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Dental homologies and evolutionary transformations in Caviomorpha (Hystricognathi, Rodentia): new data from the Paleogene of Peruvian Amazonia

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Abstract

Dental homologies and evolutionary transformations within caviomorph rodents have long been disputed. Here, we join to these debates in providing new insights from the dental morphology of Paleogene caviomorphs from Peruvian Amazonia (Contamana and Shapaja). Their analyses and comparisons with many hystricognaths allows (1) to generalize some hypotheses previously proposed about occlusal morphology of caviomorph cheek teeth, and (2) to propose new ones. In caviomorphs, the third crest of upper teeth would correspond either to a mesoloph or to a mesolophule or to a combination of both. The transformation from a pentalophodont pattern to a tetralophodont pattern would be explained by the disappearance of the metaloph. Likewise, the transformation from a tetralophodont pattern to a trilophodont pattern is observed by the loss of the third crest. A direct transformation from a pentalophodont pattern to a trilophodont pattern is also observed. Concerning lower teeth, discrepancies of homologies are centered on the mesial cristids, which can be notably distinguished depending on their compositions and connections with other structures. The ancestral patterns of caviomorph lower molars and dp4s were likely tetralophodont and pentalophodont, respectively. However, schemes with five and four (even three) transverse cristids cannot be ruled out for the two loci, respectively.

Keywords: Caviomorph rodents, Peru, South America, dental morphology, hypotheses of homologies.

Introduction

Homology is usually considered as a fundamental concept in biology, which ‘occupies a central position in comparative studies’, dixit de Pinna (1991). As part of morphological analyses, the identification of structures corresponding to primary homology (*sensu* de Pinna 1991) is a prerequisite, but is not always obvious and often a matter of debate. For instance, the case of the distal crests of upper teeth in caviomorph rodents (Caviomorpha Wood, 1955 or New World hystricognaths) has long been the subject of intense discussions. The diverging proposed homologies have resulted in competing hypotheses regarding the sister group identification of caviomorphs and, hence, in diverging opinions about their geographic origin. Indeed, two main hypotheses were proposed during the twentieth century:

(1) some authors have advocated that a tetralophodont pattern would be the ancestral condition for caviomorph upper teeth, and that these rodents would be closely related to North American rodents: Paramyidae or Sciuravidae (Wood 1949) and then Franimorpha (Reithroparamyinae, Protoptychidae, *Prolapsus*, *Guanajuatomys*, and later Cylindrodontidae; Wood 1980; see also Wood 1950, 1959, 1962, 1965, 1972, 1973, 1974, 1975, 1983, 1984, 1985a, b, 1993; Wood and Patterson 1959; Patterson and Wood 1982);

(2) in contrast, some others have defended the hypothesis according to which the upper teeth of caviomorphs would be primitively pentalophodont, with a pattern similar to that of Old World hystricognaths (Phiomorpha [Thryonomyidae, Bathyergoidea, and Hystricoidea] *sensu* Lavocat 1967). On the basis of these hypotheses of morphological homologies, an African origin of caviomorphs was postulated (Lavocat 1969, 1971, 1973, 1974a, b, 1976, 1977a, b, 1980; Hoffstetter 1971, 1972, 1975, 1976; Hoffstetter and Lavocat 1970).

Since then, the reassessment of the potential links between North American reithroparamyids and hystricognaths (Dawson 1977; Korth 1984; Meng 1990), as well as the formalization of the caviomorph-phiomorph relationships via phylogenetic analyses based on morphological (e.g., George 1993; Luckett and Hartenberger 1993; Marivaux *et al*. 2002, 2004) and molecular data (e.g., Nedbal *et al*. 1996; Huchon et al. 2000, 2002, 2007; Huchon and Douzery, 2001; Montgelard *et al*. 2008; Fabre *et al*. 2012) marked the end of this hotly debated biogeographic issue. The hypothesis of an African origin for caviomorphs, put forward by Lavocat (and collaborators), is now a well-accepted consensus within the scientific community. However, critical factors such as the mode and precise timing of the Afro-South-American dispersal(s), and the pathways by which this (these) dispersal(s) occurred remain still entirely unknown.

Over the past decades, many authors have studied dental homologies and evolutionary patterns in caviomorphs (e.g., Jaeger 1989; Vucetich and Verzi 1994; Verzi *et al*. 2018), notably in erethizontoids (e.g., Candela 1999, 2002) and in octodontoids (e.g., Carvalho and Salles 2004; Candela and Rasia 2012; Candela 2015; Verzi *et al*. 2014, 2016, 2017, 2018). The debates regarding the dental homologies in caviomorphs have then shifted to other structures, such as the mesial cristids of lower teeth (Candela 2002; Carvalho and Salles 2004; Candela and Rasia 2012; Candela 2015; Verzi *et al*. 2014, 2016, 2017, 2018).

Despite the modern and Neogene high diversity of caviomorphs, the early evolutionary history of these rodents has long remained obscure. Until recently, most of the Paleogene caviomorph assemblages were primarily concentrated at middle (Bolivia, Brazil, Chili, southern Peru, and Uruguay) and high (Argentina) latitudes of South America (15/19; see Boivin et al. 2017b and citations therein). By contrast, lower latitudes have long remained poorly documented (Santa Rosa and Lircay, Peru; Foz do Breu and Cachoeira São Salvador, Brazil; Hartenberger *et al*.

1984; Frailey and Campbell 2004; Ribeiro et al. 2013, Kerber *et al*. 2017). During the last decade, the continuing field efforts in Peruvian Amazonia (Contamana and Tarapoto areas) have led to the discovery of about twenty Paleogene localities yielding many fossils of caviomorphs (mainly dental remains; Antoine *et al*. 2016; Boivin *et al*. 2017a, b, 2018). They document three South American Land Mammal Ages (SALMA): Barrancan (late Middle Eocene; Contamana), Tinguiririican (Early Oligocene; Tarapoto, Shapaja section) and Deseadan (Late Oligocene; Contamana). The late Middle Eocene localities have so far yielded the oldest known representatives of the group in South America (Antoine *et al*. 2012; Boivin *et al*. 2017a). The studies of these fossils have revealed a rich specific diversity, most of the species being new for science (Antoine *et al*. 2012; Boivin 2017; Boivin *et al*. 2017a, b, 2018). These ancient fossils have provided unusual dental morphologies for caviomophs, the descriptions and detailed comparisons of which have led us to formulate new hypotheses regarding some structural homologies, and also to further our understanding regarding some aspects of their evolutionary trends. All these observations were at the origin of an updated dental nomenclature, which was proposed in Boivin et al., 2017a, b, 2018). In this paper, we propose a detailed overview of the dental homology and evolutionary transformation hypotheses that we have formulated in light of the dental material from the Paleogene rodent-bearing localities of Contamana and Tarapoto/Shapaja. We provide here an exhaustive morphological analysis of the fossil cheek teeth from these localities, and compare these rodents from Peruvian Amazonia to other extinct New and Old World hystricognaths as well as to extant caviomorphs.

Material and methods

Material

For this study, we considered most of the caviomorph cheek teeth available from the Eocene (Antoine *et al*. 2012; Boivin *et al*. 2017a) and Oligocene (Boivin *et al*. 2017b) localities of Contamana (CTA), and the Oligocene localities of Tarapoto/Shapaja (TAR; Boivin *et al*. 2018). For comparisons, we used a large taxonomic sampling of caviomorphs, including several extinct and extant members of the four superfamilies recorded from low, middle and high latitudes of South America. Our taxonomic material used for comparisons also included some Paleogene representatives of the Old World hystricognaths, which represent among the early hystricognaths known from Asia and Africa (e.g., Wood 1968; Marivaux *et al*. 2000, 2002, 2014, 2017a; Marivaux and Welcomme 2003; Sallam et al. 2009, 2011, 2012; Coster et al. 2012; Sallam and Seiffert, 2016), and are supposed to be close to the caviomorph ancestor. The comparisons were made from the literature or directly with the material (originals or casts) of several institutions. The taxa used for comparisons are listed in Supplementary Online Material.

Dental nomenclature

The terminology used here for the rodent dentition (Figures 1 and 2) is based on:

- Wood and Wilson (1936), Lavocat (1976), Candela (1999, 2002), Marivaux *et al*. (2002, 2004) and Antoine *et al*. (2012) for the cusps, crests and cristids;
- Stirton (1935), Black and Wood (1956), Fields (1957), Candela (1999), Antoine *et al*. (2012) and Marivaux *et al*. (2014, 2017a, b) for the flexi(-ds), fossett(-ids)es and stri(-ds).

Compared with these authors, several modifications regarding the designation of some cusp(-id)s, loph(-id)s, and flexi(-ds) are the results of our own observations and interpretations of the material we have studied and used for comparisons. These modifications, based on distinct homology hypotheses, are abundantly discussed here, and were considered for the selection of characters and character states used by Boivin (2017) and Boivin et al. (submitted) for their large scale cladistic analysis of caviomorph rodents. Some of these characters and character states have already been introduced by Boivin and Marivaux in Boivin *et al*. (2017a, b, 2018), and used by Marivaux *et al*. (2017a) at a wide taxonomic scale (i.e., for Old World hystricognaths). Upper case letters are used here for the upper dentition (DP: for deciduous premolar, P: for premolar, M: for molar) and lower case letters for the lower dentition (dp: for deciduous premolar, p: for premolar, m: for molar).

Criteria for homologies

For the recognition of dental homologies, we followed the anatomical definition of homology (i.e., primary homology *sensu* de Pinna 1991), and used notably the interdependent criteria of topology and connectivity between structures (Rieppel 1988, 1994). We also used two other criteria: the position of structures relative to each other and their orientation (the latter aspect being applied only for loph(-id)s). We did not used directly the shape and size criteria for homology identification, but we considered the variations of both the shape and size (in surface and height) of the structures in one taxon or closely related taxa, which could be informative for the understanding of homology recognition and evolutionary tendencies. The latter aspect joins the third criterion of Remane (1952) for identifying homologies: criterion of continuity or connection through intermediate forms (the latter being either ontogenetic stages or systematically intermediate species). For each taxon, when the available material was sufficient, we examined the intraspecific variation (inter-individual variation) in analysing dental specimens of several individuals. We focused with special interest on juvenile specimens (when available) having germs or little worn teeth, for which the dental structure recognition was obvious (not erased by wear). The morphological comparisons between many New and Old World hystricognaths allowed the proposition of dental homology hypotheses (conjectures of homologies) that can be applicable at the caviomorph scale, or at least for the less or moderately specialized taxa. We compared our proposed hypotheses of dental homologies with alternative plausible hypotheses proposed and discussed in the literature (synthetized in the section 'Historical review and current state of caviomorph dental structures', see below). The dental homology hypotheses proposed here have been evaluated by a cladistic assessment (Boivin 2017; Boivin *et al*. submitted; i.e, test of congruence; see Rieppel 1988; de Pinna 1991; Rieppel and Kearney 2002) in order to provide a phylogenetic context and to identify structures shared from a common ancestor (secondary homology *sensu* de Pinna 1991). In this paper, the schematic line drawings focus exclusively on the occlusal morphology and transformations of some parts (specified in each case) of considered loci. The other occlusal areas and structures remain voluntarily unchanged (i.e., the schemes do not refer to any occlusal pattern of a specific taxon).

Institutional abbreviations

MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; **MLP**: Museo de Ciencias Naturales de La Plata, La Plata, Argentina; **MMP**: Museo de Ciencias Naturales de Mar del Plata, Lorenzo Scaglia, Mar del Plata, Argentina; **MNHN**: Musée national d'Histoire naturelle, Paris, France; **MNHN-Bol-V**: Museo Nacional de Historia Natural, La Paz, Bolivia; **MN-UFRJ:** Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **MPEF**: Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MPM-PV**: Museo Regional Provincial 'Padre Manuel Jesús Molina', Río Gallegos, Argentina; **MUSM**: Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Peru; **MVZ**: Museum of Vertebrate Zoology, University of California, Berkeley, USA; **UATF**: Universidad Autónoma Tomás Frías, Potosí, Bolivia; **UM**: Universite de Montpellier, Montpellier, France.

Other abbreviations

GSP: Yale-Geological Survey of Pakistan**; Z5R**: Zallah 5 Rodent Locality.

Historical review and current state of caviomorph dental structures (homologies and nomenclature)

Upper teeth

Stirton (1935), then Wood and Wilson (1936) were the first to propose/formalize a nomenclature of cusps, crests, cristids and flexi(-ids), applicable to the cheek tooth morphology of rodents, a nomenclature which was consistent with the tribosphenic plan characteristic of Theria, as defined by Simpson (1936) based on Osborn (1907). Throughout the description of *Platypittamys* (Scarritt Pockett, Argentina; Deseadan), Wood (1949) applied the Wood and Wilson nomenclature to caviomorphs. Their proposition was subsequently completed and formalized by Wood and Patterson (1959), and later by Patterson and Wood (1982). For tetralophodont teeth, these authors recognized successively on a mesiodistal axis, an antero-, meta-, hypo- and posterolophid on lower teeth, and an antero-, proto-, meta- and posteroloph on upper teeth. According to these authors, the tetralophodonty of upper molars was likely the ancestral condition in caviomorphs, and the pentalophodonty was developed secondarily in some groups, by the addition of a neoloph situated between the metaloph (then constituting the third loph) and the posteroloph (the fifth loph; Figure 3(A)). The pentalophodonty of lower molars (as well as for dp4s and p4s) was also interpreted with the addition of a neolophid (Figures 4(A) and 5(A)).

