus extinct lineages such as Neopiblemidae and the Antillean *Amblyrhiza*

Cope, 1868 (see Kramarz et al. 2013 and literature therein). Chinchillidae groups the living *Chinchilla* Bennet, 1829, *Lagidium* Meyen, 1883 and *Lagostomus*, several early to middle Miocene euhiposodont taxa related to *Lagostomus* (*Prolagostomus* and *Pliolagostomus* Ameghino, 1887), and an unnamed taxon probably related to *Chinchilla* and *Lagidium* (Flynn, Croft, et al. 2002). Besides, several protohiposodont to euhiposodont early Oligocene-early Miocene chinchillids were grouped in the genus *Eoviscaccia* (Vucetich 1989; Kramarz 2001b; Bertrand et al. 2012). These species – except the one described by Flynn, Croft, et al. (2002) – have bilaminar cheek teeth with a small fossettid in young individuals. A new phylogenetic analysis (Kramarz et al. 2013) supports *Eoviscaccia* as closely related to the living chinchillids, although it failed to resolve which of the modern genera the former is more closely related to. The species grouped in *Eoviscaccia*, even the oldest one – *Eoviscaccia frassinetti* Bertrand et al., 2012 from the Tinguirirican SALMA (early Oligocene) – are more specialised than *I. menniorum* in its higher-crowned cheek teeth, greater reduction of the fossette/id and a greater lamination of the triangular lobe. This suggests that the group represented by *Incamys* split from *Eoviscaccia* before the Tinguirirican SALMA.

Caviomorpha incertae sedis

Genus *Llitun* n. gen.

Type and only species. *Llitun notuca* n. sp.

Etymology. From Mapuche *llitun* = to promote.

Horizon and locality. Upper levels of the Sarmiento Formation (late Oligocene) at Cabeza Blanca.

Diagnosis. As for the type and only species of the genus.

Llitun notuca n. gen., n. sp.

(Figure 5, Table 2)

Holotype and only specimen. MPEF-PV 10679, right mandibular fragment with i, p4–m2 and roots of m3.

Etymology. From the Mapuche *notuca* = debate. The name of the species, *L. notuca*, makes reference to the long discussions among the authors about the homologies of the dental characters present in this and other old caviomorphs, promoted while studying the holotype.

Diagnosis. Size about 40% smaller and slightly more brachyodont than *Migraveramus beatus* Patterson and Wood, 1982; normal replacement of premolars; complicated p4 with four well-developed crests, plus a short spur from the ectolophid, and a short posterior projection of the metalophulid I and the posterior arm of the metaconid; metalophulid I separated from protoconid by a furrow in juveniles; four well-developed lophids on m1–m2 and a

