

# Upper molar morphology, homologies and evolutionary patterns of chinchilloid rodents (Mammalia, Caviomorpha)

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## Abstract

Chinchilloidea are a clade of caviomorph rodents that includes seven living species, the Dinomyidae *Dinomys branickii*, the Chinchillidae *Lagostomus maximus*, two species of *Chinchilla* and three species of *Lagidium*. In addition, two extinct families are traditionally considered chinchilloids – Neopiblemidae and Cephalomyidae. The phylogeny of the Chinchilloidea has so far not been well established and is based on partial analyses. Studying the anatomy and ontogeny of extinct and extant taxa, we propose homologies for the upper molars of Chinchilloidea for which these homologies have not been previously proposed: that is the Chinchillidae *Prolagostomus*, *Lagostomus*, *Lagidium* and *Chinchilla*, and the Neopiblemidae *Neopiblema* and *Phoberomys*. We identify patterns of occlusal simplification within Chinchilloidea and evaluate its importance in an evolutionary context. A phylogenetic analysis recovered Dinomyidae, Chinchillidae and Neopiblemidae as clades. ‘Cephalomyidae’ have not been recovered as a monophyletic group and ‘cephalomyids’ are closely related to Neopiblemidae. *Branisamys* is not included within the Dinomyidae and appears to be a basal chinchilloid.

**Key words:** dental anatomy; ontogeny; phylogeny; Rodentia.

## Introduction

Chinchilloidea form a clade of caviomorph rodents today represented by the pacaraná (*Dinomys branickii* Peters, 1873) of the Dinomyidae, and the chinchillas (*Chinchilla*), mountain vizcachas (*Lagidium*) and plains vizcacha [*Lagostomus maximus* (Desmarest, 1817)] of the Chinchillidae (e.g. Nowak, 1991; Upham & Patterson, 2015). Living chinchilloids are distributed in western and southern South America (Nowak, 1991; Redford & Eisenberg, 1992; Mares & Braun, 2016; Spotorno & Valladares Faúndez, 2016). In addition, chinchilloids include two extinct groups, the Neopiblemidae and the Cephalomyidae (e.g. Kraglievich, 1940; Bondasio et al. 1975; Vucetich, 1985; Kramarz, 2001a, 2005), as well as some taxa not allocated to any family (see below; e.g. Kramarz et al. 2013; Vucetich et al. 2015; Kerber et al. 2016).

With four genera that include seven living species, Chinchilloidea are not as diverse as other caviomorph lineages such as Octodontoidea, which include 30 genera and more than 170 species, or Caviioidea, which display nine genera

and more than 40 species (e.g. Nowak, 1991; Redford & Eisenberg, 1992; Wilson & Reeder, 2005; Mares & Braun, 2016; Spotorno & Valladares Faúndez, 2016).

The Dinomyidae (late Oligocene to recent times) include a single living species, *Dinomys branickii*, inhabiting Andean forests in northwestern South America (White & Alberico, 1992; Mares & Braun, 2016), but the group had a great diversity in the past, with more than 30 genera and 50 species (e.g. Fields, 1957; Mones, 1986). Some of the oldest dinomyids, such as the late Oligocene *Branisamys* (e.g. Patterson & Wood, 1982), were brachyodont. Another primitive dinomyid, *Scleromys*, was protohypsodont and has been recorded in the late Oligocene–Early Miocene of Peru (e.g. Boivin et al. 2017) and early Miocene of Argentina (e.g. Ameghino, 1887, 1894; Kramarz, 2006; Cerdeño & Vucetich, 2007) and Chile (Flynn et al. 2008). Dinomyids were very diverse and widely distributed during the late Miocene (e.g. Nasif, 2010; Nasif et al. 2013) and were the largest rodents that have ever lived (e.g. Kraglievich, 1926; Francis & Mones, 1966; Mones, 1986; Rinderknecht & Blanco, 2008). Dinomyidae have been included in the Chinchilloidea and also in Caviioidea, Erethizontoidea and Dinomyoidea (see White & Alberico, 1992). Recent molecular studies have proposed close relationships between Dinomyidae and Chinchillidae (e.g. Huchon & Douzery, 2001; Spotorno et al. 2004; Voloch et al. 2013).

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Within the Chinchillidae (early Oligocene to recent times), two subfamilies are traditionally recognized (e.g. Pocock, 1922; Spotorno & Valladares Faúndez, 2016): the Chinchillinae, including species of *Chinchilla* and *Lagidium*, which inhabit Andean regions from Ecuador to southern Argentina and Chile, and the monospecific Lagostominae with *Lagostomus maximus*, inhabiting lowland habitats of Argentina, Paraguay and Bolivia (e.g. Redford & Eisenberg, 1992; Jackson et al. 1996). Living chinchillids have euhippodont teeth and the occlusal morphology of the cheek teeth consists of laminar loph/lophids, three in the P4-M3 and p4-m3 of Chinchillinae and the M3 of Lagostominae, and two in the P4-M2 and p4-m3 of Lagostominae. The oldest known chinchillid is *Eoviscaccia*, dating from the early Oligocene of Chile (Bertrand et al. 2012), the late Oligocene of Argentina and Bolivia (Vucetich, 1989; Pérez et al. 2018) and the early Miocene of Argentina (e.g. Kramarz, 2001b). *Eoviscaccia* has protohippodont teeth, cusps in early wear stages, and persistent fossettes/ids with advanced wear. *Prolagostomus* and *Pliolagostomus* are extinct lagostomines known from the early Miocene to middle Miocene which have similar cheek teeth features than the living *Lagostomus maximus*, having bilophodont P4-M2 and p4-m3, and trilophodont M3 (e.g. Ameghino, 1887; Vucetich, 1984; Kramarz, 2002). The genus *Lagostomus* has been recognized from the late Miocene in Argentina (e.g. Rasia & Candela, 2017a), with abundant records in the latest Neogene and Quaternary of Argentina, Uruguay, Bolivia and Brazil (e.g. Ameghino, 1889; Francis & Mones, 1968; Marshall & Sempere, 1991; Kerber et al. 2011; Rasia & Candela, 2013, 2017b). Besides the many studies dealing with the systematics of this group (e.g. Ameghino, 1887, 1889; Vucetich, 1984, 1989; Kramarz, 2001b, 2002; Rasia & Candela, 2017a, b), the homologies of loph/ids of cheek teeth of extant and extinct chinchillids (except for *Eoviscaccia*; see Vucetich, 1989; Kramarz, 2001b) have not been adequately clarified based on ontogeny and paleontological evidence.

The extinct Neopiblemidae (late Oligocene–late Pliocene) include four genera (*Perimys*, *Doryperimys*, *Neopiblema* and *Phoberomys*) including small-bodied to giant forms that are characterized by euhippodont cheek teeth composed of parallel lophs and lophids (e.g. Ameghino, 1887; Kraglievich, 1926; Bondesio & Bocquentin-Villanueva, 1988; Negri & Ferigolo, 1999; Kramarz, 2002; Carrillo & Sánchez-Villagra, 2015; Kramarz et al. 2015; Kerber et al. 2017a; Rasia & Candela, 2018). There are competing hypotheses regarding the relationships of Neopiblemidae, which has been considered to be closely related either to the Dinomyidae (e.g. Horovitz et al. 2006; Kramarz et al. 2013) or to the Chinchillidae (e.g. Kerber et al. 2017a,b; Rasia & Candela, 2018). *Perimys* has been reported from the early Miocene of Argentina and Chile (e.g. Ameghino, 1887; Flynn et al. 2002; Kramarz, 2002), *Doryperimys* from the early Miocene of Argentina (Kramarz et al. 2015), *Neopiblema* have been found from the middle Miocene–

Pliocene of Argentina, Brazil, Peru and Venezuela (e.g. Ameghino, 1889; Negri & Ferigolo, 1999; Vucetich et al. 2010; Antoine et al. 2015; Carrillo & Sánchez-Villagra, 2015; Tejada-Lara et al. 2015) and *Phoberomys* from the late Miocene–Pliocene of Argentina, Brazil, Peru and Venezuela (e.g. Kraglievich, 1926; Mones, 1980; Horovitz et al. 2006; Kerber et al. 2017a). As for chinchillids (see above), the homologies of the loph/lophids of cheek teeth of Neopiblemidae have not been properly established, except for *Perimys* (see Kramarz, 2001a).

The Cephalomyidae clade, including late Oligocene to late Miocene taxa such as *Cephalomys*, *Cephalomyopsis*, *Litodontomys*, *Soriamys* and *Banderomys* (e.g. Vucetich, 1985; Kramarz, 2001a, 2005; Busker & Dozo, 2018), has long not been recognized as a natural group (e.g. Wood & Patterson, 1959; Patterson & Wood, 1982). This group includes taxa with different degrees of hypsodonty and cheek teeth simplification of the occlusal pattern. *Banderomys leanzai* Kramarz, 2005 is recognized from the early Miocene of Neuquén and Chubut (Argentina; Kramarz, 2005; Busker et al. 2017) and would represent the most primitive cephalomyid (Kramarz, 2005). *Soriamys* was described from the early Miocene of Chubut, Argentina (Kramarz, 2001a), and *Cephalomys* from the late Oligocene of Patagonia, Argentina (see Ameghino, 1897; Wood & Patterson, 1959) and the middle Miocene Quebrada Honda, Bolivia (Frailey, 1981). Cephalomyids are often considered to be closely related to cavioids (Kramarz, 2005; Busker & Dozo, 2018).