After studying the fossil rodents from Salla (Bolivia; Deseadan), Hoffstetter and Lavocat (1970) and Lavocat (1976) proposed, however, another interpretation of the crest homologies for describing the pentalophodonty of upper molars, a view which was compatible with that of Schaub (1953) (Figure 3(B)). For these authors, the configuration of the teeth would be similar to that found in the Theridomyidae and Old World hystricognaths (Phiomorpha *sensu* Lavocat 1967): the third crest would be a mesoloph (that can be linked to a transversal crest stemming from the anterior arm of the hypocone; Lavocat 1976, figure 4, p. 71) labially connected to a mesostyle, and the fourth crest would be a metaloph labially connected to the metacone (Figure 3(B)). They interpreted the tetralophodonty of caviomorphs as a simplification (i.e., loss of the metaloph) from a pentalophodont ancestral state. They provided several arguments in favor of this hypothesis:

- in addition to the formerly known pentalophodont taxa *Protosteiromys* (Cabeza Blanca and La Flecha, Argentina; Deseadan; Wood and Patterson 1959), the fact that three new genera from Salla (*Branisamys*, *Incamys*, and *Sallamys*) also exhibited a pentalophodont pattern of upper molars, revealed that the pentalophodonty was rather common among early caviomorphs (known in the 1970s) and likely primitive;

- the taxa with a well-defined and long metaloph (*Branisamys* and *Protosteiromys*) exhibit brachydont teeth, a crown state which would rather indicate a plesiomorphous condition for the metaloph configuration;
- *Incamys* shows a vestigial metaloph as in *Thryonomys* (i.e., the modern African cane rat), in which this crest originates from the well-developed metaloph of Miocene 'phiomorphs';
- *Sallamys* has a P4 that is structurally much simpler than the condition observed in *Platypittamys*, and also exhibits a very large infraorbital foramen, a condition which would suggest that the absence of P4 complexity is not primitive;
- the Salla rodents are very similar to the early 'phiomorphs' known in the 1960s (i.e., Early Oligocene of Fayum, Egypt; Wood 1968), notably in the morphology of their upper molars. Their pattern can be explained by the reductions or loss of connections between crests from a fundamental pattern illustrated by the African *Phiomys andrewsi* (Early Oligocene; Wood 1968; Lavocat 1976, figure 4(D), p. 71).

The two competing hypotheses have generated hotly debated issues regarding caviomorph geographic origins, notably the North American origin defended by Wood (and collaborators) *versus* the African origin defended by Lavocat (and collaborators) (see Introduction). It is worth noting that Butler (1985) questioned Wood's hypothesis of homologies (Wood 1949), inasmuch as the dental pattern of upper molars would be a non-functional configuration (i.e., the paracone being closer to the metacone than the protocone to the hypocone). This argument was later used by Candela (1999) who also noted in erethizontoids that the third labial cusp is larger in both surface and height than the second one, thereby suggesting a pattern including a mesostyle-metacone complex, the latter topology being more consistent with the Lavocat's hypothesis of homologies (Lavocat 1976). Jaeger (1989) and Vucetich and Verzi (1994) followed Lavocat's view but diverged regarding the pattern of simplification leading to a tetralophodonty from a pentalophodont scheme. Based primarily on Salla rodents, Jaeger (1989) interpreted the third crest of tetralophodont upper molars of *Sallamys* as the result of a fusion between the metaloph and the mesoloph. In this context, the latter was not considered to be the homologuous structure as that observed in Old World hystrognaths. These crests, although occupying an analogous position would be developed independently in each group as a result. Vucetich and Verzi (1994) also analyzed the Salla rodent fauna in performing a more extensive comparative analysis, and considering many other extinct and extant taxa. According to them, the transformation from a pentalophodont to a tetralophodont pattern would also include the fusion of the metaloph with another crest, but the latter would be the posteroloph instead of the mesoloph. These authors recognized that a fusion between the mesoloph and the metaloph is possible, like on the M2 of the *Branisamys* holotype (MNHN SAL 102, Lavocat 1976: plate 2.4). Nevertheless, this fusion would be particular in *Branisamys*, generating a part of the intraspecific variation observed in this taxon. Bryant and McKenna (1995) also advocated that the pentalophodonty of upper molars is the ancestral condition of caviomorphs, but in considering that the third crest of Old World hystrognaths and caviomorphs is neither a mesoloph nor a metaloph, but rather a mesolophule (Figure 3©). This structure was originally defined by Flynn *et al*. (1986) in Baluchimyinae (Chapattimyidae *sensu* Flynn *et al*. 1986; Hystricognathi *incertae sedis sensu* Marivaux *et al*. 2002) as being the crest originating from the metaconule and running towards the labial edge of the tooth (Flynn *et al*. 1986; Marivaux 2000; Marivaux *et al*. 2000, 2002, 2004; Marivaux and Welcomme 2003). In studying the morphology of the upper molars of fossil and modern erethizontoids, Candela (1999) showed that the third crest is either continuous or discontinuous in this superfamily. When discontinuous, this crest is formed by a lingual portion linked to a metaconule (corresponding to a mesolophule) and a neoformed labial portion stemming from the mesostyle (Figure 3(D)). Given these observations, Candela (1999) proposed a pre-pentalophodont step as the ancestral condition in erethizontoids, a pattern in which the metaloph is still connected to the hypocone. Subsequently, this connection would be lost, and the metaloph would be linked to the posteroloph. A continuous third crest would be formed by the fusion of the mesolophule with the neocrest of the mesostyle.

Over the past three decades, the hypothesis of an African origin of caviomorphs, closely related to the 'phiomorphs', has gained strong support. The phiomorph-caviomorph relationship derives from a corpus of morpho-anatomical and genetic data (see Introduction), other than the dental morphology only. Such a strongly supported phylogenetic relationship between Old and New World hystricognaths then supports Lavocat's dental homology hypothesis, which has now reached a well-accepted consensus, althrough some authors have continued to follow the nomenclature proposed by Wood (Carvalho and Salles 2004; Frailey and Campbell 2004). Since the 1990s, the discussions have progressively focused on the homology of the third crest on upper molars, considered as either a mesoloph or a mesolophule (see above). Marivaux (2000) studied the early radiation of Paleogene rodents via a phylogenetic approach, in order to better understand the patterns of dental transformations through time, and to identify homoplasic structures. In related papers, Marivaux *et al.* (2002, 2004) proposed a general dental terminology applicable to the whole group (at least to their Paleogene representatives and more recent forms moderately derived from a dental point of view). In this nomenclature, the third crest of upper molars can be formed by (1) a lingual part, the mesolophule (*sensu* Flynn *et al*. 1986) that is connected to the metaconule (conule that can disappear in some groups like caviomorphs and advanced ‘phiomorphs’), and (2) a labial part, named mesoloph, originating from the mesostyle and running lingually (Figure 3(E)). This nomenclature was consistent with that proposed by Candela (1999). However, Marivaux *et al*. (2004) recognized only a mesolophule as the third crest in the sampled Paleogene Ctenohystrica (caviomorphs included, but limited to few Deseadean forms; the Afro-Asian hystricognaths being also less known and documented at that time), the mesoloph being observed only in some Ischyromyiformes (Anomaluroidea, Zegdoumyidae, Eutypomyidae, Gliridae, Sciuravidae, and Theridomyidae). This terminology has been applied by Marivaux for the original description of caviomorphs from CTA-27, which are among the most ancient representatives of the group known thus far (Barrancan; Antoine *et al*. 2012; Figure 3(F)). The dental morphology of some of these rodents (*Cachiyacuy* and *Canaanimys*), characterized by pentalophodont upper molars, is very similar to that of Old World hystricognaths and especially to some Paleogene African forms. The discovery of these early caviomorph taxa from the late Middle Eocene of Peruvian Amazonia has provided key elements, which have strengthened support for Lavocat’s hypotheses regarding caviomorph origin and dental evolutionary patterns (i.e., African origin of caviomorphs and ancestral pentalophodont pattern of upper molars in this group; Hoffstetter and Lavocat 1970; Lavocat 1976).

Lower teeth

Although less controversial than for upper teeth, the structural homologies on lower teeth have often been questioned, notably regarding the identification of the mesial cristids. According to Candela (2000), based on Wood and Wilson (1936), the second cristid of lower molars in erethizontids would be a metalophulid II or a mesolophid, depending on the connected cuspids (protoconid-metaconid or mesoconid-mesostylid, respectively; Figure 4(B)). Candela (2002) studied the dp4 morphology of extinct and extant erethizontids and compared it with that of dp4s of some fossil Old World hystricognaths (i.e., *Baluchimys*, *Gaudeamus*, *Lindsaya*, *Phiomys*, and *Tsaganomys*). The morphologies being very similar, she concluded that they are probably homologous, and that the ancestral pattern of erethizontid dp4s (and probably, more generally, of hystricognaths dp4s) is pentalophodont, contrary to Wood and Patterson (1959). On lower teeth, based on Wood and Wilson (1936), she recognized successively an anterolophid, metalophulid II, mesolophid, hypolophid and posterolophid (Figure 5(B1)). The tetralophodont scheme would be developed subsequently in *Hypsosteiromys* and some specimens of *Erethizon dorsatum* by the loss of the mesolophid (Figure 5(B2)). The hexalophodont pattern of some erethizontids (i.e., *Eosteiromys homogenidens*, *E. dorsatum*, *Steiromys detentus*, *S. duplicatus*, and *Coendou prehensilis*) would be also achieved from the pentalophodont ancestral configuration, by the addition of a neolophid between the anterolophid and the metalophulid II (Figure 5(B1)). Candela (2002) identified the same hexalophodont morphology on one dp4 of *Branisamys* (UM GN 014; Hartenberger 1975; Patterson and Wood 1982), a taxon from Salla initially described as a dasyproctid cavioid (Lavocat 1976). Based on this observation, as well as on other cranial and dental features characterizing erethizontids, Candela (2002) advocated a potential affiliation of *Branisamys* to the New World porcupines.

The nomenclatures used so far for the studies on hystricognaths (and more generally other rodent groups) have often been inconsistent across authors. This lack of uniformity (standard usage) has somewhat engendered a degree of confusion in the terminology: e.g., cingulum/anterior cingulid, anterolophid, paracristid/paralophid, metalophid, metalophid I, protolophid/protocristid, metalophid II, metalophulid I, metalophulid II, and posterior arm of the protoconid (e.g., Wood 1968; Dawson 1984; Flynn *et al*. 1986; Korth 1994; Kumar *et al*. 1997; Wang 1997; Meng and Wyss 2001). The nomenclature proposed by Marivaux *et al*. (2004), modified from that of Wood and Wilson (1936), allowed, to some extent, for a first step of clarification of these issues, notably on the homologous structures used for discriminating the anterior cristids of lower molars. Following this terminology, basal rodentiaforms display a trigonid with a paralophid/paracristid linking the protoconid to the reduced paraconid, as well as a metalophulid II (protolophid/protocristid = long posterior arm of protoconid) connecting the protoconid to the metaconid (e.g., *Tribosphenomys*). The paraconid is subsequently lost and the paralophid joins lingually the metaconid, then becoming a metalophulid I (e.g., *Archetypomys*, *Cocomys*). A low anterior cingulid can be present in some “ctenodactyloids” and “ischyromyoids”. In the latter group, this cingulid iteratively developed to reach a lophid status, becoming the anterolophid, and in some cases replacing the metalophulid I, which is lost in some forms (for a synthesis, see Marivaux *et al*. 2004, p. 120). In this context, Marivaux et al. identified on caviomorph lower molars a metalophulid I, a metalophulid II, a hypolophid, and a posterolophid (Figure 4(C)). According these authors, these same cristids are present on dp4s, and a mesolophid can be additionally developed between the metalophulid II and the hypolophid (Figure 5(C)). This terminology was used by Antoine *et al*. (2012). Candela and Rasia (2012) extended this nomenclature to dp4s and lower molars of echimyids (the more diversified octodontoid group) and questioned previous terminologies of Patterson and Wood (1982; Figures 4(A) and 5(A)) and Carvalho and Salles (2004; Figures 4(A) and (D), 5(A) and (D)) based on cladistic assessments (Figures 4(E) and 5(E)). Following their results, the tetralophodonty would be the ancestral condition of lower molars in echimyids, the pentalophodonty and trilophodonty (which appears at least three times independently) would be derived. Candela and Rasia (2012) shared, however, the view of Patterson and Wood (1982) and Carvalho and Salles (2004) in the interpretation of the second cristid of pentalophodont lower molars (in *Hoplomys*), which would be a neoformed structure called neolophid (Figure 4(E1)). As for erethizontids (Candela 2002), the pentalophodonty would be the plesiomorph condition for echimyid dp4s, and the tetralophodonty would be the apomorph state. Lastly, these authors interpreted the “crest C” of dp4s and lower molars of some echimyids (i.e., *Clydomys*, *Euryzygomatomys*, *Lonchothrix*, *Mesomys*, *Proechimys*, *Therisomysops*, or *Trinomys*) as being a metalophulid II, more or less long and curved (Figures 4(E2) and 5(E2)). This cristid was originally defined by Carvalho and Salles (2004) as a metalophid merged with a neolophid (Figures 4(D) and 5(D)). Recently, Verzi *et al*. (2014, 2016, 2017) have considered the second cristid of lower molars in some octodontoids as a mesolophid (*Myocastor*, *Acaremys* in Verzi *et al*. [2014, figure 5(D), p. 763]; *Acaremys* and gen. et sp. nov. in Verzi *et al*. [2017, figure 5(B) and (F), p. 418]) or a combination of a metalophulid II with a mesolophid (e.g., *Proechimys*, *Myocastor*, *Acarechimys* in Verzi *et al*. [2016, figures 1–3, p. 96–98]; and potentially *Acarechimys*, *Plesiacarechimys*, and *Protacaremys* in Verzi *et al*. [2017, figures 4(C), (F) and (G), p. 417]; Figure 4(F1)). In the case of the lower molars of *Hoplomys*, Verzi *et al*. (2016) have interpreted the second cristid (“crest C”/neolophid *sensu* Carvalho and Salles [2004] and Candela and Rasia [2012], respectively) as a metalophulid II, and the third cristid (metalophulid II *sensu* Candela and Rasia [2012]) as a mesolophid (Figure 4(F2)). Following Arnal (2012) and Candela and Rasia (2012), Candela (2015) questioned the hypothesis advanced by Verzi *et al*. (2014, and subsequently Verzi *et al*. 2016, 2017). According to Candela (2015), in all octodontoids, the second cristid of lower molars would correspond to a metalophulid II with notable variation in orientation, size and shape, but not to a mesolophid. Recently, Verzi *et al*. (2018), analyzing dp4s of caviomorphs of the four superfamilies and ancient representatives of New and Old World hystricognaths, have considered that a hexalophodont scheme is the ancestral condition for this locus in caviomorphs. This scheme would be characterized by an anterolophid, metalophulid I, metalophulid II, mesolophid, hypolophid and posterolophid (Figure 5(F)). From this ancestral condition, more simple patterns would derive with firstly the loss of the metalophulid I.