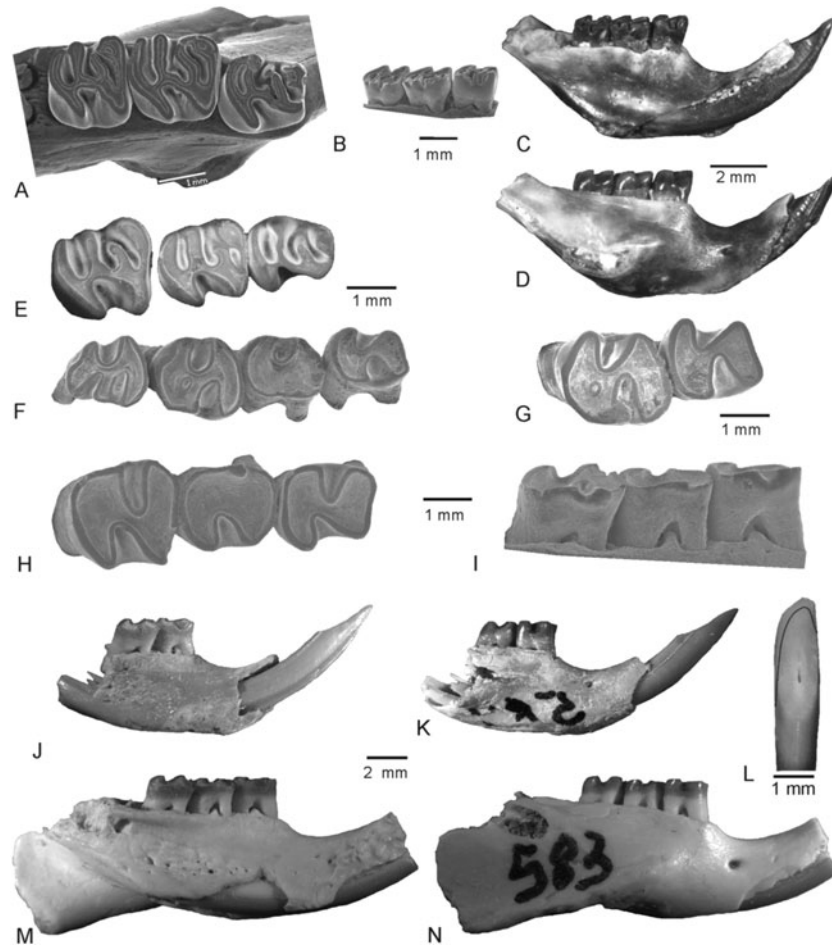


Figure 5. Caviomorpha incertae sedis. (A–D) *L. notuca* n. gen., n. sp. MPEF-PV 10679 holotype, right mandible with p4–m2. (A) occlusal view; (B) labial view (reversed); (C) internal view (reversed); (D) external view. (E–N) *L. zeffiae* n. gen., n. sp. (E) MPEF-PV 585, right p4–m2 occlusal view; (F) MPEF-PV 586, left p4–m3 occlusal view; (G and J–L) MPEF-PV 584 left p4–m1: (G) occlusal view; (J) mandible internal view; (K) mandible external view (reversed); (L) incisor occlusal view. (H,I,M,N) MPEF-PV 583 holotype, right mandible with p4–m2: (H) occlusal view; (I) labial view (reversed); (M) mandible internal view (reversed); (N) mandible external view. Anterior to the right except (L).

fifth anterior lophid formed by a posterior projection of the metalophulid I united with a posterior arm of the metaconid, longer than in *M. beatus*, metalophulid II long and zigzag-shaped; very short mesolophid in m1, absent on m2; m2 smaller than m1, unlike *M. beatus*; hypoflexid wide especially in m2. Mental foramen anteriorly located with respect to *M. beatus*.

Description and comparisons

The cheek teeth are slightly high crowned, lophodont, with cusps barely differentiable from crests (Figure 5(A),(B)). The p4 has a complex structure. The anterior crest is incomplete, formed by a short metalophulid I that reaches up to half of the anterior face, and is separated from the protoconid by a large gap, unlike *M. beatus*. On the posterior face of metalophulid I, there are two structures posteriorly directed: a short posterior arm of the

metaconid and a short posterior extension of the metalophulid I. Between these latter there are two isolated small cusps of uncertain affinities (Figure 4(A)). The protoconid is lingually with respect to the hypoconid. The metalophulid II is oblique, postero-lingually oriented, and although long, it does not reach the lingual border. Unlike *M. beatus*, this crest extends from the ectolophid instead from the protoconid. Behind the labial end of the metalophulid II, there is a lingual isolated cuspule that could be interpreted as a mesostylid. A spur from the middle of the ectolophid could be interpreted as part of a mesolophid, a structure not present in *M. beatus*. The hypoconid is very elongated transversely. The hypolophid is slightly curved, anteriorly concave and long, and contacts the entoconid enclosing a large kidney-shaped posterofossettid. The hypoflexid is wide, very oblique and oriented towards the posterofossettid.

The m1 and m2 resembles superficially those of *M. beatus*. The m1 is the largest of the preserved teeth (Table 2), larger than m2 unlike *M. beatus*. The metalophulid I is straight and complete, whereas the posterolophid is strongly curved and somewhat shorter than the hypolophid. The metaconid is not distinguishable, but the area for this cusp is large and backward projected into a well-developed posterior arm. This area includes a short posterior projection of the metalophulid I. These structures form a tiny anterolabial fossettid, smaller and more circular than in *M. beatus*. The posterior arm of the metaconid comprises almost half the anteroposterior diameter in the m1, whereas in *M. beatus* only comprises 25% of this diameter. The metalophulid II is gently zigzag-shaped, more evident in m1, long and reaches the posterior arm of the metaconid. A tiny spur from the middle of the ectolophid could be interpreted as part of a mesolophid, a structure not present in *M. beatus*. The hypolophid is long, reaching the lingual border, and transversely oriented. The posterolophid is a little shorter than the hypolophid and anteriorly concave; its lingual end is closer to the entoconid than in *M. beatus*. Nevertheless, the posterofossettid is not formed in this stage of wear. The hypoconid is transversely enlarged as in the p4. The mesoflexid is linguallly narrow, but it enlarges in its labial end by an anterolabial extension. The posteroflexid is homogeneous in width. The hypoflexid is as wide as in the p4 and also directed to the posteroflexid. It is much more penetrating than in *M. beatus* as it reaches almost half the width of the occlusal surface, whereas in *M. beatus* it reaches 25% of the width.