Some caviomorph taxa are considered *incertae sedis* Chinchilloidea (see Kramarz et al. 2013; Vucetich et al. 2015; Kerber et al. 2016). This is the case for *Incamys bolivianus* Hoffstetter & Lavocat, 1970, which was described from Salla in Bolivia and Cabeza Blanca in Argentina (late Oligocene; e.g. Hoffstetter & Lavocat, 1970; Patterson & Wood, 1982; Busker & Dozo, 2017) and was considered a dasypsectid cavioid by Patterson & Wood (1982). More recently, Vucetich et al. (2015) described *Incamys menniorum* Vucetich et al. 2015 from the Sarmiento Formation (late Oligocene) in Cabeza Blanca (Chubut Province, Argentina) and considered it a chinchilloid, but did not include it in any family. *Loncolicu tretos* Vucetich et al. 2015, known from a few dental remains, was described from the upper levels of the Sarmiento Formation (late Oligocene) in Cabeza Blanca (Chubut Province, Argentina; Vucetich et al. 2015) and was also considered to be a chinchilloid but not included in any family. *Garridomys curunuquem* Kramarz et al. 2013 was reported from the early Miocene Cerro Bandera Formation (Neuquén, Argentina; Kramarz et al. 2013) as an *incertae sedis* chinchilloid probably related to the origin of Chinchillidae. *Niedemys piauiensis* Kerber et al. 2016 was reported from the late Quaternary of Brazil and treated as a chinchilloid but not assigned to any family (Kerber et al. 2016). *Ucayalimys crassidens* Boivin et al. 2017 is a possible Chinchilloidea from the late Oligocene of Contamana, Perú (Boivin et al. 2017) with tetralophodont M2. The *incertae sedis*

caviomorph *Aenigmys diamantensis* Vucetich et al. 2005, from the Pleistocene of Argentina, has been related to the families Dinomyidae, Neopiblemidae and Heptaxodontidae (Vucetich et al. 2005).

Among these *incertae sedis* chinchilloids, *Incamys*, *Loncolicu* and *Garridomys* have tooth morphologies that resemble that of *Eoviscaccia* and have been considered to be related to the origin of the Chinchillidae (e.g. Kramarz et al. 2013; Vucetich et al. 2015). However, the affinities of at least some taxa (i.e. *Incamys* and *Loncolicu*) within Chinchilloidea are still uncertain, given that they have not been included in phylogenetic analyses.

As in other groups of caviomorphs (e.g. Carvalho & Salles, 2004; Vucetich et al. 2010; Antoine et al. 2012; Candela & Rasia, 2012; Candela, 2016), the systematics of fossil chinchilloids are essentially based on dental characters. However, homologies of the dental structures of many genera of chinchilloids have not been established.

The cheek teeth modification of the occlusal pattern, with parallel laminar lophs/lophids, and the reduction in number of these laminae observed in living chinchillids, is also present in other chinchilloids, notably in the extinct neopiblemids and some cephalomyids (e.g. *Cephalomys*, *Soriamys*). Homologies of the cheek teeth of different genera of Chinchilloidea have not been studied in detail, and it has been assumed that cheek teeth with the same number of laminae are homologous (e.g. Kramarz et al. 2013; Rasia & Candela, 2018).

In this work, we study the upper molar morphology of extinct and extant Chinchilloidea, identifying cusp and loph homologies, taking into account ontogenetic variations. We propose hypotheses for dental structure homologies in taxa where no homology has previously been established and, on this basis, evaluate how simplified cheek teeth and reduction of the number of lophs could have been acquired in the different chinchilloid lineages.

## Material and methods

We studied specimens of the living chinchilloids (*Dinomys branickii*, *Chinchilla* spp., *Lagidium* spp. and *Lagostomus maximus*), including individuals with different ontogenetic states (see Supporting Information Data S1). We also studied fossil material of extinct chinchilloids, including Dinomyidae, Chinchillidae, Neopiblemidae and Cephalomyidae (see Data S1).

We propose primary homology hypotheses (*sensu* de Pinna, 1991) for the cusps and lophs of upper molar of different groups of chinchilloids through comparisons of tooth morphology based on topological relations (Rieppel, 1988). We based our interpretations on topological and ontogenetic criteria, but once the homologies were established, we extend primary homology hypotheses for taxa within the same taxonomic rank and with identical topographical positions of their molar structures.

The terminology of main upper molar cusps, valleys and lophs used in this work (Fig. 1) follows the proposal of Candela (1999). When the mesoloph/mesolophule was absent, we considered the presence of a meso-metaflexus, given that the resulting flexus does

not correspond either to a mesoflexus or to a metaflexus (i.e. the two flexi are confluent).

For the construction of the data matrix, we used the free software MESQUITE 3.5 (Maddison & Maddison, 2018). We used a combination of the data matrix of Rasia & Candela (2018), a modification of the matrix from Kramarz et al. (2013) and Kramarz (2001a, 2005) (see Supporting Information Data S2 for a detailed list of characters). There were 11 new characters in this study (see Data S2). The character 'number of transverse crests on M1-M2 in adult stages' of Rasia & Candela (2018) was replaced by five characters: 70 – Reduction of protoloph in adult M1-M2; 71 – Presence/absence of mesoloph/mesolophule in adult M1-M2; 72 – Development of mesoloph/mesolophule in adult M1-M2; 73 – Relation of metaloph with anterior structures in adult M1-M2; 74 – Relation of metaloph with anterior structures in adult M1-M2.

The data matrix resulted in 80 characters and 19 taxa (Supporting Information Data S3). The phylogenetic analysis was performed following cladistic methodology (e.g. Hennig, 1968; Farris, 1983) using the program TNT 1.5 (Goloboff & Catalano, 2016) available from the Willi Hennig Society. The heuristic searches consisted on 200 Wagner trees replications, followed by a Tree Bisection Reconnection, saving 50 trees per replication. To calculate support values, we used the absolute Bremer index.

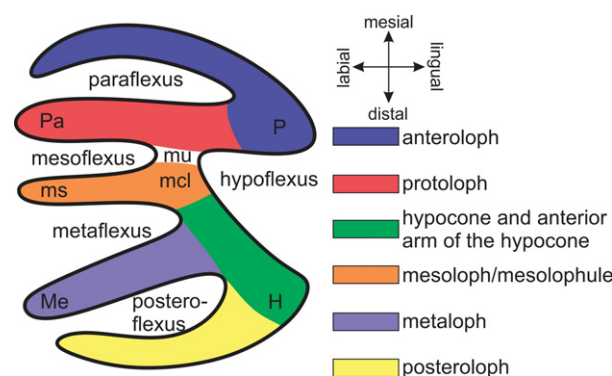
## Institutional abbreviations

Museo de La Plata – mammal collection, La Plata, Argentina (MLP-Ma); Museo de La Plata – paleovertebrate collection (MLP-Pv); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' – mammal collection, Buenos Aires, Argentina (MACN-Ma); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' – National Collection Florentino Ameghino (MACN-A); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' – paleovertebrate collection (MACN-Pv); Muséum National d'Histoire Naturelle, Paris, France (MNHN).

## Results

### Morphology, homologies and ontogeny of Chinchillidae

The ontogeny of upper cheek teeth of many chinchilloids (e.g. *Soriamys*, *Garridomys* and *Dinomys*; see Kramarz,