Results

Upper teeth

The third transverse crest

Marivaux (2000) and Marivaux *et al*. (2002, 2004) have highlighted the third crest of the upper molars, which can comprise a lingual part, the mesolophule stemming from the metaconule (conule that can disappear in caviomorphs), and a labial part, the mesoloph originating from the mesostyle. Based on the available taxonomic sample, it was shown that the mesoloph is present more specially in some Ischyromyiformes (*sensu* Marivaux et al. 2004), and that the third crest of the upper molars in Ctenohystrica (including caviomorphs [but limited to *Incamys*, *Branisamys*, *Sallamys*, and *Platypittamys*]) corresponds only to a mesolophule (see section 'Historical review and current state of caviomorph dental structures'). However, the New World hystricognaths included in the analysis were limited and inufficient to appreciate variability of the third crest configuration (works otherwise focused on Old World hystricognaths). In parallel, Candela (1999) observed that the third crest of erethizontid upper molars can be discontinuous, and in this case, in addition to a mesolophule, there is a labial crest neoformed from the mesostyle.

Following the nomenclature proposed by Marivaux *et al*. (2004), this labial crest is an equivalent of the mesoloph.

On several upper teeth of early caviomorphs from the Eocene of Contamana (e.g., MUSM 1873, 2801, 2819, 2832), the third crest is clearly discontinuous and formed by two portions: a mesoloph and a mesolophule (Figure 6). The study of the entire fossil material from Contamana and Tarapoto/Shapaja has revealed that the third crest morphology is very variable (Boivin *et al*. 2017a, b, 2018). Indeed, it can be composed of the mesoloph and mesolophule, connected either with each other (Figure 6(A)) or not (Figure 6(B)). It can also be only formed by the mesolophule (e.g., general case of upper molars of *Mayomys*; Figure 6(C) and (D)) or only by the mesoloph (e.g., general case of upper molars of three species of *Eoincamys* from Tarapoto/Shapaja; Figure 6(E) and (F)) (Boivin *et al*. 2018). Besides, the mesoloph and mesolophule are also strongly variable in terms of length (Figure 6(A–F)), orientation and connections with other elements (i.e., with the mesostyle, anterior arm of the hypocone, metaloph, or posteroloph). The third crest composition is sometimes hardly interpretable, notably when (1) this crest is fully transverse from the mesostyle to anterior arm of hypocone without discontinuity or mesiodistal pinch-point (Figure 6(G)), or (2) it displays several discontinuities or mesiodistal pitch-points (Figure 6(H)). When no interpretation/distinction can be made, the term “third transverse crest” is then used. In addition to erethizontoids (Candela, 1999), other fossil and modern caviomorphs, such as species of Santa Rosa, those of Salla, but also *Australoprocta*, *Garridomys*, *Eoviscaccia*, *Willidewu*, *Protadelphomys*, *Proechimys*, or *Mesomys* display upper molars with a mesoloph, accompanied or not by a mesolophule (Lavocat 1976; Patterson and Wood 1982; Vucetich and Bond 1984; Vucetich and Verzi 1991; Kramarz 1998, 2001a; Frailey and Campbell 2004; Kramarz *et al*.

2013). In this context, the observations made by Candela (1999) on erethizontoid upper molars must be generalized to the whole caviomorph group and for all upper loci (i.e., P4, DP4, and M1–3).

Terminology of flexi

The flexus nomenclature of upper teeth used in Boivin *et al*. (2017a,b) follows that of Candela (1999). For pentalophodont teeth, this nomenclature recognizes, labially a paraflexus, mesoflexus, metaflexus and posteroflexus, and lingually the hypoflexus. Nevertheless, it is not consistent with the original definitions of the metaflexus and mesoflexus proposed by Black and Wood (1956). According to these authors, the metaflexus is distal to the mesoflexus and should be the posteroflexus *sensu* Candela (1999). The third crest being a secondary formation with respect to the ancestral pattern of rodents (see Marivaux *et al*. 2017a, b), the mesoflexus *sensu* Black and Wood (1956) corresponds to the mesoflexus plus metaflexus *sensu* Candela (1999). In Boivin *et al*. (2018), we proposed a new terminology in order to distinguish both flexi separated by the third crest: the mesial mesoflexus (mesoflexus *sensu* Candela 1999) and the distal mesoflexus (metaflexus *sensu* Candela 1999) (Figure 7).

Pentalophodont, tetralophodont and trilophodont patterns

Old and New World fossil evidence and phylogenetic inference (e.g., Marivaux et al. 2002, 2004; Antoine et al. 2012; Sallam and Seiffert, 2016; Boivin 2017; Boivin et al. 2017a, submitted) substantiate the hypothesis that the ancestral occlusal pattern of caviomorph upper molars is composed of five transverse crests (see section 'Historical review and current state of caviomorph dental structures'). As for the upper molars, the ancestral condition of P4s and DP4s is aslo considered as a pentalophodont scheme. However, on the basis of the phylogenetic results of Boivin (2017) and Boivin *et al*. (submitted), the characters corresponding to the presence/absence of the metaloph on P4s and DP4s (see coding of the characters 68 and 115 in Boivin 2017 and Boivin *et al*. submitted) have an ambiguous distribution in the basal branches of caviomorphs. These ambiguities can be explained by an important polymorphism of these characters in stem-caviomorphs (e.g., *Cachiyacuy contamanensis* or *Tarapotomys subandinus*) and their non-coding for some taxa without documented P4 and/or DP4. According to the nomenclature developed and adopted in this paper (Figures 1 and 2; see the paragraph 'The third transverse crest' above), an anteroloph, protoloph, third transverse crest (mesoloph and/or mesolophule), metaloph and posteroloph can therefore be distinguished on pentalophodont upper teeth.

In caviomorphs, the tetralophodont pattern, deriving from the pentalophodont ancestral scheme (transformation cladistically supported in Boivin 2017 and Boivin *et al*. submitted), is frequently developed on upper molars (Figure 8). Several taxa from Contamana (primarily Eocene localities) and Tarapoto/Shapaja demonstrate of the transformation from a pentalophodont pattern to a tetralophodont pattern: *Eoespina* sp. from CTA-51, *Cachiyacuy contamanensis*, *Cachiyacuy kummeli*, *Canaanimys maquiensis* and cf. *Eoespina* sp. from CTA-27, *Pozomys ucayaliensis* and *Cachiyacuy* cf. *contamanensis* 2 from CTA-29, *Chambiramys sylvaticus* from CTA-61 (Late Oligocene), as well as *Eoincamys valverdei* and cf. *Tarapotomys* sp. from TAR-20 and TAR-21, *Tarapotomys subandinus*, *Tarapotomys mayoensis* and *Mayomys confluens* from TAR-01 (see Boivin *et al*. 2017a, b, 2018). In these taxa, the metaloph tends to be lost: it is reduced and seems to merge with the posteroloph, especially in advanced stages of wear

(Figure 8). In these taxa, the metacone is usually linked to the posteroloph and tends also to merge with the latter (subsumed), thereby forming a posteroloph-metacone-metaloph complex in the posterolabial part of the tooth (Figure 8). Nevertheless, the metacone is sometimes still distinct and well-defined, as in *Eoincamys valverdei*. Similar observations were previously made in other caviomorphs (e.g., *Incamys* or *Draconomys*; Vucetich and Verzi 1994; Vucetich *et al*. 2010a; Verzi *et al*. 2016) that led Vucetich and Verzi (1994) to propose the hypothesis according to which a tetralophodont pattern would derive from a pentalophodont pattern, notably by the reduction of the metaloph subsumed within the posteroloph (Figure 8; see section 'Historical review and current state of caviomorph dental structures'). This pattern of occlusal transformation seems to be the rule in caviomorphs and to have occurred iteratively during the Paleogene. Some specimens (e.g., MUSM 2792–2794 from CTA-27) show a metaloph reduced to a very short spur nonetheless. Therefore, a loss of the metaloph (by complete reduction not by incorporation within the posteroloph) cannot be ruled out in some cases (Figure 8). Vucetich and Verzi (1994, p. 66) also seem to consider as possible complete reduction (= loss) of the metaloph: '*primero*, *el metalofo se reduce o se fusiona al pósterolofo*, *dando como resultado el primer patrón tetralofodonte*'. Contrary to some Old World hystricognaths such as *Paraphiomys* and *Thryonomys*, no caviomorph seems to develop a tetralophodont pattern as the result of the reduction of the third crest on upper molars.

Vucetich and Verzi (1994) defined two main types of tetralophodont patterns on upper molars, depending on the morphology of the third crest (mesoloph *sensu* Vucetich and Verzi 1994). The first pattern is characterized by a complete third crest stretching from the mesostyle to the anterior arm of the hypocone, whereas for the second pattern, this same crest is more reduced and is lingually linked to the posteroloph (Figure 8). In the first case, the third crest can be composed of a mesoloph and/or a mesolophule, whereas in the second case, it would correspond to a mesoloph (backwardly curved), the mesolophule being absent (or lost).

The first scheme is typical of octodontoids but it is also observed in some erethizontoids (*Eopululo*, *Hypsosteiromys*, ?*Neosteiromys tordillense*, *Steiromys detentus*, *Neosteiromys bombifrons*, and *Protosteiromys pattersoni*; Vucetich *et al*. 1993, 2010b; Candela 2000, 2004; Frailey and Campbell 2004; Pérez *et al*. in press) and in several taxa considered here as stem-caviomorphs (e.g., *Cachiyacuy*, *Canaanimys*, *Eoespina*, *Pozomys*, *Ucayalimys*, *Plesiosteiromys*, or *Tarapotomys*; see Boivin 2017 and Boivin *et al*. submitted). In octodontoids (e.g., *Platypittamys* or *Dudumus*; Wood 1949; Arnal *et al*. 2014), the tetralophodont pattern of upper molars is associated with four main cusps: the paracone, protocone, hypocone and a cusp situated labiodistally, usually joined to the posteroloph with wear. Owing to its large size (in height and surface) and its distal position on the occlusal surface, the latter cusp has often – and logically – been considered as a metacone (e.g., Vucetich and Kramarz 1993; Vucetich and Verzi 1996; Arnal and Vucetich 2015; Arnal *et al*. 2014). However, in some cases, this distolabial cusp may be a large and displaced mesostyle. This new nomenclatural assumption is supported by several observations:

- some upper molars of the octodontoid *Protadelphomys* (Vucetich and Bond 1984; Vucetich *et al*. 1992) retain a reduced metaloph associated with a metacone positioned very distally and slightly lingually, and which appears smaller than the mesostyle;
- some octodontoids (e.g., *Galileomys antelucanus*; Vucetich and Kramarz 2003) have on some of their upper molars a third transverse crest, which clearly originates from this labiodistal

cusp. In *Galileomys antelucanus*, the third crest is lingually extended and connected to the anterior arm of the hypocone. A short mesolophular spur is sometimes distinct. This morphology recalls the condition found in some taxa such as *Cachiyacuy* and *Eobranisamys javierpradoi*, and thus can be interpreted as a third crest essentially formed by a long mesoloph stemming from the mesostyle. A metacone-metaloph complex is highly doubtful, the metaloph being very rarely connected to the anterior arm of the hypocone in caviomorphs. A metaloph-anterior arm of the hypocone connection is only observed in two ancient caviomorphs (and basal): *Cachiyacuy* and *Canaanimys*. Aditionnally, the metaloph seems to disappear in octodontoids, as observed in *Plesiacarechimys* or *Draconomys* (Vucetich and Vieytes 2006; Vucetich *et al*. 2010a);

- lastly, the abundant taxon in TAR-01, *Mayomys confluens*, shows affinities with octodontoids (Boivin 2017; Boivin *et al*. 2018, submitted). The morphology of its upper molars appears intermediary (for considered characters), between the ancestral pentalophodont pattern and the tetralophodont pattern typical of octodontoids. Such a configuration highlights the understanding regarding the identification of the labiodistal cusp. In *Mayomys*, the tetralophodont scheme is dominant, with a metaloph sometimes vestigial but absent in most cases. A metacone, distal to the mesostyle, is clearly distinct on some M3s (MUSM 3462 and 3480; Boivin et al. 2018, figure 4S, p. X) and merged with the posteroloph and/or the mesostyle with wear (e.g., MUSM 3461; Boivin et al. 2018, figure 4N, p. X). On M1–2s, only one labiodistal cusp is present. It is interpreted as a mesostyle due to, (1) its position moderately close to the paracone; (2) a third crest (usually a mesolophule) broadly transverse and aligned with this cusp (both structures can be joint), and (3) the presence of a very extensive distal flexus. The metacone is subsumed within the posteroloph in most cases. The MUSM 3462 M3 has a large and distally displaced mesostyle, with a labiodistal-linguomesial obliquity of the third crest, and a marked expansion of the distal flexus, which are typical features of octodontoids (e.g., *Caviocricetus*, *Dudumus*).

However, it is worth noting that on some specimens of *Sallamys pascuali* from Salla (MNHN-Bol-V-004256, -007382, -007589, -007823, and -011054), the mesostyle appears associated (i.e., very closely situated or twinned) to a distal cusp, interpretable as a metacone. On these specimens, the mesostyle can be larger than the metacone (MNHN-Bol-V-007589), but the reverse is also observed (MNHN-Bol-V-007382 and -011054). Hence, total loss of the metacone may not have occurred in all octodontoids. A fusion between the mesostyle and the metacone is also possible (as in the erethizontoid *Erethizon* and *Coendou*; Boivin 2017 and Boivin et al. submitted), and as such the hypothesis of loss of the mesostyle instead of the metacone cannot be completely excluded in this superfamily.