Besides its smaller size, the m2 differs from m1 in a larger area for the metaconid bearing a larger fossettid (Figure 4(A)). The metalophulid II is shorter and gently oblique. In this stage of wear, it is isolated from the metaconid area. The posterolophid is a little shorter, barely reaching the lingual border; its lingual end turns anteriorly almost closing the posterofossettid. The hypoconid is more lingual than in m1, as in *M. beatus*. The mesoflexid is narrower and less expanded in its labial end than in m1. By contrast, the hypoflexid is conspicuously wider.

The lower incisor is slender, with the transverse diameter somewhat shorter than the anteroposterior incisor with a curved anterior face. It is long, with its base below the m3 (Figure 4(C)). The occlusal surface is long and concave, and the enamel layer is thin.

The diastema is somewhat shorter than the p4–m3 row, very concave unlike *M. beatus*, and its anterior border is at the level of the occlusal surface of the p4 (Figure 4(C), (D)). The mental foramen is large, facing anteriorly, a little anterior to the middle of the diastema and above the middle point of its height, unlike *M. beatus*. The base of the coronoid process is lateral to the posterior root of m3. The notch for the masseter medialis pars infraorbitalis is very robust, and below the posterior root of p4 and the

anterior root of m1, and almost at the middle of the mandible height.

Comments. Although at first glance m1–m2 of *L. notuca* resemble those of *M. beatus*, they have many important differences that suggest these species represent different, although probably closely related, lineages. Most important in this sense is the very different morphology of the p4. As explained above, such differences have been interpreted as indicatives of different genera among related species.

Genus *Leucokephalos* n. gen.

Type and only species. *Leucokephalos zeffiae* n. gen., n. sp.

Etymology. From the Greek leuco = white, and kephalos = head in reference to the name of the locality.

Horizon and locality. Upper levels of the Sarmiento Formation (late Oligocene) at Cabeza Blanca.

Diagnosis. As for the species.

Leucokephalos zeffiae n. sp.

(Figure 5, Table 2)

Holotype. MPEF-PV 583, right mandibular fragment with p4–m2, and broken incisor.

Etymology. In memory of Silvia N. Zeff (Zeffi), dearest friend of one of the authors (MGV).

Diagnosis. Small caviomorph; cheek teeth slightly hypsodont, tetralophodont when young turning to figure eight-shaped and even kidney-shaped when adult; normal replacement of the premolars; p4 tetralophodont, anterior wall straight with metalophulid I anteroposteriorly wide, separated from the protoconid in young individuals by a furrow on the anterior face; metalophulid II short, reaching up to half the width of the occlusal surface, shorter than in *M. beatus* and *L. notuca*, entoconid large as in *M. beatus* and *L. notuca* with well-developed hypolophid; m1–m2 with metalophulid II short; hypoflexid wide and long, reaching up to the middle of the occlusal surface width; posterolophid as long as the hypolophid; m3 reduced posteriorly; lower incisor long with its posterior end posterolateral to m3; large mental foramen slightly anterior to p4, diastema shallow.

Referred material. MPEF-PV 585, right mandibular fragment with p4–m2 of a juvenile; MPEF-PV 586, left p4–m3 series; MPEF-PV 10680, isolated right p4; MPEF-PV 584, left mandibular fragment with p4-m2 and the incisor; MPEF-PV 10680, isolated right p4.