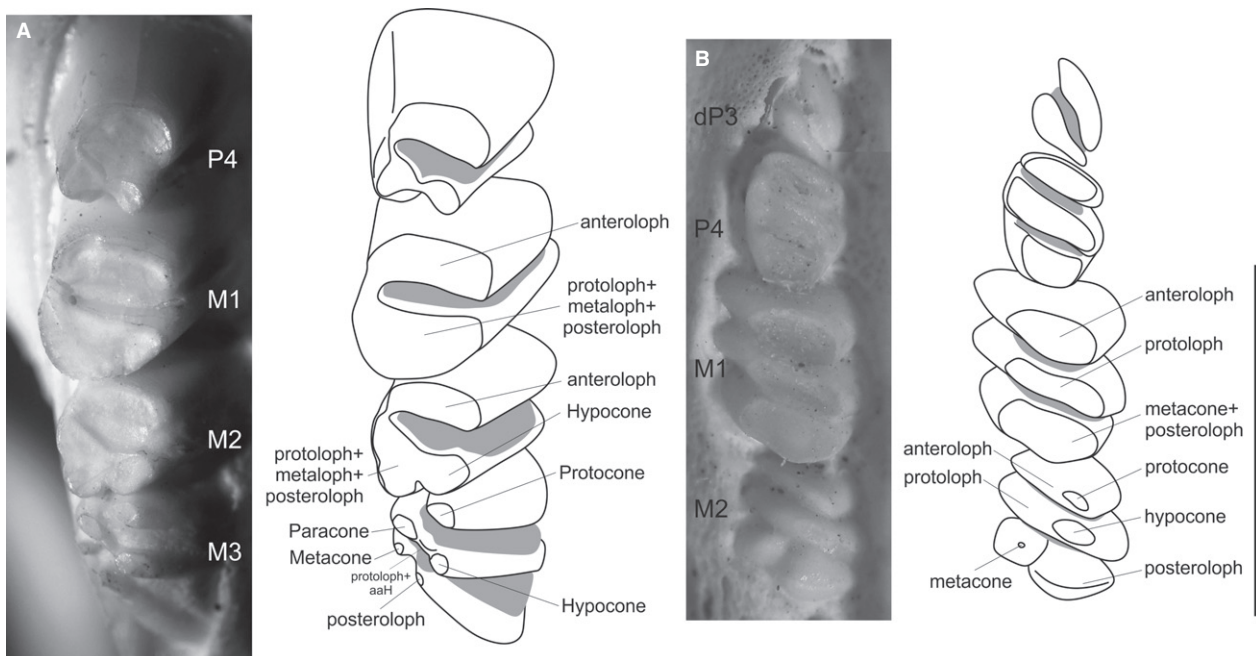
**Fig. 1** Upper molar terminology. H, hypocone; mcl, metaconule; Me, metacone; ms, mesostyle; mu, mure; P, protocone; Pa, paracone (Modified from Candela, 1999).

2001a; Kramarz et al. 2013; Nasif & Abdala, 2016) is well known, but there are almost no studies on chinchillids on this regard, except for *Eoviscaccia* (Vucetich, 1989; Kramarz, 2001b). We identified different ontogenetic states in the Chinchillidae *Eoviscaccia*, *Prolagostomus*, *Lagostomus* and *Lagidium* (Figs 2–4), and the main cusps and lophs were identified in unworn molars of the living chinchillids *Lagostomus maximus* and *Lagidium* sp. (see Fig. 2A,B).

In the M3 of a newborn specimen (MACN-Ma 49.238; Fig. 2A) of *Lagostomus maximus*, we identified a tetralophodont pattern. There is a mesiolingual cusp that we interpreted by its topology as the protocone. Mesiolabially, there is a cusp that could be identified as the paracone, united with the distolingual hypocone by an oblique crest that probably corresponds to the protoloph+mure+anterior arm of the hypocone. The protocone and the paracone+protoloph+mure+anterior arm of the hypocone+hypocone are separated by the paraflexus+hypoflexus, what allows identification with certainty of both lingual cusps as protocone and hypocone. Distal to the paracone, there is a small metacone, and between these two labial cusps, there is a meso-metaflexus that opens distolingually and labially. The recognition of a mesoloph/mesolophule and a metaloph, and the associated labial cusps (mesostyle and metacone, respectively), has been subject of discussion, constituting one of the most critical aspects on dental anatomy recognition in caviomorph rodents (e.g. Candela, 1999; and works cited therein). The identification of the second labial cusp in *Lagostomus maximus* as a metacone, and not as a mesostyle, is because of its topological location, almost at the

same level as the hypocone, which is the expected position of the metacone in a generalized upper molar pattern in rodents (e.g. Candela, 1999). If this cusp is indeed a mesostyle, then the metacone (and metaloph) were fused to the posteroloph since eruption of the teeth. Also, there is no observable mesostyle or mesoloph/mesolophule in early stages of wear of related chinchilloids such as *Eoviscaccia* or *Garridomys* (see below). In the distal portion of the tooth, there is a short posteroloph, isolated from the rest of the structures by a short posteroflexus that opens lingually and labially.

A similar morphology is observed in the M2 of an unborn specimen of *Lagidium* sp. (MACN-Ma 50.280; Fig. 2B). There is a mesial anteroloph with a lingual protocone. Distal to the anteroloph is the protoloph, which joins the mure+anterior arm of the hypocone+hypocone. The paracone is entirely submerged within the protoloph and therefore not visible. Distolabially, there is a large cusp interpreted as the metacone. As in the newborn specimen of *Lagostomus maximus* described above, the identification of this cusp as a metacone, and not as a mesostyle, is due to the topographic position of the cusp, at the same level than the hypocone, and there is no evidence that the most distal loph corresponds to a fusion of metaloph and posteroloph. Also, there is an absence of mesostyle or mesoloph/mesolophule in closely related forms with identical molar patterns. Note that in *Eoviscaccia* and *Garridomys* with little wear, there is no evidence of mesostyle or mesoloph/mesolophule (see below, see also Kramarz, 2001b; Kramarz et al. 2013). Instead, as noted by Kramarz et al. (2013) in an early stage



**Fig. 2** Juvenile upper dentition of living Chinchillidae. (A) *Lagostomus maximus*, MACN-Ma 49.238, photograph and schematic interpretation of right P4-M3. (B) *Lagidium* sp., MACN-Ma 50.280, photograph and schematic interpretation of right dP3-M2. Scale bar: 10 mm.

of wear of *Garridomys*, the second labial cusp of the M1/M2 of this genus shows a topographical location (aligned to the hypocone) corresponding to the position of the typical metacone, and the associated loph to this cusp can be homologized to the metaloph. The posteroloph is located distolingually.

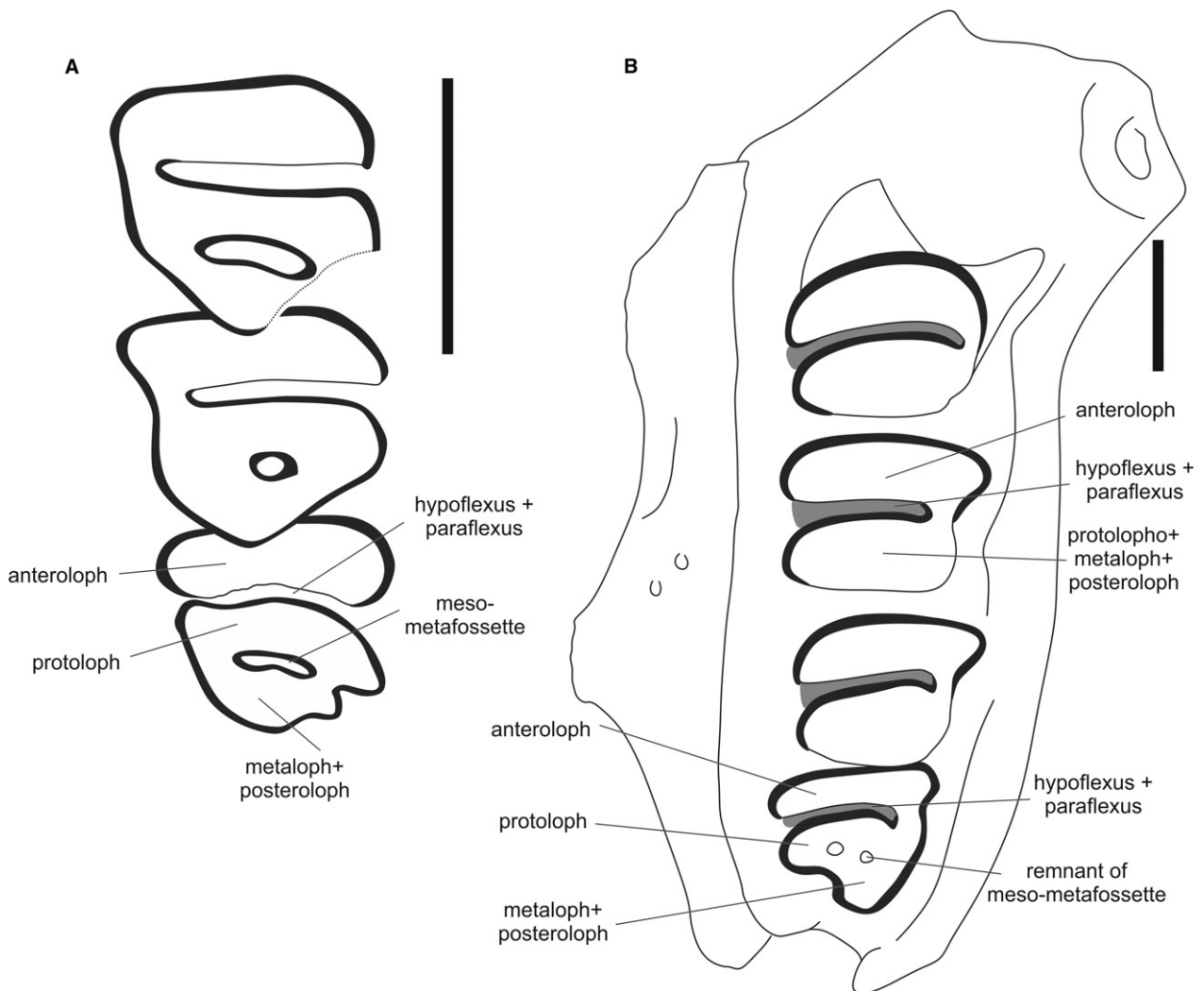
In little-worn molars of *Prolagostomus* sp. (Fig. 3A,B), a trilophodont pattern can be observed, the first loph being interpreted as the anteroloph, the second as the protoloph+hypocone, and the third as the fusion of the metaloph+posteroloph (assuming that in earlier stages of wear, it has an independent metaloph or metacone, as in *Eoviscaccia* and *Lagostomus maximus*).