The second scheme of tetralophodonty defined by Vucetich and Verzi (1994) would be a characteristic of chinchilloids. Indeed, this morphology is developed in several fossil chinchilloids (e.g., *Scleromys angustus*, *Eoviscaccia australis*, and *Garridomys curnunuquem*; Ameghino 1887; Kramarz 2001a; Kramarz *et al*. 2013), taxa originally described as dasyproctids but which would show closer affinities with chinchilloids (e.g., *Microscleromys cribriphilus*, *Eoincamys pascuali*, and *Eoincamys parvus*; Walton 1997; Frailey and Campbell 2004; Boivin *et al*. 2018), and in the octodontoid *Protadelphomys latus* (Vucetich and Bond 1984). Such a case of tetralophodonty also tends to be developed in other taxa such as: the chinchilloid *Eoincamys ameghinoi*, *Eoincamys valverdei*, *Chambiramys sylvaticus*, *Incamys bolivianus*, *Maquiamys praecursor*, *Scleromys quadrangulatus* and *Microscleromys paradoxalis*, and the octodontoid *Sallamys pascuali* (Lavocat 1976; Patterson and Wood 1982; Walton 1997; Frailey and Campbell

2004; Kramarz 2006a; Boivin 2017; Boivin *et al*. 2017b, 2018, submitted). In these species, the mesoloph is reduced and it loses its connection(s) with the anterior arm of the hypocone or the mesolophule (which is strongly reduced or absent), its lingual part is oriented toward the posteroloph and, in some cases, connects to the latter. In some of these taxa (*E. valverdei*, *C. sylvaticus*, *I. bolivianus*, *S. pascuali*, and *P. latus*), a short metaloph can be still present. With wear, the mesoloph and mesostyle tend to be subsumed within the posteroloph (and the metaloph, if it is still present), thus forming a large distolabial complex/platform as observed on upper molars of *S. pascuali*, *E. valverdei*, and species of *Scleromys*. This complex is suspected on M1–2s of *Willidewu*, which have three transverse crests including a very thick posteroloph (Vucetich and Verzi 1991, 1994). This configuration being very similar to that observed for the metaloph, Vucetich and Verzi (1994) and Verzi *et al*. (2016) have proposed that the transformation from a tetralophodont pattern to a trilophodont pattern can be explained by the loss of a crest (i.e., mesoloph *sensu* Vucetich and Verzi 1994; mesolophule *sensu* Verzi *et al*. 2016; called third transverse crest here) merging with the posteroloph. This transformation allows explaining the dental pattern of upper molars of *Chambiramys shipiborum* from CTA-32 (Late Oligocene). Indeed, this taxon displays trilophodont upper molars, with a mesostyle distally displaced and strongly linked to the posteroloph and structures associated to the posteroloph, which are likely the relicts of the third crest or its connection with the posteroloph (on MUSM 2849 and 2852; Boivin *et al*. 2017b, figure 4B, C, p. 77). With wear (MUSM 2851; Boivin *et al*. 2017b, figure 4D, p. 77), all of these structures merge and form a large complex (i.e., platform).

The observations made here, supported by phylogenetic results of Boivin (2017) and Boivin *et al*. (submitted) and consistent with the proposition of Vucetich and Verzi (1994), allow to explain the transformation from a pentalophodont pattern to a tetralophodont pattern: the metaloph would merge with the posteroloph or it would be lost. Concerning the tranformation from a tetralophodont pattern to a trilophodont pattern, in this case it is the third crest (mesoloph *sensu* Vucetich and Verzi 1994; mesolophule *sensu* Verzi *et al*. 2016) which would merge *in fine* with the posteroloph or would disappear, the metaloph being already absent or subsumed (indistinct) within the posteroloph (Figure 8). Nevertheless, these transformations do not necessarily occur in an ordored fashion (i.e., a trilophodont scheme deriving from a tetralophodont scheme, itself deriving from the pentalophodont scheme). As a matter of fact, some taxa, such as *E. valverdei*, still have a metaloph in addition to the reduced third crest, all of these structures tending to merge with the posteroloph. These taxa would then illustrate a direct transformation from a pentalophodont to a trilophodont pattern (Figure 8).

Interestingly, in the extant octodontoid *Euryzygomatomys*, the trilophodonty of upper molars seems not to follow a scheme of occlusal transformations presented above. Indeed, its trilophodont pattern would be linked to the loss of the labial protoloph instead of the third crest (always present). The slightly worn teeth of a specimen attributed to this taxon (MLP 16 VII0211; Figure 9) are characterized by an isolated cusp, positioned to the labial extremity of the first transverse crest (i.e., anteroloph), and another labial cusp connected to the apparent second crest. With dental wear, the first cusp tends to be connected to the anteroloph. It can be interpreted as a paracone. In that context, the cusp directly posterior to this paracone would then be a mesostyle, and the crest linked to this style would be the third transverse crest (mesoloph/mesolophule), thereby forming a transverse crest in second position. However, the possibility exists that this isolated buccal cusp is rather a neoformation, which would invalidate our interpretation regarding the trilophodonty of this taxon.

The posteroloph spur

A short and longitudinal spur (Figure 10), situated on the mediolingual part of the posteroloph, can be observed in several taxa from Contamana (Eocene and Oligocene) and Tarapoto/Shapaja: *Cachiyacuy contamanensis*, *Eobranisamys javierpradoi*, *Chambiramys shipiborum*, *Maquiamys praecursor*, *Palaeosteiromys amazonensis*, *Eoincamys valverdei*, *Eoincamys parvus*, cf. *Tarapotomys* sp. of TAR-20 and TAR-21, *Tarapotomys subandinus*, *Tarapotomys mayoensis*, *Kichkasteiromys raimondii*, and *Shapajamys labocensis* (Boivin 2017; Boivin *et al*. 2017a, b, 2018, submitted). It is also present in other caviomorphs such as the species of Santa Rosa, those of Salla, *Draconomys*, *Australoprocta*, *Garridomys*, *Microscleromys*, or *Coendou* (Walton 1997; Kramarz 1998; Kramarz *et al*. 2013; Vucetich *et al*. 2010a; see the coding of the character 214 in Boivin 2017 and Boivin *et al*. submitted). Being usually associated to the metaloph, this spur has often been interpreted as a part or a relict of this crest (Boivin *et al*. 2017a, b, 2018), but from our observations and comparisons, it seems likely that this spur is a neoformation because:

- it is developed from the posteroloph;
- it is slightly connected to the metaloph in most cases, and it is sometimes independent of it (Figure 10(A) and (B));
- it can be present althrough the metaloph is absent (or completely subsumed within the posteroloph) (Figure 10(C) and (D));
- it can be also connected to the third crest and notably to the mesoloph (e.g., *E. valverdei*, *E. parvus*, and *T. mayoensis*) (Figure 10(D)).

Lower teeth

Posterior arm of the protoconid, neomesolophid, mesolophid and neocristids on lower molars

In most caviomorphs, the second transverse cristid of lower molars would correspond to a posterior arm of the protoconid (= metalophulid II; Candela 2000, 2015; Marivaux 2000; Marivaux *et al*. 2002, 2004; Arnal and Vucetich 2011, 2015; Antoine *et al*. 2012; Arnal, 2012; Candela and Rasia 2012; Kramarz *et al*. 2013; Arnal *et al*. 2014; see section 'Historical review and current state of caviomorph dental structures'). Some authors recognize that a mesolophid can form the second cristid instead of a metalophulid II (in erethizontoids; Candela 2000) or in association with the metalophulid II (in octodontoids; Verzi *et al*. 2014, 2016, 2017). However, there are competing interpretations regarding that second cristid, notably in octodontoids. Indeed, contrary to the opinion of Verzi et al. (2014, 2016, 2017), Arnal (2012), Candela and Rasia (2012) and Candela (2015) consider that in octodontoids, the second cristid of lower molars is not a mesolophid but a metalophulid II that varies in orientation and length (see section 'Historical review and current state of caviomorph dental structures').

Like the third crest of upper teeth, the configuration of the second transverse cristid is highly variable on lower molars and p4s of taxa from Contamana and Tarapoto/Shapaja, especially in *Cachiyacuy contamanensis* (CTA-27). In the latter, the second transverse cristid of lower molars is usually formed by two portions of fluctuating length and orientation: (1) a labial portion stemming from the protoconid (the posterior arm of the protoconid), and (2) a lingual portion originating from the mesostylid (Figure 11(A) and (B)). The latter, not previously identified, has been recently called a neomesolophid in Boivin *et al*. (2017a, b, 2018). It is worth noting that the posterior arm of the protoconid and the neomesolophid can be connected together (Figure 11(A)) or disconnected (Figure 11(B)), and in some cases, only the posterior arm of the protoconid (Figure 11(C) and (D)) or the neomesolophid (Figure 11(E) and (F)) forms the second cristid (see

Boivin *et al*. 2017a, figure 8, p. 21). A posterior arm of the protoconid and neomesolophid are also recognisable on p4s of *C*. *contamanensis* (Boivin *et al*. 2017a, figure 7, p. 20). As for the third crest of upper teeth, it is sometimes difficult to determine the composition of the second cristid of lower teeth (Figure 11(G) and (H)). The other taxa described from Contamana and Tarapoto/Shapaja have lower molars that differ regarding the development of these two cristids: both cristids are present (e.g., *Cachiyacuy kummeli*, *Canaanimys maquiensis*, *Palaeosteiromys amazonensis*, cf. *Tarapotomys* sp. of TAR-20 and TAR-21, and *Tarapotomys mayoensis*), only the neomesolophid is developed (e.g., *Chambiramys sylvaticus*, *Eoincamys* cf. *pascuali* of TAR-01, *Tarapotomys subandinus*, and *Tarapotomys mayoensis*), only the posterior arm of the protoconid is developed (e.g., *Mayomys confluens*), or neither cristid is present (*Chambiramys shipiborum* and *Tarapotomys mayoensis*) (see Boivin *et al*. 2017a, b, 2018). Other fossil and modern caviomorphs, such as species of Santa Rosa, those of Salla, *Hypsosteiromys*, *Steiromys*, *Australoprocta*, *Garridomys*, *Scleromys*, *Drytomomys*, *Prostichomys*, *Erethizon*, *Myocastor*, *Proechimys* or *Mesomys* (Fields 1957; Lavocat 1976; Patterson and Wood 1982; Kramarz 1998, 2001b, 2006a; Candela 2000; Frailey and Campbell 2004; Kramarz *et al*. 2013), clearly have a neomesolophid, which is associated or not with a posterior arm of the protoconid. The “crest C” defined by Carvalho and Salles (2004) on lower molars of some echimyids (e.g., *Clydomys*, *Euryzygomatomys*, *Lonchothrix*, and *Mesomys*) was interpreted by Candela and Rasia (2012) as being a metalophulid II, which would have lost its connection with the protoconid, and developed a link with the metalophulid I (see section ‘Historical review and current state of caviomorph dental structures’). Nevertheless, this cristid would correspond most likely to a neomesolophid, with the labial extremity connected to the metalophulid I.

Several p4s and lower molars of *C. contamanensis* (CTA-27, late Middle Eocene; MUSM 1879, 1914, 1915, 2676–2678, 2689, 2692, 2701, 2708, and 2714; Antoine et al. 2012; Boivin et al. 2017a) show additional and unusual structures (cristids and/or cuspids) between the second transverse cristid and the hypolophid. Some of these structures are developed from the hypolophid, and as such, are considered as neoformations. Otherwise, it is difficult to establish criteria of homology for these structures, notably those stemming from the ectolophid, which can be interpreted either as neoformations or as residual parts of an ancestral mesolophid (Boivin *et al*. 2017a; Figure 12). Among all p4s and lower molars attributed to *C. contamanensis*, only one specimen (the MUSM 2678 p4) displays one of these additional cristids stemming from a cuspid situated at the level of the ectolophid, and that could be interpreted as a mesoconid. Some lower molars seem to bear a mesoconid-like cuspid, but without supernumerary cristid associated with it. These structures are not found in other taxa from Contamana or Tarapoto/Shapaja. The mesolophid is commonly developed but very variable and slender in some 'baluchimyines' and 'phiomorphs' of the Old World from the Eocene to the Oligocene: *Bugtimys*, *Hodsahibia*, '*Acritophiomys*', *Phiomys*, '*Waslamys*', and *Gaudeamus hylaeus* (see Marivaux and Welcomme 2003; Jaeger et al. 2010; Sallam et al. 2009, 2011, 2012). Otherwise, the mesolophid is present and well developed in many groups of Ischyromyiformes (e.g., Anomaluroidea, Theridomorpha and Cricetidae; see Marivaux *et al*. 2004, 2017b). It is therefore possible that basal caviomorphs (including *C. contamanensis*) inherited this structure from their African common ancestor. It is usually considered that the ancestral pattern of caviomorph lower molars is tetralophodont (e.g., metalophulid I, second cristid, hypolophid, and posterolophid). But, considering that earliest caviomorphs would have inherited a mesolophid from their African hystricognath ancestor (and not developed this structure independently), the possibility exists that a pentalophodont pattern characterized earliest caviomorphs. This ancestral pattern would have been rapidly supplanted by the tetralophodont scheme (i.e., without mesolophid; Figure 12).

It is worth noting that the modern caviomorph *Dasyprocta* can have pentalophodont lower molars (Figure 12) characterized by:

- a second transverse cristid clearly formed by a posterior arm of the protoconid and another cristid stemming from the metaconid (metaconid cristid or metaconid spur, see below);
- a third cristid between the second transverse cristid and the hypolophid. It is composed of a lingual part corresponding potentially to a neomesolophid, and a labial part stemming from the ectolophid, which can be interpreted as a mesolophid.

In other taxa observed and compared to the material of Contamana and Tarapoto/Shapaja in the context of this study (*Coendou*, *Branisamys*, *Cephalomys*, and *Luantus*), the second transverse cristid can be distally displaced on lower molars, and notably on m3s. The second cristid is then close to the hypolophid and would correspond to a mesolophid (at least for its labial part, sometimes connected to a neomesolophid; Figure 12). In addition, some specimens of extant erethizontoids (MNHN MO-1909-241 and MNHN MO-1909-242, originally assigned to *Sphiggurus insidiosus* and probably attributable to *Coendou insidiosus* following the synonymy proposed by Voss 2011) have pentalophodont lower molars, characterized by the simultaneous presence of a posterior arm of the protoconid and a mesolophid (Figure 12). The presence of a mesolophid in erethizontoids had previously been indicated by Candela (2000). Verzi *et al.* (2014, 2016, 2017) consider that the second cristid of lower molars of some octodontoids is a mesolophid or the association of a metalophulid II with a mesolophid. As noted by Verzi *et al*. (2016, figure 3, p. 98), a very short mesolophid can be developed posteriorly to the second transverse cristid in *Protacaremys prior* and *Caviocricetus lucasi* (Figure 14(G) and (J)). In contrast, in other taxa figured by Verzi *et al*. (2016, figures 1 and 2, p. 96–97; Figures 13, 14), the second cristid is positionned anteriorly, and it is linked to the protoconid and/or the mesostylid, and/or the metaconid (see below). Given these connections, this cristid seems not to correspond to a mesolophid (Figures 13, 14), which is in agreement with the hypothesis selected by Arnal (2012), Candela and Rasia (2012) and Candela (2015).