Description and comparisons

The p4, with little wear (Figure 5(E)), has the metalophulid I straight and with a notch between the

protoconid and the much larger metaconid, as in *L. notuca*. The protoconid is lingual respect to the hypoconid, as in *M. beatus* and *L. notuca*. The metalophulid II is well developed and extends from the anterior portion of the ectolophid as in *L. notuca*; its lingual end slightly exceeds half of the occlusal surface and is postero-lingually oriented. The ectolophid is long and oblique. The hypolophid is long and connected to the entoconid, which is the highest and most lingual of the occlusal structures. The posterolophid is gently curved and a little shorter than the hypolophid. The hypoconid is transversely elongated as in *L. notuca*. The hypoflexid is postero-lingually oriented, with a long and oblique anterior wall, and a posterior wall short and transverse. The posterior most lingual flexid is transverse. The anterior-most lingual flexids are broad and divided into two arms by the metalophulid II at the midpoint of the occlusal surface. With wear, the metalophulid II merges with the proto and metaconid forming an anterior lobe (Figure 5(F),(G),(H)), and the hypolophid merges with posterolophid forming a posterior lobe. In this way, the tetralophodont p4 develops a bilobular, vaguely octodontiform, appearance. The hypoflexid is much deeper than the anterior most lingual flexid.

The m1 and m2 are similar in size and structure, with the protoconid and hypoconid anteroposteriorly aligned unlike the p4. The metalophulid I is connected with the protoconid by a weak isthmus. The metalophulid II is as long as in the p4, shorter in m1 than in m2 in which surpasses the midpoint of the occlusal surface (Figure 5(E)). The hypolophid is as long as the antero- and the posterolophid not projecting lingually beyond the other lophids as in the p4. The posterolophid is gently curved. At the stage of wear of MPEF-PV 585, the hypoflexid of m2 is very wide, whereas it is smaller in m1 (Figure 5(E)). When wear increases, the posterior-most flexid disappears first producing an eight-shaped pattern (Figure 5(F),(G)). Then, the anterior-most flexid also disappears, at least in m1, giving the tooth a vaguely kidney-shaped appearance (Figure 5(H),(I)). In the smallest specimen (MPEF-PV 586), the anterior-most lingual flexus of p4 and m2 are wider than in the other specimens.

The m3 is only present in the smallest specimen; it is smaller than m1–m2, and the posterolophid is shorter than the other lophids (Figure 5(F)). At this stage of wear, it has no metalophulid II.

The lower incisor is very long, with its posterior end behind and external to the m3 (Figure 5(K),(N)). It is slender, with a long occlusal face. The anterior face is gently curved. The enamel layer extends short along the medial wall, but is longer on the distal wall (Figure 5(L)).

The mandible is gracile (Figure 5(J),(K),(M),(N)). The diastema is long and gently curved. The mental foramen is large, round and facing anteriorly (Figure 5(N)). In the smallest specimen (Figure 5(K)), the mental foramen is

higher, close to the dorsal border of the diastema and facing slightly upward instead of laterally. The notch for the tendon is oblique, poorly developed and continuous with the masseteric crest. The latter is moderately developed and poorly laterally extended. The masseteric fossa is very shallow. The base of the coronoid process is at the level of the m3 delimiting a wide retromolar fossa.

The smallest specimen (MPEF-PV 586) has some differences in dental and mandibular morphology that suggest it could represent a different species. But we prefer to consider them as individual variation until further material is available to re-evaluate their meaning.

Litodontomys chubutensis Loomis, 1914 is another small caviomorph from Cabeza Blanca with eight-shaped lower cheek teeth, but it differs from *Leucokephalos* by having a particular p4 with a very long anterior portion, m1–m3 with very wide flexids with cement. These differences suggest that the eight-shaped lower molars may be the result of convergence rather than indicative of close relationships.

Comments. We consider that *Llitun*, *Leucokephalos* and *Migraveramus* represent a clade by shearing a combination of characters not present in other caviomorphs: molarised tetralophodont p4 with posterolophid, hypolophid, metalophulid I and II well developed; tetralophodont m1 and m2 with well-developed posterior arm of the metaconid and a posterior extension of the metalophulid I, and in the mandible a large and anteriorly directed mental foramen. Within this general pattern, they show variations in the degree of development of cusps and lophids having *Leucokephalos* the most simplified occlusal pattern.