The lochs observed in unworn or little-worn upper molars of *Lagostomus maximus*, *Lagidium* and *Prolagostomus* are in accordance with those described by Vucetich (1989) in little-worn molars of *Eoviscaccia boliviana* Vucetich, 1989; in

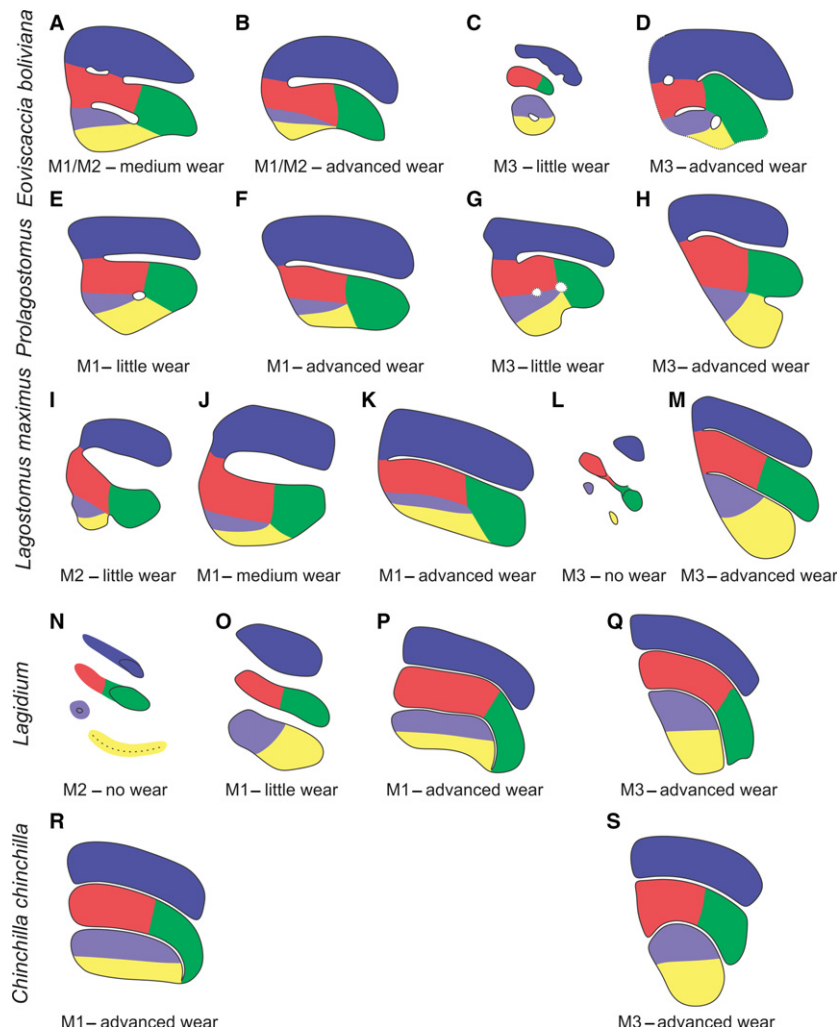
bearing an anteroloph, an oblique protoloph fused with the region of the hypocone, and a distolabial metaloph and posteroloph delimiting a posterofossette (see Fig. 4C). The same tetralophodont morphology of juvenile *Eoviscaccia* was observed (e.g. Kramarz, 2006; Kramarz et al. 2013) in little-worn molars of other Chinchilloidea such as *Garridomys* and *Scleromys* (see below).

### Pentalophodont pattern

The primitive *Branisamys* is considered a basal pentalophodont Dinomyidae (e.g. Patterson & Wood, 1982; Nasif, 2010) with a molar pattern (see Fig. 1) comparable to that of extinct Erethizontidae (see Hoffstetter & Lavocat, 1970; Nasif, 2010), with an anteroloph, a protoloph, a mesoloph/mesolophule, a metaloph and a posteroloph. In addition, *Incamys bolivianus* shows a pentalophodont



**Fig. 3** Juvenile upper dentition of *Prolagostomus*. (A) *Prolagostomus* sp., MLP-Pv 15-87 (holotype of '*Scotaeumys imminutus*'), right P4-M2. (B) *Prolagostomus* sp., MLP-Pv 15-180 (holotype of '*Sphaeramys irruptus*'), palate fragment with left dP4-M3. Scale bar: 20 mm.



**Fig. 4** Upper molars of Chinchillidae. *Eoviscaccia boliviana* (A) left M1 or M2, (B) left M1 or M2, (C) left M3, (D) MNHN-BLV 164 (holotype), right M3. *Prolagostomus* sp. (E) MLP-Pv 15-87 (holotype of '*Scotaeumys imminutus*'), right M1; (F) MLP-Pv 15-180 (holotype of '*Sphaeromys irruptus*'), left M3, (H) MLP-Pv 15-152, right M3. *Lagostomus maximus* (I) MACN-Ma 49.238, right M2; (J) MACN-Ma 49.238, right M1; (K) MACN-Ma 49.13, right M1; (L) MACN-Ma 49.238, right M3; (M) MACN-Ma 49.13, right M3. *Lagidium* sp. MACN-Ma 50.280, (N) right M2; (O) right M1; *Lagidium viscacia*, MLP-Ma 1431, (P) right M1; (Q) right M3. *Chinchilla chinchilla*, MLP-Ma 1768, (R) right M1; (S) right M3. (A-D) modified from Vucetich (1989); (A,B,C,G) reversed. Colours indicate dental anatomy as in Fig. 1. Note that the limits in fused structures are interpretative.

pattern in early stages of wear (see Hoffstetter & Lavocat, 1970).

The dinomyid '*Scleromys*' *schurmanni* has tetralophodont upper molars, but a pentalophodont pattern in early stages of wear is inferred due to its similarity to other pentalophodont dinomyids such as '*Scleromys*' *colombianus* and *Drytomomys aequatorialis* (see Fields, 1957).

Little-worn M2 of *Dinomys branickii* have five lophs, identified as anteroloph, protoloph, mesoloph/mesolophule, metaloph and posteroloph (Figs. 5O,P).

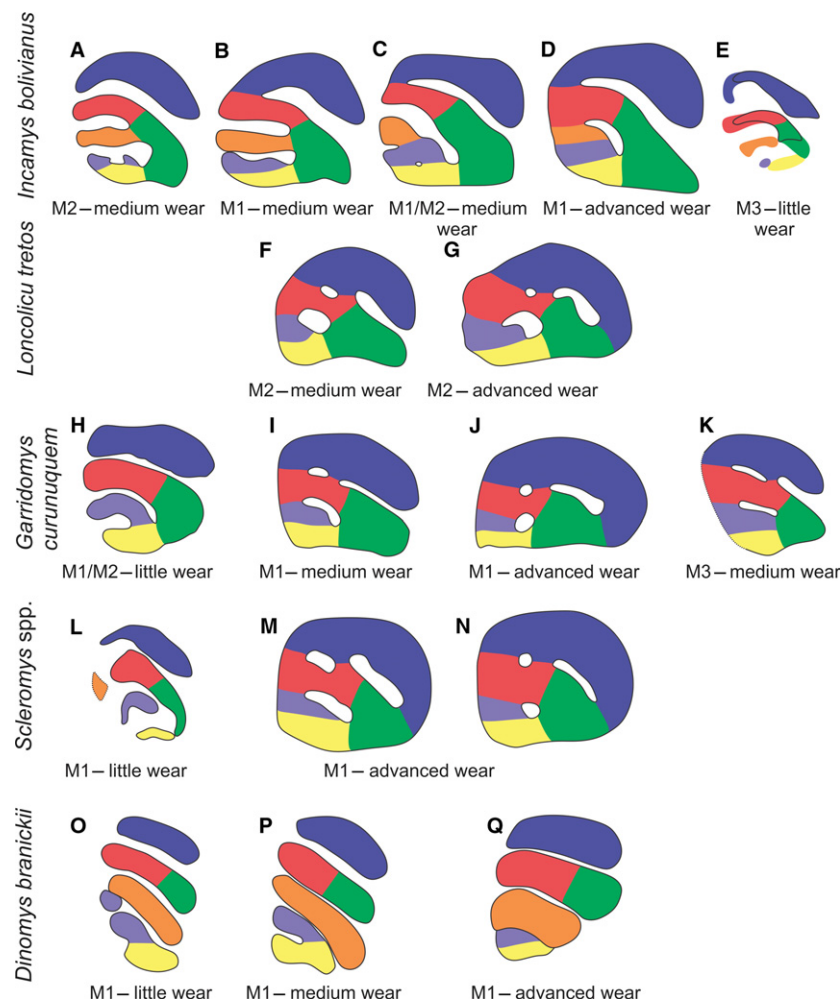
Little-worn M1-M2 of Cephalomyidae such as *Banderomys*, *Soriomys* and *Cephalomys* are pentalophodont, with an anteroloph, protoloph, mesoloph/mesolophule, metaloph and posteroloph (see Kramarz, 2001a, 2005).