Another type of pentalophodonty, different from that previously mentioned for *Dasyprocta* and *Shiggurus*, is found on lower molars of the octodontoid *Hoplomys* (Carvalho and Salles 2004; Figure 13(A1, A3)) and several fossil erethizontoids (e.g., *Branisamyopsis australis*, *Branisamyopsis praesigmoides*, *Steiromys duplicatus*, and *Neosteiromys pattoni*; Candela 2000, 2003, 2004; Kramarz 2004). It corresponds to an addition of a neolophid in the anteroflexid, situated between the metalophulid I and the second cristid (Patterson and Wood 1982; Candela 2000, 2003, 2004; Carvalho and Salles 2004; Candela and Rasia 2012; Figures 12 and 13(A3)). This neolophid often originates from a mesiolingual cuspid, which is also neoformed (neoconid), and situated between the metaconid and the mesostylid. MUSM 2861 is the only lower molar from CTA-32 that is assigned to *Palaeosteiromys amazonensis* (Boivin *et al*. 2017b, figure 4L, p. 77). With a neolophid in the anteroflexid, this molar displays a pattern equivalent to that of *B. australis*, *B. praesigmoides*, *S. duplicatus*, *N. pattoni* and *Hoplomys* (Boivin *et al*. 2017b).

In several caviomorphs (including *Dasyprocta*), a cristid is developed in the anteroflexid of lower molars. This cristid is neither a posterior arm of the protoconid, nor a mesolophid, nor a neomesolophid, and nor to the neolophid aforementioned. It extends labially from the metaconid, being usually short or very short. It is named here metaconid cristid or metaconid spur (Figures 12 and 13; Boivin 2017; Boivin *et al*. submitted). For most taxa displaying that metaconid cristid, the developement of this structure is very variable. Besides, for a given species, this cristid can be present or absent (see coding of the character 369 in Boivin 2017 and Boivin *et al*. submitted). It can be then expected that the development of this structure is convergent among several taxa. It is frequently found in octodontoids (e.g., *Platypittamys*, *Sallamys*, *Willidewu*, *Acaremys*, *Dudumus*, and *Galileomys*; Wood 1949; Lavocat 1976; Patterson and Wood 1982; Vucetich and Verzi 1991; Kramarz 2004; Arnal and Vucetich 2015; Arnal *et al*. 2014). In that group, this metaconid cristid can be connected to the posterior arm of the protoconid, and in some cases accompanied by other cristulids stemming from the metalophulid I, the metaconid or even the posterior arm of this cuspid (when the latter is still present; Figures 13, 14). Verzi *et al*. (2016, 2017) recognized a metalophulid II and a mesolophid on lower molars of some octodontoids (the two cristids can be associated to form the second transverse cristid; see above). Nevertheless, given its position, orientation and connections with other structures, the cristid interpreted by Verzi *et al*. (2016, figures 1–2, p. 96–98; Figure 13(K); Figure 14(B–H), (J) and (K)) as a metalophulid II seems more likely a metaconid cristid (in *Acarechimys minutus*, *Acaremys*, *Caviocricetus lucasi*, *Deseadomys arambourgi*, *Sallamys pascuali*, *Protacaremys prior*, *Protadelphomys* sp., and *P. latus*), and/or a supernumerary cristulid (in *Proechimys cuvieri*, *P. roberti*, *Protadelphomys* sp., and *Sallamys quispea*; Figure 13(B), (D) and (I); Figure 14 (C) and (E)). Similarly, the cristid considered as a mesolophid by Verzi *et al*. (2016, figures 1 and 2, p. 96–97) corresponds more likely to:

- a neomesolophid (in *Mesomys hispidus* and *Trinomys dimidiatus*; Figure 13(E) and (F));

- a posterior arm of the protoconid seperated from a neomesolophid (m2 of *Proechimys cuvieri* in Verzi *et al*. (2016, figure 1b', p. 96; Figure 13(B));
- a posterior arm of the protoconid linked to a neomesolophid (in *Myocastor coypus*, m1 of *Proechimys cuvieri* in Verzi *et al*. (2016, figure 1b', i', p. 96; Figure 13(B), (I) and (J));
- a posterior arm of the protoconid, seperated from a metaconid cristid (in *Acarechimys minutus*, *Protacaremys prior*, *P. latus*, *Protadelphomys* sp., *Sallamys pascuali*, and *S. quispea*; Figure 13(K); Figure 14(C–G));
- a posterior arm of the protoconid, connected to a metaconid cristid (*Protacaremys prior*; Figure 14(H)).

On lower molars of *Lonchotrix emiliae*, *Proechimys poliopus*, *P. roberti*, *Trinomys elegans* figured by Verzi *et al*. (2016), the homology of the cristid situated in second position, stemming from the lingual margin of the molars, and which is labially connected to the metalophulid I, is somewhat ambiguous. This cristid would correspond either to a neomesolophid or to a metaconid cristid (Figure 13(C), (D), (G) and (H)). Verzi *et al*. (2017, figure 4F, G, p. 417) described a "lingual extension of the metaconid" on m1s of *Plesiacarechimys* and *Protocaremys*, which would not correspond to the metaconid cristid (it is not directly connected to the metaconid), but rather to a neoformation.

Among the Oligocene taxa from Contamana and Tarapoto/Shapaja, several of them show a tendency toward a reduction of the second cristid of lower molars: *Chambiramys sylvaticus*, *Eoincamys* cf. *pascuali*, *Tarapotomys subandinus*, *Tarapotomys mayoensis* and *Mayomys confluens* (Boivin *et al*. 2017b, 2018). In caviomorphs, this reduction seems to have occurred convergently several times, and two usual types of patterns can then be distinguished (Figure 12):

- in the first, the posterior arm of the protoconid tends to disappear and the neomesolophid to be reduced (e.g., *Tarapotomys subandinus*, *T. mayoensis*, *Chambiramys sylvaticus*, *Eoincamys*, *Incamys*, *Garridomys*, and *Eoviscaccia*; Lavocat 1976; Patterson and Wood 1982; Kramarz 2001a; Frailey and Campbell 2004; Kramarz *et al*. 2013; Boivin *et al*. 2017b, 2018);
- in the second, the neomesolophid tends to disappear and the posterior arm of the protoconid (or ?mesolophid) to be reduced (e.g., *Luantus*, *Mayomys*, *Draconomys*, *Leucokephalos*, and *Xylechimys*; Patterson and Pascual 1968; Kramarz 2006b; Vucetich *et al*. 2010a, 2015; Boivin *et al*. 2018).

In caviomorphs, several taxa display trilophodont lower molars (e.g., *Tarapotomys mayoensis*, *Chambiramys shipiborum*, *Phoberomys*, *Luantus*, *Sallamys*, *Ethelomys*, and *Deseadomys*; Wood and Patterson 1959; Lavocat 1976; Patterson and Wood 1982; Kramarz 2006b; Vucetich *et al*. 2015; Rasia and Candela 2017; Boivin *et al*. 2017b, 2018). The trilophodont pattern is achieved by the loss of the second cristid, and seems to be linked or to have implied (Figure 12):

- the fusion of a reduced neomesolophid with the metalophulid I. This fusion is observed for instance on worn molars of *T. mayoensis*, *Incamys* and *Scleromys*. This structural rearrangement recalls that observed on upper molars, notably the fusion of the metaloph and third crest with the posteroloph (see above);

- the fusion of the metaconid cristid (or associated cristulids; see previous paragraph) with the metalophulid I. This fusion occurs on worn molars of *Sallamys*;

- the complete disappearance of the neomesolophid and/or the posterior arm of the protoconid (or ?mesolophid; e.g., *T. mayoensis*, *C. shipiborum*, *Luantus*, and *Sallamys*).

In caviomorphs, p4s develop equivalent structures to those observed on lower molars (i.e., posterior arm of the protoconid, mesolophid, neomesolophid, neolophid, and metaconid cristid). The second transverse cristid can also be reduced or lost on p4s (e.g., *Draconomys*, *Leucokephalos*, and *Deseadomys*), as well as the metalophulid I (e.g., *Cephalomys arcidens*, *Asteromys*, *Perimys*, or *Galileomys*; Wood and Patterson 1959; Kramarz 2002, 2004). The hypolophid, entoconid and posterolophid are merged and form a distal thick cristid on p4s of some octodontoids (*Platypittamys*, *Deseadomys*, *Galileomys*, *Acaremys*, and *Sciamys*). However, the fossil taxa being more rarely documented by p4s than lower molars, the evolution of these different structures on p4s is more difficult to appreciate.

Nomenclature of the dp4s

According to Candela (2002) and Candela and Rasia (2012), the ancestral pattern of the dp4s of echimyids and erethizontids (and more broadly of hystricognaths) is pentalophodont. These authors recognize on dp4s of these groups: a metalophulid I, a metalophulid II, a mesolophid, a hypolophid and a posterolophid. In contrast, Verzi *et al*. (2018) consider that a hexalophodont scheme is the ancestral condition for this locus in caviomorphs. This scheme would be characterized by the presence of an anterolophid, in addition to the metalophulid I, metalophulid II, mesolophid, hypolophid and the posterolophid (see section 'Historical review and current state of caviomorph dental structures').

Considering the Old and New World hystricognaths, the identification of the mesialmost cristid seems to be somewhat more complicated than that proposed by Candela (2002), Candela and Rasia (2012) and Verzi *et al*. (2018). In some caviomorphs, the anterior cristid on dp4s appears to be a metalophulid I, which is formed by the anterior arm of the protoconid and/or the anterior arm of the metaconid. In Eocene and Oligocene Old World hystricognaths, the trigonid of the dp4s is strongly variable and can display an anterior cingulid/anterolophid/anteroconid, and/or elements of the metalophulid I (which are usually separated and reduced), and/or the posterior arm of the protoconid/metaconid cristid. In some of these Old World hystricognaths (e.g., *Baluchimys barryi*, *Lindsaya derbugtiensis*; Flynn *et al*. 1986), there is no direct connection between the anterior cingulid/anterolophid/anteroconid and the anterior arms of the protoconid and metaconid, but the latter arms are often oriented toward the anterior cingulid/anterolophid/anteroconid. In contrast, in some others (‘*Acritophiomys*’ *bowni*, *Birkamys korai*, *Hodsahibia azrae*, *Lophibaluchia*, *Phiomys hammudai*, *Protophiomys aegyptensis*, and *Protophiomys algeriensis*; Jaeger *et al*. 1985, 2010; Flynn *et al*. 1986; Sallam *et al*. 2009, 2012; Sallam and Seiffert 2016), the anteroconid (and often its anterior and posterior arms as well) and/or the anterior cingulid, can be connected to the metalophulid I. So, the anterior cristid on dp4s in caviomorphs (and in *Gaudeamus* too) could be a more complex structure, composed of a metalophulid I, an anteroconid, its arms, and of an anterior cingulid/anterolophid. We propose here to name this mesialmost cristid on caviomorph dp4s an anterocristid.

Rk1: the specimen GSP 21352 illustrated by Verzi *et al*. (2018, figure 1A, p. 2) and originally described as a dp4 of *Baluchimys ganeshapher* by Flynn *et al*. (1986, figure 17J, p. 30), does not correspond in fact to this baluchimyine taxon, but more likely to *Downsimys*, a taxon with potential anomalurid or even cylindrodontid or bathyergid affinities (see Marivaux 2000; Marivaux *et al*. 2004, 2017b). In contrast, we consider that GSP 21353 described as a p4 of *B. ganeshapher* by Flynn *et al*. (1986, figure 17I, p. 30), would be rather a dp4. The p4 of *B.*

ganeshapher would be not documented (this assumption was already assumed in former works of Marivaux et al. (2002, 2004, etc.).

Rk2: the specimen Z5R-163 illustrated by Verzi *et al*. (2018, figure 1B, p. 2) was originally described by Coster *et al*. (2012, figure 4N, p. 243) as a dp4 of *Metaphiomys* aff. *schaubi*. However, according to Marivaux *et al*. (2017a), the specimens attributed to this taxon rather correspond to a morphology corresponding to *Acritophiomys* (*A. bowni*), a genus also considered as a junior synonym of *Phiomys*. In this context, the material of *Metaphiomys* aff. *schaubi* from Zallah (Central Libya; Coster *et al*. 2012) should be rather designated as belonging to a species of *Phiomys*.

The dp4s from CTA-27 (late Middle Eocene) attributed to *Cachiyacuy contamanensis* and *C. kummeli* are pentalophodont, except one, MUSM 1880, attributed to *C. contamanensis*, with almost hexalophodont scheme (Antoine *et al*. 2012, figure 2k, p. 1322). Except for the mesialmost cristid (see above), the nomenclature proposed by Candela (2002) and Candela and Rasia (2012) is applicable on all dp4s. However, some clarifications are appropriate:

- the second transverse cristid does not always correspond to a long posterior arm of the protoconid (= metalophulid II). Indeed, it can be composed of a posterior arm of the protoconid plus a short cristid developed from the metaconid (MUSM 1880, 1888, 2663, 2665, and 2673; Boivin *et al*. 2017a; Figure 15(A–E)). This short cristid is the equivalent of the metaconid cristid or metaconid spur of p4s and lower molars;
- the mesolophid can be aligned and connected to a lingual cristid stemming from the mesostylid (MUSM 1880; Figure 15(A) and (E–H)). This lingual cristid is the equivalent of the neomesolophid of p4s and lower molars;

- mesial and distal ectolophids can be recognized (Figures 14 and 15). The distal ectolophid is longitudinal and links the mesolophid to the hypolophid. The mesial ectolophid is longitudinally oriented in its anterior part and linguodistally oriented in its posterior part. It links the protoconid to the mesolophid and the distal ectolophid. On some dp4s of *C. contamanensis* (MUSM 1880, 2464, and 2671), the mesial ectolophid appears composed of different structures: two cristulids on MUSM 2464 and 2671, and one large cuspid with anterior and posterior arms on MUSM 1880 (Antoine et al., 2012; Boivin *et al*. 2017a). This cuspid is connected to a cristid situated between the second cristid and the mesolophid, and which seems to be composed of two cristulids. This cuspid would be a mesoconid labially displaced, but it is interpreted here as a neocuspid, as well as the cristid that is connected to it (neolophid; Figures 16, 17). Indeed, these structures are developed on only one dp4 of *C. contamanensis* (MUSM 1880). Paleogene Old World hystrognaths do not have structures with equivalent morphology and position (e.g., '*Acritophiomys*', *Protophiomys*, *Phiomys*, '*Waslamys*', *Metaphiomys*, *Gaudeamus*; Wood 1968; Sallam *et al*. 2009, 2011, 2012; Jaeger *et al*. 2010; Coster *et al*. 2012; Marivaux *et al*. 2014). Conversely, the mesoconid, at the intersection of the two ectolophids and mesolophid, tends to disappear in these taxa.