Family CEPHALOMYIDAE Ameghino, 1897

Genus *Cephalomys* Ameghino, 1897

Type species. *Cephalomys arcidens* Ameghino, 1897.

Species content. The type species, *Cephalomys plexus* Ameghino, 1897, and *Cephalomys bolivianus* Lavocat, 1976.

Horizon and locality. Sarmiento Formation and Salla Beds (late Oligocene), Patagonia and Bolivia.

Diagnosis. Teeth high-crowned but rooted, with unilateral hypsodonty, particularly in upper molars; no cement on crowns; crown pattern of unworn cheek teeth essentially resembling that of *Neoreomys*, also basically similar to that of *Platypittamys* but with P4/4 much more advanced than in the latter; pattern disappearing fairly rapidly with wear, much less persistent than in *Neoreomys*; enamel interrupted on lingual and anterior sides of lower teeth and buccal and posterior sides of upper teeth after considerable wear (only cheek teeth; Wood and Patterson 1959).

Table 4. Dental measurements of *C. ceciae*.

	ml? m2?			m3?			ACH	PCH	Hh	Index
	AP	AW	PW	AP	AW	PW				
MPEF-PV 10687				1.89	1.77	1.77	3.66	4.27	3.35	2.25
MPEF-PV 10693	2.55	2.07	1.88				5.24	5.43	4.57	
MPEF-PV 10690	2.22	2.11	1.92							2.44
MPEF-PV 10691	2.22	2.15	2.14				5.18	4.88	4.53	2.20
MPEF-PV 10692	2.22	2.15	2.29				3.37	3.70	3.03	1.67
MPEF-PV 10694	2.31	1.89	1.95				3.35	3.05	2.8	
MPEF-PV 10695	2.13	1.95	1.95					2.80	2.19	

	M1			M3			ACH	Index
	AP	AW	PW	AP	AW	PW		
MPEF-PV 10688	1.85	1.70	1.52				4.44	2.40
MPEF-PV 10689				1.66	1.63	1.19		

***Cephalomys ceciae* n. sp.**

(Figure 5, Table 4)

Holotype. MPEF-PV 10693, left lower m1 or m2.*Etymology.* In honour of Cecilia M. (Ceci) Deschamps for her permanent good tempered participation in the rodent team at the Museo de La Plata, and her contribution to the biostratigraphy of the late Miocene–Pleistocene of Argentina.*Diagnosis.* Very high-crowned cephalomyid with crown higher than in the other species of *Cephalomys*, but with roots; size within the size range of *C. plexus*; hypoflexid and mesoflexid deep and opposite to each other producing an irregular eight-shaped occlusal surface with two lobes different in shape and size, the posterior larger than the anterior lobe; other flexids absent since early stages of wear; enamel continuous near the apical portion of the crown, but with dentine tracks at the base of the anterior wall and the postero-lingual corner; upper teeth with a wide and shallow inflexion on the labial wall, M3 with posterior lobe extremely reduced; cement absent.*Referred material.* MPEF-PV 10690, left lower molar; MPEF-PV 10691, right lower molar; MPEF-PV 10692, right lower molar; MPEF-PV 10687, right lower molar; MPEF-PV 10694, right m1 or m2; MPEF-PV 10695, left m1 or m2; MPEF-PV 10688, isolated M1 or M2; MPEF-PV 10689, isolated M3 (the last two probably of a single individual).*Horizon and locality.* Upper levels of the Sarmiento Formation (late Oligocene) at Cabeza Blanca.**Description and comparisons**

The lower teeth are very similar to those of *C. arcidens* and *C. plexus* (see Wood and Patterson 1959, Figure 19), but higher-crowned (Figure 6). One of the most characteristic specimens (Figure 6(A)) is a tiny left lower molar with the anterior lobe smaller than the posterior lobe,

sub-rhomboidal in outline and with very acute labial and lingual ends. The posterior lobe is irregular in outline, with the lingual end blunt, result of the fusion of the postero- and hypoflexid. None of the specimens show a remnant of the anterior labial flexids present in the other two Patagonian species, although the crowns are very high (Figure 6). Only in the holotype (Figure 6(B),(C)), the specimen with the highest crown in the sample (Table 4), a posterofossettid is present. In this specimen, the lingual