#### Tetralophodont pattern

In some Dinomyidae, such as the living *Dinomys branickii*, the M1-M2 show a tetralophodont pattern. These four crests are interpreted as anteroloph, protoloph+hypocone, mesoloph/mesolophule and metaloph+posteroloph (Fig. 5Q; see also Nasif, 2010).

The Cephalomyidae *Banderomys* has tetralophodont M1-M2 (Fig. 6B,C), with an anteroloph, protoloph, mesoloph/mesolophule and metaloph+posteroloph after the postero-fossette disappears (see Kramarz, 2005).

Little-worn molars of *Incamys bolivianus* are tetralophodont (Fig. 5B) and we recognize an anteroloph, a protoloph+hypocone, a mesoloph/mesolophule and a

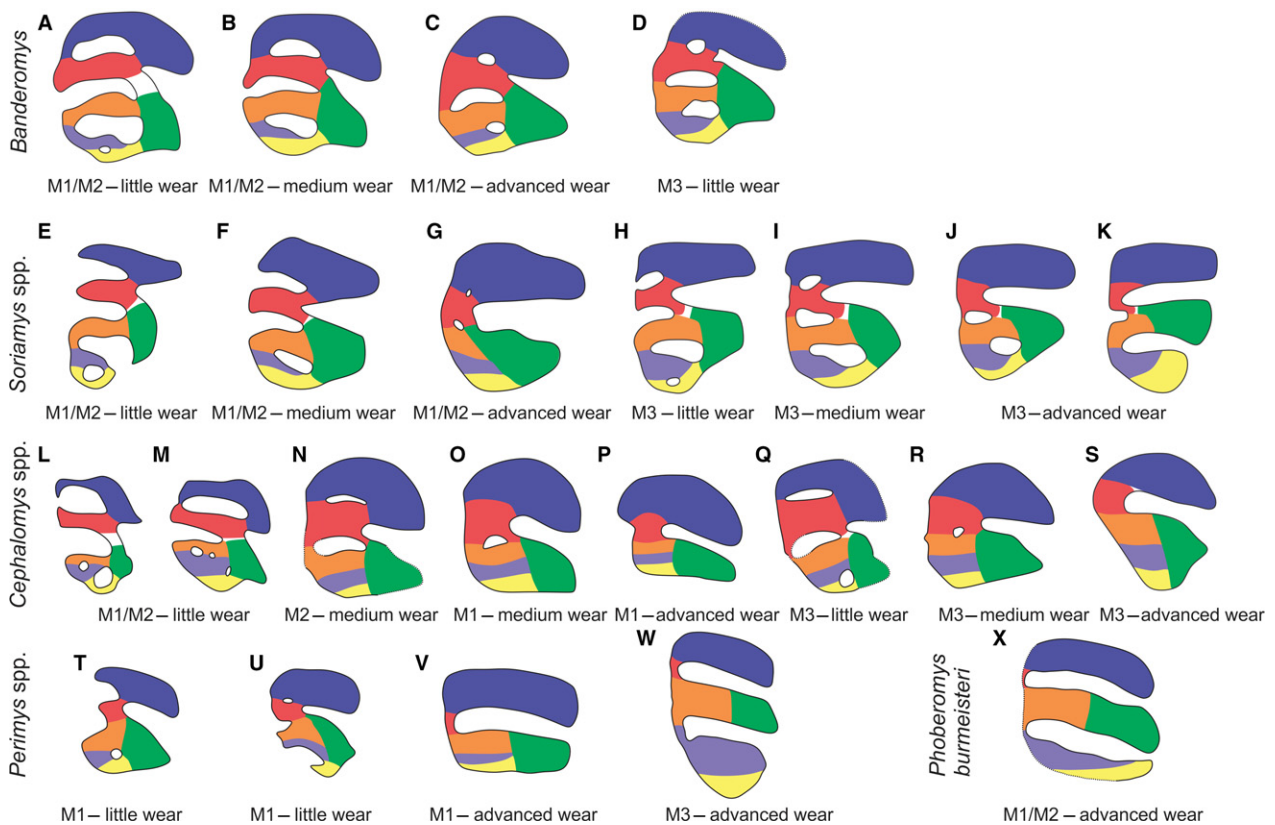


**Fig. 5** Upper molars of Chinchilloidea *incertae sedis* and Dinomyidae. *Incamys bolivianus* (A) right M2; (B) right M1; (C) left M1 or M2; (D) left M1; (E) right M3. *Loncolicu tretos* (F) left M2; (G), left M2. *Garridomys curunuquem* (H) left M1 or M2; (I) right M1; (J) right M1; (K) right M3. *Scleromys quadranguatus* (L) left upper molar. *Scleromys osbornianus* (M) MACN-A 10121, left M1. *Scleromys angustus* (N) MACN-Pv 4363, right M1. *Dinomys branickii* (O) MACN-Ma 12962, right M1; (P), left M1; (Q) right M1. (A,B,E) modified from Hoffstetter & Lavocat (1970); (C,D) modified from Patterson & Wood (1982); (F,G) modified from Vucetich et al. (2015); (H-K) modified from Kramarz et al. (2013); (L) modified from Kramarz (2006); (P,Q) modified from Nasif & Abdala (2016); (C,D,F-H,L,M,P) reversed. Colours indicate dental anatomy as in Fig. 1. Note that the limits in fused structures are interpretative.

metaloph+posteroloph. In some juvenile specimens of *Incamys bolivianus*, there is a cusp near the labial margin of the teeth and anterior to the metaloph (see Fig. 5C), interpreted here as a mesostyle, which represents a remnant of the reduced mesoloph/mesolophule. In adult trilophodont molars of *Incamys bolivianus*, the mesoloph/mesolophule forms the third loph, fused with the metaloph and posteroloph (see below).

Many taxa that show a trilophodont pattern in worn upper molars, such as *Garridomys* and *Scleromys*, have tetralophodont unworn or little-worn M1-M2 (see Fig. 5H,L), with an anteroloph separated from the protocone+hypocone by a paraflexus+hypoflexus, and posteriorly the metaloph and posteroloph delimiting a posteroflexus/posterofossette (see Kramarz, 2006; Kramarz et al. 2013). In

unworn upper molars of *Garridomys*, the second labial cusp, aligned with the hypocone, was identified as the metacone. The associated loph to this cusp is the metaloph, which curves distolabially to reach the posteroloph (see Kramarz et al. 2013). A labial cusp was observed in some tetralophodont little-worn specimens of *Scleromys quadrangulatus* Kramarz, 2006 (Fig. 5L), interpreted as a mesostyle because of its topographical position, in agreement with Kramarz (2006). Moreover, in some upper molars of *Scleromys* (see Boivin et al. 2017), there is a reduced loph distal to the paracone that we interpret as the mesoloph. The identification of a mesostyle and a reduced mesoloph, distal to the paracone, is a strong argument for interpreting as a metaloph the third loph of little-worn upper molars with tetralophodont pattern of *Scleromys*.



**Fig. 6** Upper molars of Cephalomyidae and Neopiblemidae. *Banderomys leanzai* (A) MOZ-Pv6833, right M1 or M2; (B) PVPH 363, right M1 or M2; (C) PVPH 364, left M1 or M2; (D) PVPH 365, right M3. *Soriamys gainanensis* (E) MACN-CH 1805, left M1 or M2; (F) MACN-CH 1807, right M1 or M2; (G) MACN-CH 1809, left M1 or M2; (H) MACN-CH 1812, left M3; (I) MACN-CH 1814, left M3; (J) MACN-CH 1815, left M3. *Soriamys ganganensis* (K) MACN-CH 1765, right M3. *Cephalomys arcidens* (L) MNHN 1903-3-20, left M1 or M2; (M) MNHN 1903-3-22, left M1 or M2; (N) CNHM P 14652, left M2; (O) CNHM P 14652, left M1; (Q) CNHM P 14652, left M3; (R) ACM 3099, right M3. *Cephalomys* sp. (P) ACM 3109, left M1; (S) ACM 3109, left M3. *Perimys* sp. (T) MLP-Pv68-1-17-80, right M1. *Perimys intermedius* (U) MACN-Pv SC 3998, left M1; (V) MACN-Pv SC 2123, left M1; (W) MACN-Pv SC 2123, left M3. *Phoberomys burmeisteri* (X) right M1 or M2. (A,B,C,D) modified from Kramarz (2005); (E-K,T) modified from Kramarz (2001a); (L-S) modified from Wood & Patterson (1959); (U-W) modified from Kramarz (2002); (C,E,G-Q),S,U-W reversed. Colours indicate dental anatomy as in Fig. 1. Note that the limits in fused structures are interpretative.