As for the p4s and lower molars, the metaconid cristid and neomesolophid are present on dp4s of other fossil taxa from Contamana (e.g., *Cachiyacuy* cf. *contamanensis* 1 of CTA-51; Boivin *et al*. 2017a) and Tarapoto/Shapaja (e.g., Caviomorpha indet. 1. of TAR-21, *Eoincamys* cf. *pascuali* of TAR-01, and *Mayomys*; Boivin *et al*. 2018), and elsewhere in South America (e.g., *Branisamys*, *Incamys*, *Drytomomys*, *Eosallamys*, and *Galileomys*; Fields 1957; Patterson and

Wood 1982; Frailey and Campbell 2004; Kramarz 2004; see coding of the characters 317 and 329 in Boivin 2017 and Boivin *et al*. submitted). Verzi *et al*. (2017, figure 4A, F, G, p. 417 and figure 5A, p. 418) have described a "lingual extension of the metaconid" on dp4s, in notably *Ameghinomys constans*, *Protocaremys avunculus*, *Plesiacarechimys koenisgwaldi* and in *Acaremys* (*Sciamys principalis*). This would be the metaconid cristid in *Ameghinomys* and *Protocaremys*, whereas it could be rather a neoformation in the other taxa (in which it seems to be not directly connected to the metaconid). As for the lower molars, the "crest C" defined by Carvalho and Salles (2004) on dp4s of some echimyids (see Candela and Rasia (2012) and 'Historical review and current state of caviomorph dental structures') would correspond more likely to a neomesolophid with a labial extremity connected to the anterocristid. Within caviomorphs, the mesial ectolophid of the dp4s has variable morphology (Figure 16): it is more or less long, mesially connected or not to the protoconid, with or without neocuspid, and it can be aligned with the third cristid (mesolophid and/or neomesolophid; e.g., Caviomorpha indet. 5 and Cavioidea or Chinchilloidea indet. of CTA-29, *Eobranisamys*, *Branisamys*; Patterson and Wood 1982; Frailey and Campbell 2004; Boivin *et al*. 2017a) or with the distal ectolophid and hypolophid (e.g., *E*. cf. *pascuali* of TAR-01, *Eoviscaccia*, *Drytomomys*; Fields 1957; Kramarz 2001a).

Considering our interpretation of the mesialmost cristid homology on caviomorph dp4s, the ancestral condition of the dp4s would not then be hexalophodont in caviomorphs. However, although an ancestral pattern of dp4s in caviomorphs would be probably pentalophodont, a scheme with four (even three) transverse cristids is not entirely excluded, because:

- the morphology of the dp4s in the oldest known caviomorphs strongly varies, notably in the development of the second and third cristids, which are sometimes short (e.g., MUSM 1895, 2670; Antoine *et al*. 2012; Boivin *et al*. 2017a);
- two other dp4s, MUSM 2645 and 2651, from two more ancient levels yielding caviomorphs (CTA-47 and CTA-51), have undeveloped third cristid (Boivin *et al*. 2017a, figure 5.1, 5.5, p. 10; Figure 17);
- the dp4s of some African hystricognaths (‘*Acritophiomys*’, *Protophiomys*, *Phiomys*, ‘*Waslamys*’, *Metaphiomys*, and *Talaphiomys*; Wood 1968; Sallam *et al*. 2009, 2012; Jaeger *et al*. 2010; Coster *et al*. 2012; Marivaux *et al*. 2014) variably have second and third cristids complete, reduced or absent.

If we take into consideration that the tetralophodonty (or trilophodonty) is the ancestral condition on caviomorph dp4s, the development of the third (even of the second) cristid would be a convergent feature between Old World hystrognaths and caviomorphs.

Like MUSM 1895 and 2670, other dp4s (e.g., MUSM 2843, 2845, and 3302) from Contamana (Late Oligocene) and Tarapoto/Shapaja (Early Oligocene), exhibit a tetralophodont pattern, which is explained by the absence of the third cristid (Boivin *et al*. 2017b, 2018; Figure 17). The dp4s attributed to *Mayomys* are variable and can be tetralophodont (Boivin *et al*. 2018). On these dp4s, the mesolophid can be either complete or reduced, or even absent, and the posterior arm of the protoconid can be complete or reduced, but always present (Boivin *et al*. 2018; Figure 17). Candela (2002) interpreted the tetralophodont pattern of the dp4s of *Hypsosteiromys* and some specimens of *Erethizon dorsatum*, as resulting from the loss of the mesolophid. The cristid in second position on the dp4s of *Hypsosteiromys* (MACN 52-176, MACN A 52-177, MLP 84-111-10-1, and MNHN col 54) seems to be however formed by two connected cristids (Figure 17), which are:

- a lingual part, which is transverse (MLP 84-111-10-1 and MNHN col 54) or labiomesially oriented (MACN 52-176 and MACN A 52-177), very distally positioned and stemming from a cuspid on the lingual margin of the teeth. Given its position and orientation, this cristid likely corresponds to a neomesolophid linked to a mesostylid;
- a second part, which is linguodistally oriented, and appearing in a position intermediate between the usual posterior arm of the protoconid and mesolophid. Although it is located far from the protoconid (especially on the dp4 of the specimen MLP 84-111-10-1), it would more likely correspond to a posterior arm of the protoconid, notably owing to its obliquity.

According to Candela (2002), some erethizontids (i.e., *Eosteiromys homogenidens*, *E. dorsatum*, *Steiromys detentus*, *S. duplicatus*, and *Coendou prehensilis*) have dp4s with a hexalophodont pattern, which is characterized by the addition of a neolophid in the anteroflexid, between the anterocristid (anterolophid *sensu* Candela 2002) and the second cristid (metalophulid II *sensu* Candela 2002), and mesially to the metaconid (Figure 17). Other extinct taxa such as *Shapajamys labocensis* (Boivin *et al*. 2018), *Eobranisamys romeropittmanae* (Frailey and Campbell 2004), *Branisamys luribayensis* (Hartenberger 1975; Patterson and Wood 1982; Candela 2002), *Incamys bolivianus* (e.g., MNHN-Bol 008499), *Drytomomys typicus* (Candela and Nasif 2006) and *Luantus propheticus* (Kramarz 2006b), seem to have developed this pattern (see coding of the character 320 in Boivin 2017 and Boivin *et al*. submitted). Nevertheless, the recognition of the cuspids (protoconid and metaconid) and anterior cristids (posterior arm of the protoconid, mesolophid, neomesolophid, metaconid cristid, and neolophid) is often ambiguous on dp4s of erethizontoids. Moreover, some representatives of this superfamily would develop another type of neolophid located not mesially to the metaconid but distally to this cuspid (see coding of the character 318 in Boivin 2017 and Boivin *et al*. submitted). For instance, the specimen MACN A 4160, attributed to *Steiromys detentus*, shows a short neocristulid stemming from the lingual edge in the anteroflexid. This neocristulid, situated between the anterocristid and the second cristid, is distally located to the metaconid (Figure 17). The oblique 'second cristid' would correspond to the posterior arm of the protoconid, which is connected to a neomesolophid (i.e., a combination of branches forming the second and third cristids of the pentalophodont scheme, respectively). The MACN 52-176 dp4 of *Hypsosteiromys* presents a similar cristulid to that observed in MACN A 4160, which is positioned distally to the metaconid.

Conclusions

The exhaustive analysis of the material from Contamana and Tarapoto/Shapaja, and its comparisons with other hystricognath specimens (fossil and modern New and Old World hystricognaths) further our understanding regarding the homology and the evolutionary patterns of the dentary structures in caviomorphs. Our analytical results (1) support and/or allow to generalize some hypotheses formerly proposed about the occlusal morphology of caviomorph cheek teeth and associated evolutionary transformations (e.g., Vucetich and Verzi 1994; Candela 1999, 2002; Candela and Rasia 2012), and (2) propose new hypotheses of dental homologies and evolutionary trends. In caviomorphs, the third crest of the upper teeth is highly variable and would correspond either to a mesoloph (stemming from the mesostyle), or a mesolophule (originating from the mesial extremity of the anterior arm of the hypocone [i.e., former position of the ancestral metaconule]), or a combination of both. In most early and subsequent caviomorphs, the transformation from a pentalophodont pattern to a tetralophodont pattern would be explained by the reduction/loss of the metaloph or its merging with the posteroloph, and the tranformation from a tetralophodont pattern to a trilophodont pattern, by the reduction/loss of the the third crest or its merging with the posteroloph. A direct transformation from a pentalophodont pattern to a trilophodont pattern is also observed. On the mesial part of lower teeth, the development of distinct cristids can be recognized, depending primarily on their connections with other structures and secondarily on their position and orientation: metalophulid I (for p4s and lower molars)/anterocristid (for dp4s), posterior arm of the protoconid, metaconid cristid, neomesolophid, mesolophid, and different types of neolophids. Given our observations on ancient fossil specimens, the ancestral pattern of lower molars in caviomorphs was likely tetralophodont, and that of dp4s pentalophodont. However, schemes with five and four (even three) transverse cristids can not be ruled out for the two loci, respectively. The trilophodont pattern of lower molars was mostly secondarily achieved by the loss of the second cristid, a loss which seems to have occurred distinctly, iteratively and at different times in several superfamilies (notably chinchilloids *vs* octodontoids) and genera. Caviomorphs show a significant disparity of occlusal patterns on their cheek teeth throughout their evolutionary history, which is the result of a complex evolution, involving many comtemporaneous and non-comtemporaneous convergences and parallelisms for each locus. It would be now interesting to assess the correlative effects of the modifications in the number of loph(-id)s and cusp(id)s with other characters (dental, but also mandibular and cranial), to determine if they could be key innovations for this rodent group, and then to explore the modalities of their appearance/selection.

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Figure captions

Figure 1. Nomenclature of upper teeth used in this study. (A) occlusal view of upper molar (based of two different specimens); (B) occlusal view of DP4; (C) occlusal view of P4; (D) lingual view of upper tooth; (E) labial view of upper tooth. The nomenclature is based on the dental terminology of different authors (see text) and on the observations carried out in the context of this study. 1, paracone; 2, protocone; 3, metacone; 4, hypocone; 5, parastyle; 6, mesostyle; 7, anteroloph; 8, anterior arm of the protocone; 9, lingual protoloph (= posterior arm of the protocone); 10, posterior outgrowth of the protocone; 11, protoloph (= labial protoloph); 12, mure; 13, third transverse crest (= central transverse crest); 14, mesolophule; 15, mesoloph; 16, anterior arm of the hypocone; 17, metaloph; 18, posteroloph; 19, paraflexus; 20, parastria; 21, hypoflexus/hypofossette; 22, confluence of the paraflexus with the hypoflexus; 23, hypostria; 24, mesial mesoflexus/mesofossette; 25, mesostria; 26, distal mesoflexus/mesofossette; 27, metastria; 28, confluence of the distal mesoflexus with the metaflexus (i.e., posteroflexus); 29, posteroflexus. Abbreviations: ant., anterior; ling., lingual.

Figure 2. Nomenclature of lower teeth used in this study. (A) occlusal view of lower molar (based of two different specimens); (B) occlusal view of dp4; (C) occlusal view of p4; (D) labial view of lower tooth; (E) lingual view of lower tooth. The nomenclature is based on the dental terminology of different authors (see text) and on the observations carried out in the context of this study. 1, protoconid; 2, metaconid; 3, mesoconid; 4, entoconid; 5, hypoconid; 6, mesostylid; 7, metalophulid I; 8, anterocristid; 9, posterior arm of the metaconid; 10, posterior arm of the

protoconid; 11, neomesolophid; 12, second transverse cristid; 13, mesolophid; 14, rest of the mesolophid?; 15, ectolophid; 16, mesial ectolophid; 17, distal ectolophid; 18, hypolophid; 19, anterior arm of the entoconid; 20, posterior arm of the entoconid; 21, anterior arm of the hypoconid; 22, posterior arm of the hypoconid; 23, anterior outgrowth of the hypoconid; 24, posterolophid; 25, anteroflexid/anterofossettid; 26, anterostriid; 27, mesoflexid; 28, mesial mesoflexid; 29, distal mesoflexid; 30, mesostriid; 31, confluence of the anteroflexid with the mesoflexid; 32, hypoflexid; 33, hypostriid; 34, metaflexid; 35, metastriid; 36, confluence of the hypoflexid with the metaflexid. Abbreviations: ant., anterior; ling., lingual.

Figure 3. The hypotheses regarding the homology of structures on upper molars. (A) Wood and Patterson (1959), Patterson and Wood (1982) (caviomorphs); (B) Hoffstetter and Lavocat (1970), Lavocat (1976) (caviomorphs); (C) Bryant and McKenna (1995; 'phiomorphs' and caviomorphs); (D) Candela (1999; erethizontoids); (E) Marivaux *et al*. (2004; general nomenclature for rodents); (F) Marivaux *et al*. (2004), Antoine *et al*. (2012) (caviomorphs). 1 paracone; 2 protocone; 3 metacone; 4 hypocone; 5 mesostyle; 6 metaconule; 7 anteroloph; 8 protoloph; 9 mesolophule; 10 mesoloph; 11 neocrest *sensu* Candela (1999); 12 metaloph; 13 neoloph *sensu* Wood and Patterson (1959); 14 posteroloph; 15 paraflexus; 16 hypoflexus; 17 mesoflexus; 18 metaflexus; 19 posteroflexus; 20 neofossette *sensu* Wood and Patterson (1959). Abbreviations: ant., anterior; ling., lingual.