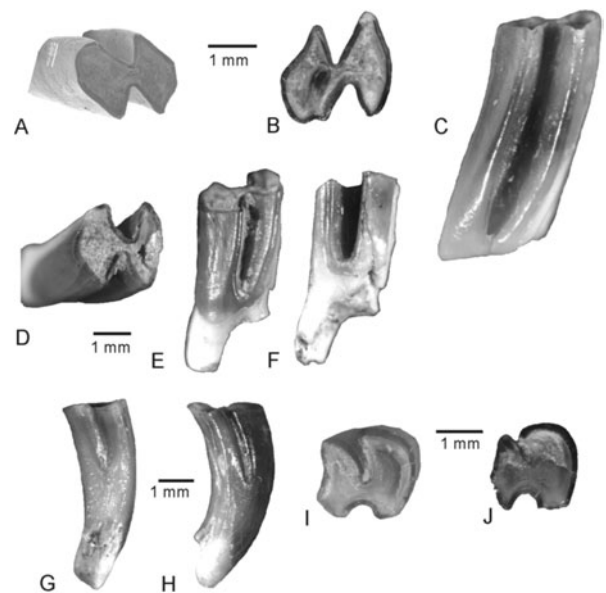


Figure 6. *C. ceciae* n. sp. (A) MPEF-PV 10687, right m3 occlusal view. (B and C) MPEF-PV 10693 holotype, left m1 or m2: (B) occlusal view and (C) labial view (reversed). (D–F) MPEF-PV 10690 right m1 or m2: (D) occlusal view, (E) labial view and (F) lingual view (reversed). (G–I) MPEF-PV 10688 left M1 or M2: (G) labial view, (H) lingual view (reversed) and (I) occlusal view. MPEF-PV 10689 left M3: (J) occlusal view. Anterior to the right.

wall of the posterior lobe has a re-entrance showing the position of the posteroflexid opening. The hypoconid is more labially placed than the protoconid and is separated from the posterolophid by a conspicuous inflexion of the wall. The enamel layer is continuous in the occlusal surface of young individuals, but with wear, dentine tracks appear on the base of the anterior wall and the posterolabial corner (Figure 6(D)–(F)). These tracks can be seen on the occlusal surface in old individuals (Figure 6(D)).

The upper teeth are referred to *C. ceciae* because of their similarity in size, degree of hypsodonty and bearing in mind the pattern of asymmetrical morphology between upper and lower teeth in *Cephalomys* and *Banderomys* Kramarz, 2005 (Wood and Patterson 1959; Kramarz 2001c, 2005). The M1 or M2 (Figure 6(G)–(I)) has the anterior lobe thick with an anteroposteriorly extended lingual wall, instead of forming a more acute apex as in the other species; the labial wall bears a conspicuous notch, much deeper than in *C. plexus*, *Cephalomys* sp. (Wood and Patterson 1959, p. 332, Figure 14C) and *C. bolivianus*, and hypoflexus less deep than *C. arcidens*. The M3 (Figure 6(J)) is similar to M1 or M2 but with the posterior lobe extremely reduced, differing from the other species in which this lobe is not reduced or is only slightly reduced as in the above-mentioned *Cephalomys* sp. This tooth is not known in *C. bolivianus*.

Comments. Deseadan cephalomyids, *Cephalomys* and *Litodontomys* Loomis, 1914, require a deep taxonomic revision in order to understand the species limits and the relationships among them. For example, a recent preliminary study of both species of *Cephalomys* from Patagonia (Busker 2013) suggests that differences in size between the *C. plexus* and *C. arcidens* do not permit to separate them, instead of the originally statement of Ameghino (1897) and Wood and Patterson (1959). However, the material here assigned to *C. ceciae* clearly differs in its degree of hypsodonty from both species as well as from *Litodontomys*. In this case, this character is mostly observed in the very ephemeral condition of the fossette/ids than in the absolute height of the crowns, as it occurs among other caviomorphs (Verzi et al. 2011).