It is noteworthy that there are alternative interpretations of the lophs considering the presence of a mesoloph subsumed under other structures. So, in little-worn upper molars of *Scleromys* (see Boivin et al. 2017), it could be identified an anteroloph, a protoloph+mure+anterior arm of the hypocone+hypocone, mesoloph and metaloph+posteroloph.

Little-worn upper molars of *Eoiviscaccia* are tetralophodont (Fig. 4C) with an identical morphology of tetralophodont molars of *Garridomys* (Fig. 5H). We recognized an anteroloph, a protoloph+hypocone, and a metaloph and posteroloph delimiting a posterofossette.

We interpret as a metacone/metaloph the third labial cusp/loph of other chinchilloids with tetralophodont little-worn upper molars (e.g. *Garridomys*, *Eoiviscaccia*, *Lagostomus*), because of its relative position with regard to the hypocone, and because there is no evidence to consider the posteriormost fourth loph to be the fusion of the metaloph and posteroloph.

Little-worn M1 of *Perimys* (Fig. 6T,U) have four identifiable lophs that rapidly became two lophs (see Kramarz, 2001a, 2002). These tetralophodont M1 were considered similar to medium-worn teeth of cephalomyids (see Kramarz, 2001a), so the lophs correspond to the anteroloph, a reduced protoloph, mesoloph/mesolophule in contact with the hypocone, and a fusion of metaloph+posteroloph.

### Trilophodont pattern

A trilophodont pattern can be found in many adult chinchilloids of different clades (Chinchillidae, Dinomyidae, Neopiblemidae and Cephalomyidae).

The M1-M2 of adult *Chinchilla* and *Lagidium* are trilophodont. The first loph corresponds to the anteroloph, which is completely separated from the rest of the structures of the tooth by the paraflexus+hypoflexus. The second loph corresponds to the protoloph+hypocone, and the third loph corresponds to the metaloph+posteroloph, given that the



metacone observed in earlier stages of wear (Fig. 4N; see above) is now completely merged with the posteroloph. The second and third lophs are separated by the mesoflexus/metaflexus, which is open labially (Fig. 4P,R).

In *Incamys*, the M1-M2 are trilophodont with advanced wear (tetralophodont in earlier stages of wear, see above), with an anteroloph, protoloph+hypocone and mesoloph/mesolophule+metaloph+posteroloph (Fig. 5D). There is a paraflexus+hypoflexus between the anteroloph and the protoloph+hypocone, and a posterior mesofossette.

The M1-M2 of *Loncolicu*, *Garridomys* and the Dinomyidae *Scleromys* (see Ameghino, 1887, 1894; Kramarz, 2006; Kramarz et al. 2013; Vucetich et al. 2015) are trilophodont, with an anteroloph, a protoloph+hypocone and metaloph+posteroloph (see Fig. 5F,G,I,J,M,N). Note that there is no evidence to consider the presence of a mesoloph/mesolophule in *Garridomys*, even at early stages of wear, but there is evidence of a reduced mesostyle or mesoloph in *Scleromys* (see above). There is a parafossette independent from the hypofossette and a posterior meso-metafossette. In *Loncolicu*, the hypoflexus becomes a hypofossette with advanced wear (Fig. 5G).

In the Neopiblemidae *Neopiblema* and *Phoberomys*, the M1-M2 are trilophodont, with the three lophs united on the labial side (Fig. 6X). Little-worn or unworn upper molars of these taxa have not been found, and therefore the identification of the cusps and lophs is difficult, but their morphology is identical to that of the M3 of *Soriamys ganganensis* Kramarz, 2001a and *Perimys* (see Fig. 6K,W). Therefore, considering the topological relations of the molar structures and different ontogenetic stages observed in *Soriamys ganganensis* and *Perimys*, the first loph of *Neopiblema* and *Phoberomys* can be homologized to the anteroloph. The protoloph is completely reduced and restricted to the labial part of the tooth, opposed the hypoflexus. The second loph includes the hypocone in its lingual portion, and the labial portion is here interpreted as the mesoloph/mesolophule. The third loph is here interpreted as a fusion of metaloph and posteroloph.

Medium-worn M1-M2 of *Eoviscaccia* (Fig. 4A) are trilophodont (see Vucetich, 1989; Kramarz, 2001b), with an anteroloph, a protoloph+hypocone and a metaloph+posteroloph, after the posterofossette disappears. The parafossette is not connected with the hypoflexus, and both separate the anteroloph from the protoloph+hypocone. There is also a meso-metafossette between the protoloph+hypocone and metaloph+posteroloph.

The M1-M2 of juvenile *Prolagostomus* are trilophodont (see above, Figs 3A and 4E), with an anteroloph, protoloph+hypocone and metaloph+posteroloph. There is a paraflexus+hypoflexus, as well as a meso-metafossette that disappears in later stages of wear.

The M3 of *Garridomys curunuquem* is trilophodont like the M1-M2, with an anteroloph, a protoloph+hypocone and the metaloph+posteroloph (Fig. 5K; see Kramarz et al.

2013). There is a parafossette not joined with the hypoflexus, and a meso-metafossette (see Kramarz et al. 2013).

In the Cephalomyidae *Soriamys ganganensis*, the lophs of the trilophodont M3 correspond to anteroloph, mesoloph/mesolophule+hypocone and metaloph+posteroloph (Fig. 6K). The protoloph is reduced and restricted labially to the hypoflexus.

The M3 of the Neopiblemidae *Perimys* is trilophodont (Fig. 6W), and with an identical morphology to the M1-M2 of *Neopiblema* and *Phoberomys* (Fig. 6X), and the M3 of *Soriamys ganganensis* (Fig. 6K; see Kramarz, 2001a).

The M3 of all Chinchillidae (i.e. *Eoviscaccia*, *Prolagostomus*, *Pliolagostomus*, *Lagostomus*, *Chinchilla* and *Lagidium*) are trilophodont, with an anteroloph, protoloph+hypocone, and metaloph+posteroloph. In Lagostominae (which traditionally includes *Eoviscaccia*, *Prolagostomus*, *Pliolagostomus*, and *Lagostomus*), the paraflexus+hypoflexus opens only lingually (see Fig. 4D, H,M), whereas in the Chinchillinae (*Chinchilla* and *Lagidium*), the paraflexus+hypoflexus opens lingually and labially (see Fig. 4Q,S). In *Eoviscaccia*, the third loph is smaller than in the other chinchillids, and the meso-metaflexus has become a meso-metafossette. In *Prolagostomus* and *Pliolagostomus*, the meso-metaflexus is short, and the second and third lophs are not completely separated. In *Lagostomus*, the meso-metaflexus separates the second and third lophs. In *Pliolagostomus* and *Lagostomus*, the meso-metaflexus opens lingually, whereas in *Prolagostomus*, it opens linguodistally or distally. In Chinchillinae, the meso-metaflexus opens lingually and labially.

### Bilophodont pattern

In the Chinchillidae *Eoviscaccia*, *Prolagostomus*, *Pliolagostomus* and *Lagostomus* (traditionally considered as Lagostominae; e.g. Vucetich, 1989), the M1-M2 are bilophodont. Following the degrees of wear observed in these genera (see above), it is possible to determine that the first loph corresponds to the anteroloph and that the second loph is a fusion of protoloph+hypocone+metaloph+posteroloph. The flexus separating both lophs is the paraflexus+hypoflexus (Fig. 4B,F,J,K).

Some Cephalomyidae, such as *Cephalomys* (Fig. 6O,P) and *Soriamys* (Fig. 6G), also have bilophodont M1-M2. In these genera, the first loph corresponds to the anteroloph, as in bilophodont Chinchillidae, but the second loph is the fusion of mesoloph/mesolophule+hypocone+metaloph+posteroloph. The protoloph is reduced and predominantly restricted to the labial portion of the teeth, opposed to the hypoflexus.

In the Neopiblemidae *Perimys*, the bilophodont M1-M2 (Fig. 6V) show a similar morphology to that in *Cephalomys* and *Soriamys*, with the first loph corresponding to the anteroloph, a reduced protoloph opposed to the hypoflexus,

the hypocone forming the lingual portion of the second loph, and mesoloph/mesolophule, metaloph and posteroloph constituting the labial portion of the second loph.

### Evolutionary patterns of upper molars in Chinchilloidea

There are some important contributions to the understanding of the phylogeny of chinchilloids (e.g. Kramarz, 2001a, 2005; Kramarz et al. 2013; Busker & Dozo, 2018; Kerber et al. 2017b; Rasia & Candela, 2018), but none of these studies has included members of all recognized clades within Chinchilloidea (i.e. Chinchillidae, Dinomyidae, Neopiblemidae and Cephalomyidae).

Although several genera among different caviomorph lineages have some degree of reduction in the number of lophs (e.g. *Lagostomus*, *Dolichotis* and *Octodontomys* with bilophodont cheek teeth), this pattern has been attained through different paths of fusion and reduction of structures and should not be considered homologous before a thorough analysis. Many recent studies (e.g. Kramarz et al. 2013; Rasia, 2016; Kerber et al. 2017b; Rasia & Candela, 2018) used the character 'number of lophs/crests in the M1-M2' in phylogenetic analyses, but in some cases, this character may not be taking into account the fusion and loss of lophs/crests than can be observed during the ontogeny of extinct and extant species.