Figure 4. The hypotheses regarding the homology of structures on lower molars. (A) Wood and Patterson (1959; caviomorphs), Patterson and Wood (1982; caviomorphs), Carvalho and Salles

(2004; non-tetralophodont echimyids); (B) Candela (2000; erethizontoids); (C) Marivaux *et al*. (2004), Antoine *et al*. (2012) (caviomorphs); (D) Carvalho and Salles (2004; tetralophodont echimyids); (E) Candela and Rasia (2010), (E1) non-tetralophodont echimyids, (E2) tetralophodont echimyids; (F) Verzi *et al*. (2014, 2016, 2017), (F1) some tetralophodont octodontoids, (F2) non-tetralophodont octodontoids. 1 protoconid; 2 metaconid; 3 mesoconid; 4 entoconid; 5 hypoconid; 6 mesostylid; 7 metalophulid I; 8 anterolophid; 9 neolophid; 10 metalophulid II ; 11 metalophid; 12 crest C (neolophid + metalophid); 13 mesolophid; 14 hypolophid; 15 posterolophid; 16 anteroflexid; 17 neoflexid; 18 mesoflexid; 19 hypoflexid; 20 metaflexid. Abbreviations: ant., anterior; ling., lingual.

Figure 5. The hypotheses regarding the homology of structures on dp4s. (A) Wood and Patterson (1959; caviomorphs), Patterson and Wood (1982; caviomorphs), Carvalho and Salles (2004; non-tetralophodont echimyids); (B) Candela (2002), (B1) non-tetralophodont erethizontoids, (B2) tetralophodont erethizontoids; (C) Marivaux *et al*. (2004; caviomorphs), Antoine *et al*. (2012; caviomorphs), Candela and Rasia (2010; non-tetralophodont echimyids); (D) Carvalho and Salles (2004; tetralophodont echimyids); (E) Candela and Rasia (2010), (E1) tetralophodont echimyids configuration 1, (E2) tetralophodont echimyids configuration 2; (F) Verzi *et al*. (2018; caviomorphs). 1 protoconid; 2 metaconid; 3 mesoconid; 4 entoconid; 5 hypoconid; 6 mesostylid; 7 metalophulid I; 8 anterolophid; 9 neolophid *sensu* Candela (2002); 10 metalophulid II; 11 neolophid *sensu* Wood and Patterson (1959); 12 metalophid; 13 crest C (neolophid + metalophid); 14 mesolophid; 15 hypolophid; 16 posterolophid; 17 anterior cingulid (anterior cingulid). Abbreviations: ant., anterior; ling., lingual.

Figure 6. Composition of the third transverse crest of upper teeth. (A) mesolophule and mesoloph connected; (B) mesolophule and mesoloph unconnected; (C) without mesoloph, long mesolophule; (D) without mesoloph, short mesolophule; (E) without mesolophule, long mesoloph; (F) without mesolophule, short mesoloph; (G, H) indeterminate (mesolophule and/or mesoloph). The schematic line drawings focus exclusively on the third transverse crest of upper teeth (on upper molars here). Abbreviations: ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Me, metacone; meta, metaloph; Mst, mesostyle; Pa, paracone; post, posteroloph; Pr, protocone; proto, (labial) protoloph.

Figure 7. Terminology of flexi on upper teeth. In red, third transverse crest (cf. Figure 6). Abbreviations: ant. anterior; H, hypocone; ling. lingual; Me, metacone; Mst, mesostyle; Pa, paracone; Pr, protocone.

Figure 8. Simplified occlusal schematic line drawings of upper molars illustrating the hypotheses of transformations from a pentalophodont pattern to a tetralophodont pattern, from a tetralophodont pattern to a trilophodont pattern, and from a pentalophodont pattern to a trilophodont pattern. These schematic line drawings focus exclusively on the transformations occurring in the distolabial area of upper molars the cited taxa are example. * *sensu* (Vucetich and Verzi 1994). Abbreviations: ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Me, metacone; meta, metaloph; Mst, mesostyle; Pa, paracone; post, posteroloph; Pr, protocone; proto, (labial) protoloph.

Figure 9. Photograph and interpretative schematic line drawing of the occlusal structures of the upper jaw (P4–M3) of MLP 16 VII0211, attributed to *Euryzygomatomys*. Abbreviations: 3rd cr, third transverse crest; ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Mst, mesostyle; Pa, paracone; post, posteroloph; Pr, protocone.

Figure 10. The posteroloph spur of upper teeth. The schematic line drawings focus exclusively on this structure (on upper molars here) and on the distolabial crests with which it can be connected. Abbreviations: ant. anterior; H, hypocone; ling. lingual; Me, metacone; Mst, mesostyle; Pa, paracone; Pr, protocone.

Figure 11. Composition of the second transverse cristid of lower molars. (A) posterior arm of the protoconid and neomesolophid connected; (B) posterior arm of the protoconid and neomesolophid unconnected; (C) without neomesolophid, long posterior arm of the protoconid; (D) without neomesolophid, short posterior arm of the protoconid; (E) without posterior arm of the protoconid, long neomesolophid; (F) without posterior arm of the protoconid, short neomesolophid; (G, H) indeterminate (posterior arm of the protoconid and/or neomesolophid). The schematic line drawings focus exclusively on the second transverse cristid. Abbreviations: ant. anterior; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; med I, metalophulid I ; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

Figure 12. Simplified occlusal schematic line drawings illustrating the hypotheses of transformations of pentalophodont, tetralophodont and trilophodont patterns on lower molars. The ancestral scheme remains ambiguous (scheme pentalophodont or tetralophodont). The schematic line drawings focus exclusively on the transformations observed on the mesial area of lower molars the cited taxa are example. Abbreviations: ant. anterior; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; med I, metalophulid I ; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

Figure 13. Photographs/drawings (1) and interpretative schematic line drawings of occlusal morphologies according to Verzi *et al*. (2016) (2) and this study (3) of transverse cristids on lower teeth (dp4–m3s) in several octodontoid taxa. (A) *Hoplomys gymnurus* USP 2001; (B, I, *Proechimys cuvieri* MN-UFRJ 20313; (C) *Lonchothrix emiliae* MN-UFRJ 4856; (D) *Proechimys roberti* MVZ 197578; (E) *Mesomys hispidus* MVZ 190653; (F) *Trinomys dimidiatus* MN-UFRJ 62275; (G) *Trinomys elegans* MN-UFRJ 43842; (H) P*roechimys poliopus* MLP 22.II.00.7; (J) *Myocastor coypus* MLP 20.XII.89.3; (K) *Acarechimys minutus* MPM-PV 4223. This figure is based on the figure 1 of Verzi *et al*. (2016, p. 96) with modifications. Abbreviations: ant. anterior; ling. lingual.

Figure 14. Photographs/drawings (1) and interpretative schematic line drawings of occlusal morphologies according to Verzi *et al*. (2016) (2) and this study (3) of transverse cristids on lower teeth (dp4–m3s) in several octodontoid taxa. (A) *Acarechimys minutus* MPM-PV 4193; (B) *Acaremys* (*Sciamys principalis*) MLP 15–349; (C) *Sallamys quispea* (based on Shockey *et al.*

2009, figure 5); (D) *Sallamys pascuali* UATF-V 5010; (E) *Protadelphomys* sp. MMP 949-M; (F) *Protadelphomys latus* MPEF 90–166; (G) *Protacaremys prior* MPEF 5652; (H) *Protacaremys prior* MPEF 7557; (I) *Prospaniomys priscus* MPEF 6447; (J) *Caviocricetus lucasi* MPEF 5076; (K) *Deseadomys arambourgi* MLP 93-XI-21-5. This figure is a compilation realised from those of Verzi *et al*. (2016, figures 1–3, p. 96–98) with modifications. Abbreviations: ant. anterior; ling. lingual.

Figure 15. Composition of the second and third transverse cristids of dp4s. (A) posterior arm of the protoconid and metaconid cristid connected, mesolophid and neomesolophid connected; (B) posterior arm of the protoconid and metaconid cristid unconnected; (C) without metaconid cristid; (D) without posterior arm of the protoconid; (E) both cristids indeterminate; (F) mesolophid and neomesolophid unconnected; (G) without neomesolophid; (H) without mesolophid. The schematic line drawings focus exclusively on the second and third transverse cristids. Abbreviations: ant. anterior; ante, anterocristid; d ectod, distal ectolophid; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; m ectod, mesial ectolophid; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

Figure 16. The ectolophids of dp4s. The schematic line drawings focus exclusively on these structures. Abbreviations: ant. anterior; ante, anterocristid; d ectod, distal ectolophid; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; m ectod, mesial ectolophid; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

Figure 17. Simplified occlusal schematic line drawings illustrating the hypotheses of transformations of hexalophodont, pentalophodont and tetralophodont patterns of dp4s. The ancestral scheme remains ambiguous (scheme pentalophodont or tetralophodont). These schematic line drawings focused exclusively on transformations of the trigonid of dp4s the cited taxa are example. Abbreviations: ant. anterior; ante, anterocristid; d ectod, distal ectolophid; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; m ectod, mesial ectolophid; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

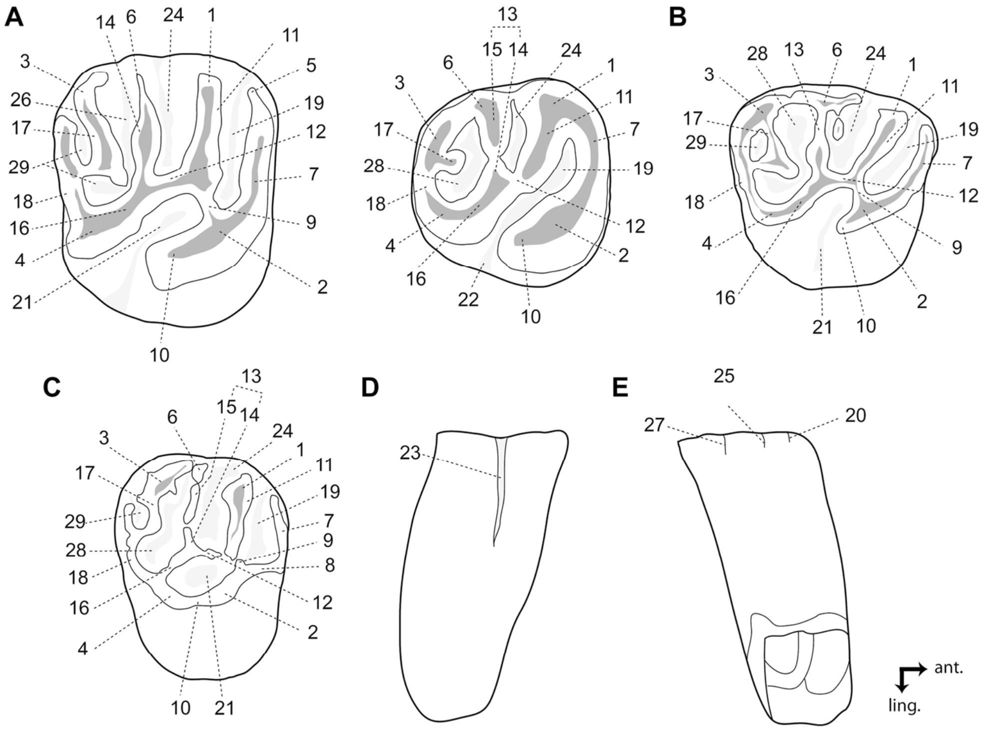

Figure 1. Nomenclature of upper teeth used in this study. (A) occlusal view of upper molar (based of two different specimens); (B) occlusal view of DP4; (C) occlusal view of P4; (D) lingual view of upper tooth; (E) labial view of upper tooth. The nomenclature is based on the dental terminology of different authors (see text) and on the observations carried out in the context of this study. 1, paracone; 2, protocone; 3, metacone; 4, hypocone; 5, parastyle; 6, mesostyle; 7, anteroloph; 8, anterior arm of the protocone; 9, lingual protoloph (= posterior arm of the protocone); 10, posterior outgrowth of the protocone; 11, protoloph (= labial protoloph); 12, mure; 13, third transverse crest (= central transverse crest); 14, mesolophule; 15, mesoloph; 16, anterior arm of the hypocone; 17, metaloph; 18, posteroloph; 19, paraflexus; 20, parastria; 21, hypoflexus/hypofossette; 22, confluence of the paraflexus with the hypoflexus; 23, hypostria; 24, mesial mesoflexus/mesofossette; 25, mesostria; 26, distal mesoflexus/mesofossette; 27, metastria; 28, confluence of the distal mesoflexus with the metaflexus (i.e., posteroflexus); 29, posteroflexus. Abbreviations: ant., anterior; ling., lingual.