Discussion and conclusions

With the description of four new genera and eight new species for the classical locality Cabeza Blanca (Chubut, Patagonia), the knowledge of the rodent diversity of the Deseadan Age is largely increased, near 25%. Furthermore, the biochrons of three lineages are lengthened in at least 3 million years: *Galileomys* and *Protacaremys* known until now for the interval Colhuehuapian–Colloncuran (early to middle Miocene), and *Acarechimys* previously known from the Colhuehuapian–Laventan (early to middle Miocene). The geographic distribution of one genus, *Incamys*,

previously known only from the Deseadan of Salla (Bolivia), is enlarged as well, adding one more genus to the taxa shared by the faunas from Salla and Patagonia. Up to date, only one genus, *Cephalomys*, was known to be shared by the faunas of Salla and Patagonia, especially Cabeza Blanca and La Flecha, and *Eoviscaccia* and *Cephalomyopsis* Vucetich, 1985 by Cabeza Blanca and Lacayani (Vucetich 1989; Vucetich et al. in press; Table 1).

About half of the taxa described in this paper are octodontoids, a group that was scantily represented in the Deseadan compared with the rich Patagonian local faunas of subsequent SALMAs (e.g. Colhuehuapian [early Miocene] for which 18 species of octodontoids have been recently recognised; Vucetich, Kramarz, et al. 2010). For Cabeza Blanca, only two octodontoid species were so far known, *D. arambourgi* and *E. loomisi*. Other two, *P. brachyodon* and a new genus and species recently described by Vucetich et al. in press, come from Scarritt Pocket – one of the classical Deseadan localities of Patagonia – and a third, *Xylechimys obliquus*, from Laguna de los Machos (Figure 1, Table 1). However, phylogenetic analyses of octodontoids chronologically calibrated showed the presence of numerous ghost lineages for this SALMA (Arnal 2012). According to recent phylogenetic analyses (Arnal 2012; Arnal et al. in press), the octodontoids from Cabeza Blanca represent several different lineages including the Acaremyidae *G. baios*, the basal octodontoids *D. arambourgi* and *A. leucotheae*, and at least two other lineages probably more closely related to the clade formed by Echimyidae + Octodontidae: *E. loomisi* and *P. ? adilos*.

Concerning the acaremyids in particular, recently Vucetich et al. (in press) described a new genus and species for Scarritt Pocket, suggesting that acaremyids must have been more diverse at this time than attested by the fossil record. The description of *G. baios*, the first Oligocene representative of this genus, confirms this hypothesis. According to the phylogenetic hypotheses of Vucetich et al. (in press) and Arnal et al. (in press), there would be three different acaremyid lineages in the Deseadan of Patagonia, represented by *G. baios*, the new genus and species of Scarritt Pocket, and the phylogenetically elusive *P. brachyodon*, plus a couple of ghost taxa (Vucetich et al. in press, Figure 5). The recent description of new taxa (Arnal and Pérez 2013, Vucetich et al. in press, and this paper) shows Acaremyidae as the most diverse lineage of extinct octodontoids. Acaremyids are known exclusively from Patagonia where they are abundant, especially during the Santacrucian SALMA (early Miocene) when they are represented by many species (Arnal 2012; Arnal and Pérez 2013; Arnal and Vucetich 2013); therefore, it seems that Acaremyidae is an austral radiation, although an acaremyid indet. has been recently mentioned for the middle Miocene of Amazonia (Antoine et al. 2013).

During the Deseadan cavioids are represented only by two genera and three species: *A. punctus* (Cabeza Blanca, Laguna de Los Machos and Punta Navas; Figure 1) and *Chubutomys simpsoni* Wood and Patterson, 1959 (Cabeza Blanca), and *C. navaensis* (Punta Navas; Figure 1). Although this group appears to be less diverse than other caviomorphs during the Deseadan SALMA, recent studies on the evolutionary history of Caviioidea (Pérez 2010b; Pérez and Pol 2012) show the presence of at least nine ghost lineages (Pérez 2010b; Pérez et al. 2012) suggesting that during this SALMA an important diversification not yet recorded would have occurred. Anyway, cavioids remain little diverse up to the Santacrucian SALMA when a second radiation is recorded, with a moderate diversity (Pérez and Pol 2012).