Heuristic searches of our phylogenetic analysis have yielded a single most parsimonious tree of 204 steps (Fig. 7).

Dinomyidae, Chinchillidae and Neopiblemidae are recovered as monophyletic groups, supported by the following synapomorphies: characters 12, 17, 27; 6, 40 and 1, 24, 25, 31, 33, 47, 48, respectively (see Data S2 for details of the characters). 'Cephalomyidae' is not recovered as a clade,

but this could be due to the lack of cranial characters in most of the studied material. *Branisamys* appears as basal to the rest of studied chinchilloids, but it is not closely related to the Dinomyidae as previously proposed (e.g. Patterson & Wood, 1982; Nasif, 2010). 'Cephalomyidae' and Neopiblemidae form a clade supported by six synapomorphies (characters 47, 49, 50, 63, 69, 75). The *insertae sedis* chinchilloids *Incamys* and *Garridomys* form a clade with Chinchillidae, supported by three synapomorphies (characters 7, 38, 61). 'Cephalomyidae'+Neopiblemidae and *Incamys*+(*Garridomys*+Chinchillidae) form a clade supported by six synapomorphies (characters 13, 16, 19, 35, 46, 48).

In order to recognize evolutionary patterns in the upper molars of Chinchilloidea, we analyzed the distribution of characters 69–74 on the most parsimonious tree (Fig. 8).

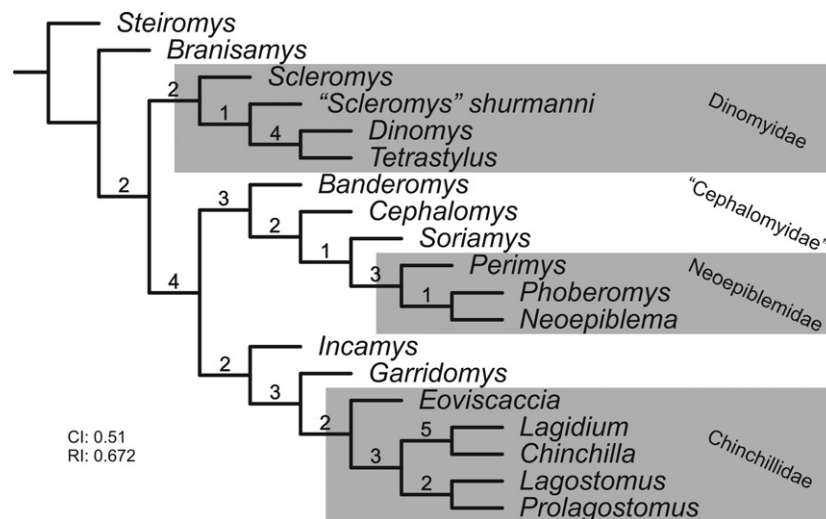
Protoloph in adult M1-M2 (character 69) is fused with the anterior arm of the hypocone (state 2) in Chinchilloidea. In the clade 'Cephalomyidae'+Neopiblemidae, the protoloph is opposed to the hypoflexus (state 1).

Reduction of the protoloph in adult M1-M2 (character 70) is present (state 1) in *Cephalomys*+(*Soriamys*+Neopiblemidae).

Mesoloph/mesolophule in adult M1-M2 (character 71) is present (state 0) in most of the studied caviomorphs and is absent (state 1) in *Scleromys* and in *Garridomys*+Chinchillidae.

Development of mesoloph/mesolophule in adult M1-M2 (character 72) is normal (state 0) in *Steiomys*, *Branisamys* and Dinomyidae, reduced (state 1) in *Incamys* (recognized at least in some specimens) and fused with the hypocone (state 2) in 'Cephalomyidae'+Neopiblemidae.

The relation between metaloph and posteroloph in adult M1-M2 (character 73) is free (state 0) in the node including all of the studied caviomorphs. In all the studied



**Fig. 7** Single most parsimonious tree of 204 steps, showing phylogenetic relationships of major clades of Chinchilloidea. Numbers indicate absolute Bremer support index; CI, consistency index; RI, retention index.

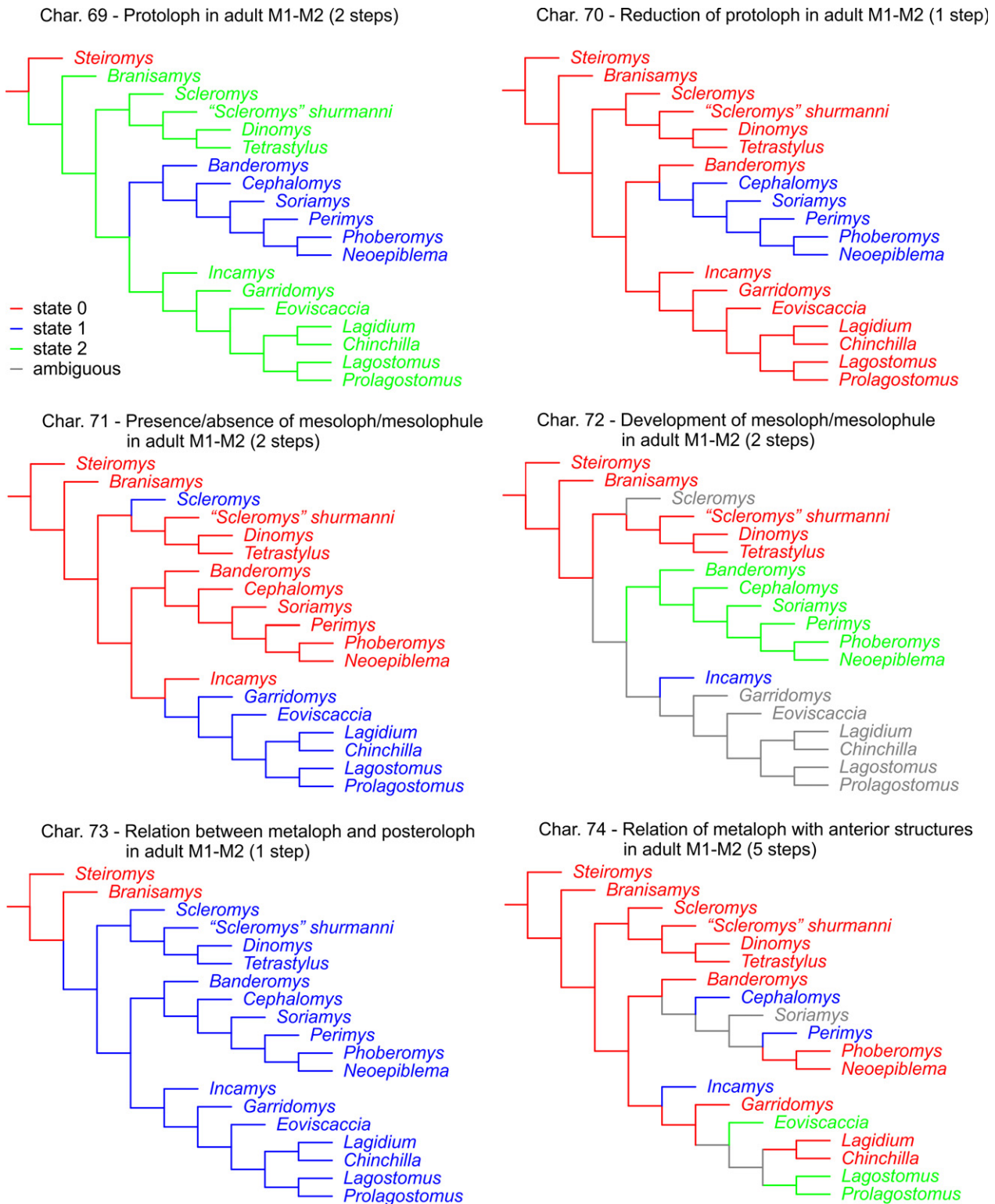


Fig. 8 Character state optimization in the most parsimonious tree. Only characters involving homologies of adult M1-M2 are shown.

Chinchilloidea, excluding *Branisamys*, the metaloph and posteroloph are fused (state 1).

The relation of the metaloph with anterior structures in adult M1-M2 (character 74) is free (state 0) in most of the

studied caviomorphs. The metaloph is fused with the mesoloph/mesolophule (state 1) in *Cephalomys*, *Perimys* and *Incamys*, and the metaloph is fused with the protoloph (state 2) in *Eoviscaccia* and *Lagostomus*+*Prolagostomus*.

Some of the characters regarding upper molar morphology (characters 63, 65, 67, 71, 73, 75, 76, 77, 79 and 80) constitute synapomorphies of major clades (see above and Supporting Information Data S2 and Data S4), highlighting the importance of a correct interpretation of dental homologies.

## Discussion

### Molar morphology

The comparison of the upper molar pattern of extinct and extant Chinchilloidea showed that early members of the group, such as *Eoviscaccia*, *Branisamys*, *Incamys*, *Scleromys* and *Banderomys*, have complex dental patterns where cusps and lophs observed in the Erethizontoid molar pattern have been identified.

In addition, our comparative analysis of upper molars of extinct and extant Chinchilloidea allowed us to identify cusps and lophs in some taxa for which homologies of these structures were not previously established (i.e. *Prolagostomus*, *Lagostomus*, *Lagidium*, *Chinchilla*, *Neoepiblema* and *Phoberomys*).

Two different patterns of upper molar morphology can be recognized among Chinchilloidea:

1 In Chinchillidae, Dinomyidae, and the *incertae sedis* Chinchilloidea *Branisamys*, *Incamys*, *Loncolicu* and *Garridomys*, the hypoflexus is opposed to the paraflexus/parafosette, separating the anteroloph from the rest of the structures of the tooth (showing a taeniodont pattern), and the protoloph is connected with the hypocone via the mure and the anterior arm of the hypocone. In addition, the metaloph and posteroloph are located in the posterolabial portion on the teeth. In the basal chinchilloid *Branisamys*, the dinomyids *Dinomys* and *Tetrastylus*, and *Incamys*, there is a well developed mesoloph/mesolophule, at least at early ontogenetic states (e.g. Hoffstetter & Lavocat, 1970; Nasif, 2010). A mesostyle is present in early stages of wear in some specimens of *Scleromys*, but apparently does not participate in any structure of the adult upper molar pattern, possibly being subsumed under the metaloph+posteroloph complex. In chinchillids, *Garridomys* and *Loncolicu*, there is no identifiable mesoloph/mesolophule. Although we did not find evidence of a mesoloph/mesolophule (even in unworn or little-worn upper molars) in *Garridomys* and Chinchillidae (i.e. *Eoviscaccia*, *Prolagostomus*, *Pliolagostomus*, *Lagostomus*, *Chinchilla*, *Lagidium*), we do not reject the possibility that future studies could change this interpretation, and that in tetralophodont unworn/little-worn molars the third loph could be considered the mesoloph/mesolophule and the fourth loph a fusion of metaloph and posteroloph, as is indeed observed in other chinchilloids such as the Dinomyidae, Neoepiblemidae and 'Cephalomyidae'.

2 In 'Cephalomyidae' and in the Neoepiblemidae *Perimys*, the hypoflexus is opposed to the protoloph. The protoloph is reduced and restricted to the labial portion of the teeth, on the labial end of the hypoflexus. This was not directly observed in the rest of the Neoepiblemidae (i.e. *Doryperimys*, *Neoepiblema* and *Phoberomys*) but the adult upper molars are similar to those of *Perimys* and some 'Cephalomyidae'. In 'Cephalomyidae', there is a mesoloph/mesolophule that is fused with the hypocone, forming the second crest or loph. This was not observed in Neoepiblemidae, but due to the resemblance to adult molars of 'Cephalomyidae', it is possible that the second loph of upper molars of this clade also corresponds to the fusion of mesoloph/mesolophule and hypocone.

Some derived taxa of several chinchilloid clades share a modification of the occlusal molar morphology to laminar lophs. These lophs can vary in number from eight (in the M3 of *Phoberomys*; e.g. Rasia & Candela, 2018) to two (in the M1-M2 of *Lagostomus*, *Perimys* and *Cephalomys*; see Figs 4 and 6). The reduction to only two lophs is found among many chinchilloid clades (e.g. Chinchillidae, Neoepiblemidae and 'Cephalomyidae'), but as we have observed here (see above), the reduction and fusion of structures of upper molars follow different paths in each group depending on the molar pattern of the group (see above). In Chinchillidae *Scleromys*, *Loncolicu* and *Garridomys* the lophs of a trilophodont upper molar correspond to the anteroloph, the protoloph+ hypocone, and the metaloph+posteroloph (in *Incamys* the third loph includes the mesoloph/mesolophule); and the lophs of a bilophodont upper molar correspond to anteroloph and protoloph+ hypocone+metaloph+posteroloph. In 'Cephalomyidae' and Neoepiblemidae, the lophs of a trilophodont upper molar correspond to the anteroloph, the mesoloph/mesolophule+hypocone and the metaloph+posteroloph, and in the bilophodont upper molars, the first loph corresponds to the anteroloph and the second loph to the mesoloph/mesolophule+hypocone+metaloph+posteroloph.

### Phylogeny

Our phylogenetic analysis is the first to include all recognized groups within Chinchilloidea, and agrees partly with previous studies (see below).

*Branisamys* does not group with Dinomyidae as previously proposed (e.g. Patterson & Wood, 1982; Nasif, 2010); instead, it appears as a basal Chinchilloidea, as in previous work (e.g. Kramarz et al. 2013; Rasia & Candela, 2018). The phylogenetic position of *Branisamys* could change if basal taxa of other groups (i.e. Erethizontoidea, Caviioidea and Octodontoidea) are added to the analysis.

'Cephalomyidae' is not recovered as a clade, probably due to the high number of missing data for skull characters,

and it is possible that this could change using different characters. Recent studies (Kramarz, 2001a, 2005; Busker & Dozo, 2018) have recovered Cephalomyidae as a monophyletic group, although none of these includes all known members of the group. As stated by Busker & Dozo (2018), an inclusion of cephalomyids within a more comprehensive analysis, using a larger taxon sampling, could help to elucidate the phylogenetic position of this group, which is still controversial (see Kramarz, 2005; Busker & Dozo, 2018).

In contrast to previous studies (Kramarz, 2001a, 2005) that proposed close relationships between Chinchillidae and Neopiblemidae, our analysis indicates a closer affinity of Neopiblemidae with 'Cephalomyidae'.

The Chinchilloidea *insertae sedis* *Incamys* and *Garridomys* form a clade with the Chinchillidae. This is consistent with the conclusions of Kramarz et al. (2013), who suggested that *Garridomys* could be related to the origin of Chinchillidae.

'Cephalomyidae'+Neopiblemidae forms a clade with *Incamys* (*Garridomys*+Chinchillidae), and it is noteworthy that the grouping of Chinchillidae, 'Cephalomyidae' and Neopiblemidae was previously proposed by Kramarz (2001a, 2005).

## Conclusions

Our comparative analysis of upper molars of living and extinct Chinchilloidea allowed us to identify cusps and lophs in some taxa for which the homologies with these structures were not previously established (i.e. *Prologostomus*, *Lagostomus*, *Lagidium*, *Chinchilla*, *Neopiblema* and *Phoberomys*).

We recognize two upper molar patterns within Chinchilloidea:

- Chinchillidae, Dinomyidae, *Branisamys*, *Incamys*, *Loncolicu*, and *Garridomys* share an upper molar pattern in which the hypoflexus is opposed to the paraflexus/parafossette, and the protoloph is in connection with the hypocone (via the anterior arm of the latter and the mure).
- 'Cephalomyidae' and Neopiblemidae share an upper molar pattern in which the hypoflexus is opposed to the protoloph. When the protoloph is reduced, the second crest or loph is formed by the mesoloph/mesolophule+hypocone.

Following changes during ontogeny, we identified the composition of the lophs in trilophodont and bilophodont upper molars of Chinchilloidea, distinguishing two different patterns:

- In Chinchillidae *Scleromys*, *Loncolicu* and *Garridomys*, the lophs of a trilophodont upper molar correspond to the anteroloph, the protoloph+hypocone and the metaloph+posteroloph (in *Incamys* the third loph including the mesoloph/mesolophule). The lophs of a

bilophodont upper molar correspond to anteroloph and protoloph+hypocone+metaloph+posteroloph.

- In Cephalomyidae and Neopiblemidae, the lophs of a trilophodont upper molar correspond to the anteroloph, the mesoloph/mesolophule+hypocone and the metaloph+posteroloph. In the bilophodont upper molars, the first loph corresponds to the anteroloph and the second loph to the mesoloph/mesolophule+hypocone+metaloph+posteroloph.

Although there are comprehensive studies of cheek teeth homologies of Erethizontoidea (e.g. Candela, 1999, 2002), Octodontoidea (e.g. Carvalho & Salles, 2004; Arnal, 2012; Candela & Rasia, 2012; Verzi et al. 2014; Candela, 2016) and Cavioidae (e.g. Pérez, 2010), the understanding of cheek teeth homologies in Chinchilloidea have so far been incomplete, and limited to family level or lower (e.g. Vucetich, 1989; Kramarz, 2001a,b, 2005; Kramarz et al. 2013). Our work has shed light on the evolution of chinchilloids based on cheek teeth homologies. Future analyses including anatomy of lower molars and upper and lower premolars, as well as the inclusion of more taxa, would increase our knowledge of the evolution of the Chinchilloidea.

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## Author contributions

LLR: study of material, homology discussion, draft of the manuscript, phylogenetic analysis. AMC: study of material, homology discussion, critical revision.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Data S1.** List of material and bibliographic sources used for the phylogenetic analysis

**Data S2.** List of characters used in the phylogenetic analysis

**Data S3.** Data matrix used in the phylogenetic analysis

**Data S4.** Most parsimonious tree showing synapomorphies