Up to date, chinchilloids were represented in the Deseadan by *Eoviscaccia*, a Chinchillidae and *Scotamys* Loomis, 1914, more closely related to Neoepiblemidae (Kramarz et al. 2013). The progress made in the knowledge of the diversity and phylogeny of chinchilloids now allows reconsider the affinities of *Incamys*, originally considered a dasyproctid (see above). Here we propose that, given the type of dental simplification seen in *Incamys*, together with certain cranial characters (see above), this genus should be more closely related to Chinchilloidea than to Caviioidea. If this hypothesis is correct, the diversity of chinchilloids during the Deseadan would have been higher than so far proposed. Recently, Kramarz et al. (2013) described *G. curunuquem* (early Colhuehuapian?, early Miocene), a chinchilloid more primitive in dental morphology than other older chinchillids such as *Eoviscaccia* (Tinguirirican–Colhuehuapian), and more closely related to the chinchillids than to other chinchilloids (i.e. Dinomyidae, Neoepiblemidae). This diversity suggests an important early diversification at generic and specific levels of the clade including the modern chinchillids, occurred at the late Eocene–early Oligocene. For the time of the Santacrucian SALMA (late early Miocene), only the Lagostominae chinchillids *Prolagostomus* and *Pliolagostomus* are recorded in Patagonia, suggesting a post Colhuehuapian extinction, followed by a moderate diversification that occurred mostly at species level during the Santacrucian and Colloncuran (early to middle Miocene; Scott 1905; Vucetich 1984). In lower latitudes, in cordilleran environments, both lagostomines and chinchillines are recorded in middle Miocene sediments (Flynn, Croft, et al. 2002). *Loncolicu*, *Garridomys* and *Incamys* would show the early processes of the development of the main dental specialisations (hypsodonty and extreme lamination) of the crown taxa of this lineage.

M. beatus was originally described as an octodontid by Patterson and Wood (1982) who considered this species as structurally ancestral to the remaining caviomorphs. However, the position of *Migraveramus* is in fact

uncertain: cladistic analyses in progress by one of the authors (MA) showed that the phylogenetic relationships of this genus are controversial within the Infraorder. Moreover, the caviomorph evolutionary scenario has changed considerably since the paper by Patterson and Wood (Antoine et al. 2012; Arnal et al. in press). Furthermore, *Migraveramus* and its structurally allied *Llitun* and *Leucocephalos* differ in many important characters (e.g. normal replacement of the dp4/4 and the complex morphology of the p4) from the remaining octodontoids. In order to establish the relationships among these species and between them and other caviomorphs, comprehensive phylogenetic analyses with the inclusion of a large number of taxa are needed.

Concerning *Cephalomys*, Cabeza Blanca is the only locality where several species are recorded together in the same levels.

The diversity of caviomorphs so far known shows that, as in Caviioidea (Pérez and Pol 2012), the Deseadan represents a time of great diversification of other caviomorph groups such as the Chinchilloidea and Octodontoidea, at least in Patagonia.

Among Paleogene mammal units, the Deseadan SALMA has the widest latitudinal distribution which, although spottily represented, covers a large geographic area from about 12°S in Peru up to 48°S in Patagonia, and from the cordillera in the west to 45°W in Brazil (Figure 1). The presence of Deseadan sediments has also been reported from Contamana, but the fauna has not been described yet (Antoine et al. 2012). The Deseadan SALMA is also a comparatively long period spanning for about 6 million years, from the late–early Oligocene to the late Oligocene (Dunn et al. 2013). Unpublished numerical ages (A. Carlini, personal Communication, 2013) indicate that La Flecha (Figure 1) is late Oligocene in age. All rodent species from this locality are also recorded in Cabeza Blanca (Table 1), suggesting that this latter is also late Oligocene in age. Important differences in composition among Deseadan faunas have been described, especially between those from Bolivia and Patagonia (e.g. Vucetich 1989; Reguero and Cerdeño 2005; Reguero et al. 2007; Billet et al. 2008). Both a certain degree of diachronism among faunas and complex biogeographic scenarios have been proposed as responsible for these differences in composition (e.g. Hoffstetter et al. 1971; Billet et al. 2008). New findings and descriptions of new taxa (Pérez et al. 2012; Vucetich et al. in press) have also contributed to unravel differences in composition among Deseadan local faunas of Patagonia. A better knowledge of the internal calibration of the Deseadan of Patagonia providing a refined temporal scenario would help to understand these differences.

A better understanding of the relationships among Deseadan rodents, and between them and other caviomorphs, as well as their early biogeographic history, needs

additional phylogenetic analyses including a larger amount of taxa and characters, which is beyond the scope of this paper.

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