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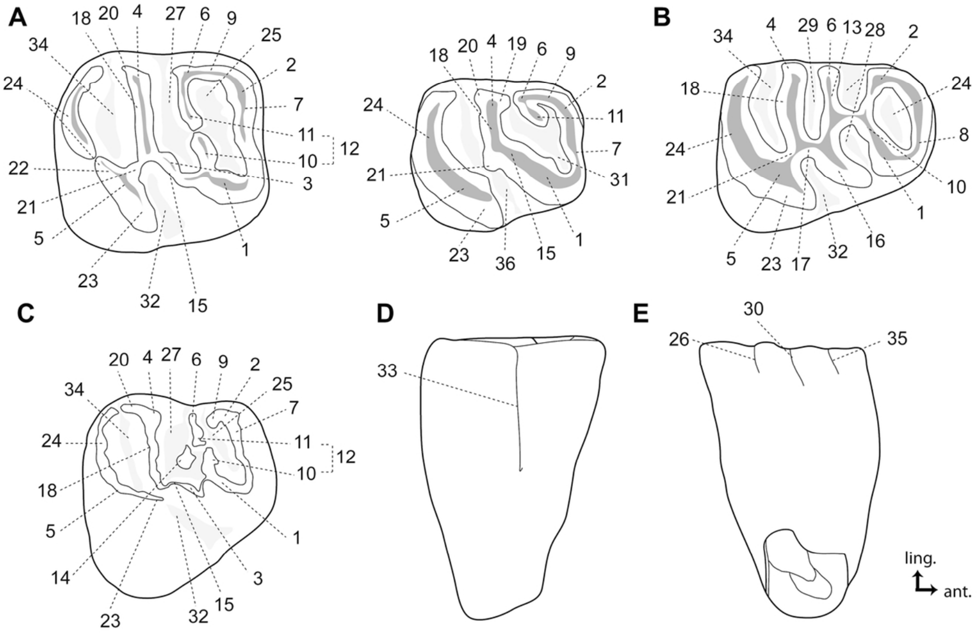

Figure 2. Nomenclature of lower teeth used in this study. (A) occlusal view of lower molar (based of two different specimens); (B) occlusal view of dp4; (C) occlusal view of p4; (D) labial view of lower tooth; (E) lingual view of lower tooth. The nomenclature is based on the dental terminology of different authors (see text) and on the observations carried out in the context of this study. 1, protoconid; 2, metaconid; 3, mesoconid; 4, entoconid; 5, hypoconid; 6, mesostylid; 7, metalophulid I; 8, anterocristid; 9, posterior arm of the metaconid; 10, posterior arm of the protoconid; 11, neomesolophid; 12, second transverse cristid; 13, mesolophid; 14, rest of the mesolophid?; 15, ectolophid; 16, mesial ectolophid; 17, distal ectolophid; 18, hypolophid; 19, anterior arm of the entoconid; 20, posterior arm of the entoconid; 21, anterior arm of the hypoconid; 22, posterior arm of the hypoconid; 23, anterior outgrowth of the hypoconid; 24, posterolophid; 25, anteroflexid/anterofossettid; 26, anterostriid; 27, mesoflexid; 28, mesial mesoflexid; 29, distal mesoflexid; 30, mesostriid; 31, confluence of the anteroflexid with the mesoflexid; 32, hypoflexid; 33, hypostriid; 34, metaflexid; 35, metastriid; 36, confluence of the hypoflexid with the metaflexid. Abbreviations: ant., anterior; ling., lingual.

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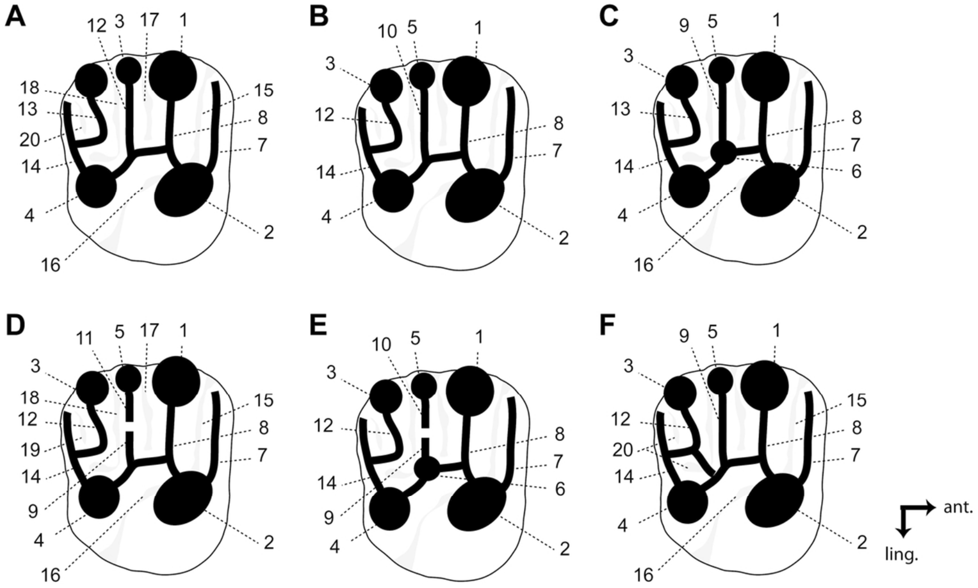

Figure 3. The hypotheses regarding the homology of structures on upper molars. (A) Wood and Patterson (1959), Patterson and Wood (1982) (caviomorphs); (B) Hoffstetter and Lavocat (1970), Lavocat (1976) (caviomorphs); (C) Bryant and McKenna (1995; 'phiomorphs' and caviomorphs); (D) Candela (1999; erethizontoids); (E) Marivaux et al. (2004; general nomenclature for rodents); (F) Marivaux et al. (2004), Antoine et al. (2012) (caviomorphs). 1 paracone; 2 protocone; 3 metacone; 4 hypocone; 5 mesostyle; 6 metaconule; 7 anteroloph; 8 protoloph; 9 mesolophule; 10 mesoloph; 11 neocrest sensu Candela (1999); 12 metaloph; 13 neoloph sensu Wood and Patterson (1959); 14 posteroloph; 15 paraflexus; 16 hypoflexus; 17 mesoflexus; 18 metaflexus; 19 posteroflexus; 20 neofossette sensu Wood and Patterson (1959). Abbreviations: ant., anterior; ling., lingual.

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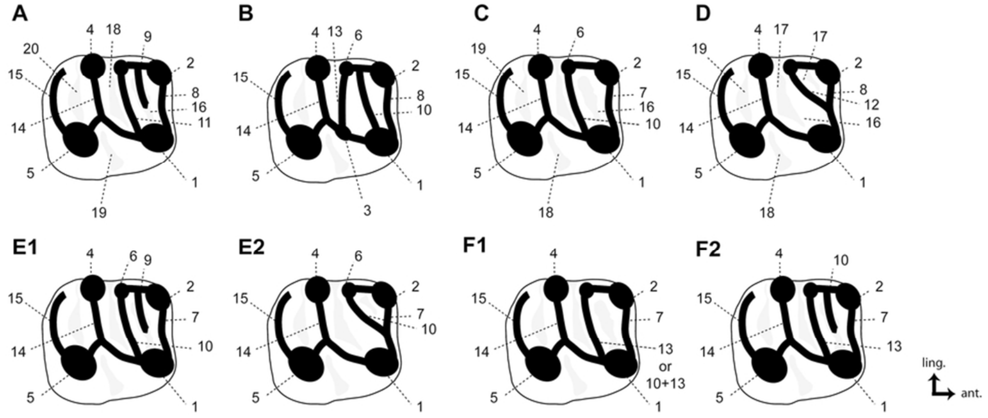

Figure 4. The hypotheses regarding the homology of structures on lower molars. (A) Wood and Patterson (1959; caviomorphs), Patterson and Wood (1982; caviomorphs), Carvalho and Salles (2004; non-tetralophodont echimyids); (B) Candela (2000; erethizontoids); (C) Marivaux et al. (2004), Antoine et al. (2012) (caviomorphs); (D) Carvalho and Salles (2004; tetralophodont echimyids); (E) Candela and Rasia (2010), (E1) non-tetralophodont echimyids, (E2) tetralophodont echimyids; (F) Verzi et al. (2014, 2016, 2017), (F1) some tetralophodont octodontoids, (F2) non-tetralophodont octodontoids. 1 protoconid; 2 metaconid; 3 mesoconid; 4 entoconid; 5 hypoconid; 6 mesostylid; 7 metalophulid I; 8 anterolophid; 9 neolophid; 10 metalophulid II ; 11 metalophid; 12 crest C (neolophid + metalophid); 13 mesolophid; 14 hypolophid; 15 posterolophid; 16 anteroflexid; 17 neoflexid; 18 mesoflexid; 19 hypoflexid; 20 metaflexid. Abbreviations: ant., anterior; ling., lingual.

82x36mm (300 x 300 DPI)

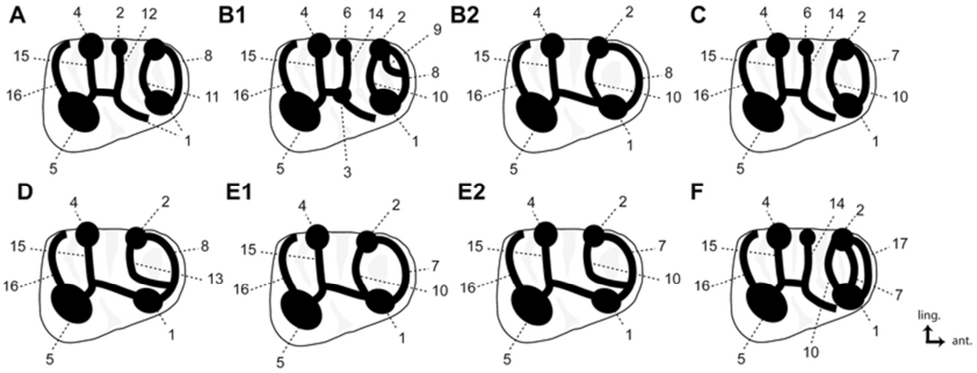

Figure 5. The hypotheses regarding the homology of structures on dp4s. (A) Wood and Patterson (1959; caviomorphs), Patterson and Wood (1982; caviomorphs), Carvalho and Salles (2004; non-tetralophodont echimyids); (B) Candela (2002), (B1) non-tetralophodont erethizontoids, (B2) tetralophodont erethizontoids; (C) Marivaux et al. (2004; caviomorphs), Antoine et al. (2012; caviomorphs), Candela and Rasia (2010; non-tetralophodont echimyids); (D) Carvalho and Salles (2004; tetralophodont echimyids); (E) Candela and Rasia (2010), (E1) tetralophodont echimyids configuration 1, (E2) tetralophodont echimyids configuration 2; (F) Verzi et al. (2018; caviomorphs). 1 protoconid; 2 metaconid; 3 mesoconid; 4 entoconid; 5 hypoconid; 6 mesostylid; 7 metalophulid I; 8 anterolophid; 9 neolophid sensu Candela (2002); 10 metalophulid II; 11 neolophid sensu Wood and Patterson (1959); 12 metalophid; 13 crest C (neolophid + metalophid); 14 mesolophid; 15 hypolophid; 16 posterolophid; 17 anterior cingulid (anterior cingulid). Abbreviations: ant., anterior; ling., lingual.

72x28mm (300 x 300 DPI)

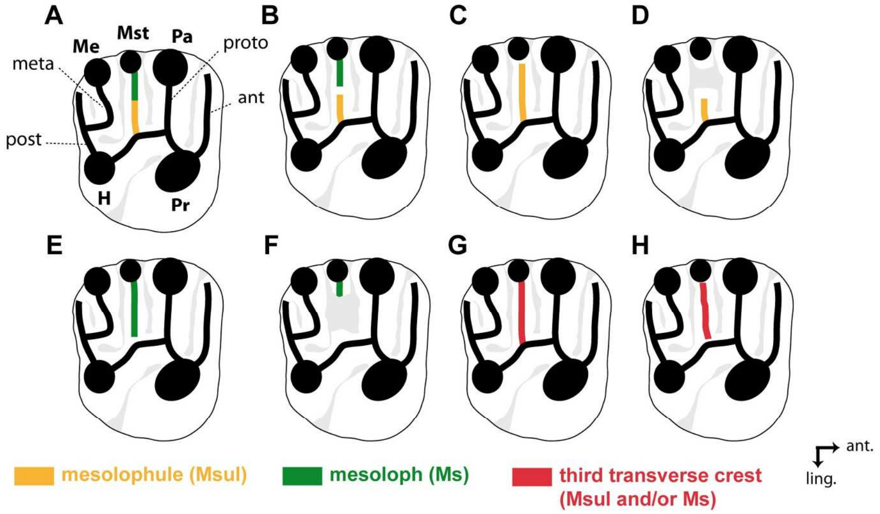

Figure 6. Composition of the third transverse crest of upper teeth. (A) mesolophule and mesoloph connected; (B) mesolophule and mesoloph unconnected; (C) without mesoloph, long mesolophule; (D) without mesoloph, short mesolophule; (E) without mesolophule, long mesoloph; (F) without mesolophule, short mesoloph; (G, H) indeterminate (mesolophule and/or mesoloph). The schematic line drawings focus exclusively on the third transverse crest of upper teeth (on upper molars here). Abbreviations: ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Me, metacone; meta, metaloph; Mst, mesostyle; Pa, paracone; post, posteroloph; Pr, protocone; proto, (labial) protoloph.

172x91mm (300 x 300 DPI)

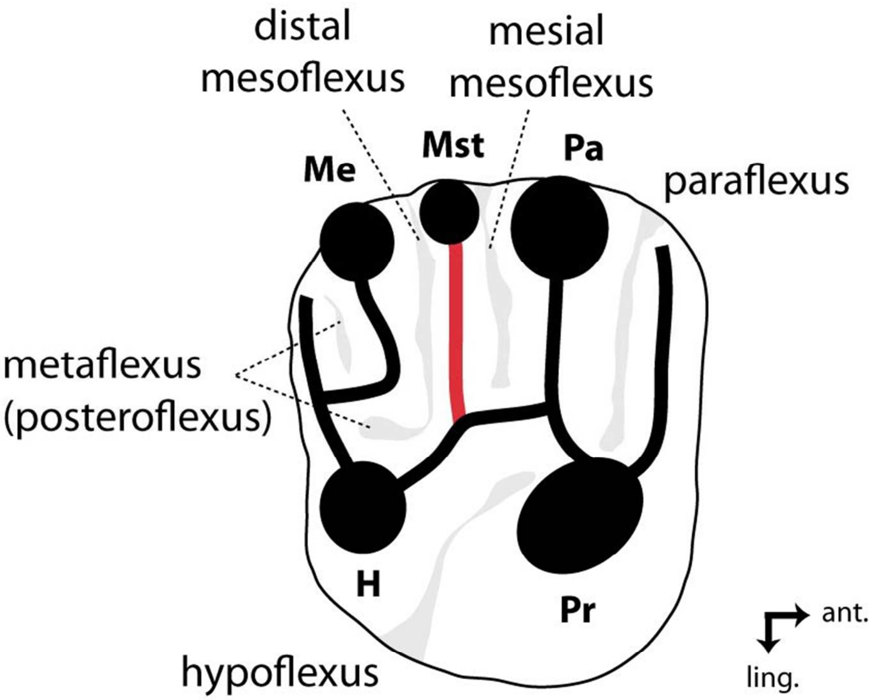

Figure 7. Terminology of flexi on upper teeth. In red, third transverse crest (cf. Figure 6). Abbreviations: ant. anterior; H, hypocone; ling. lingual; Me, metacone; Mst, mesostyle; Pa, paracone; Pr, protocone.

82x63mm (300 x 300 DPI)

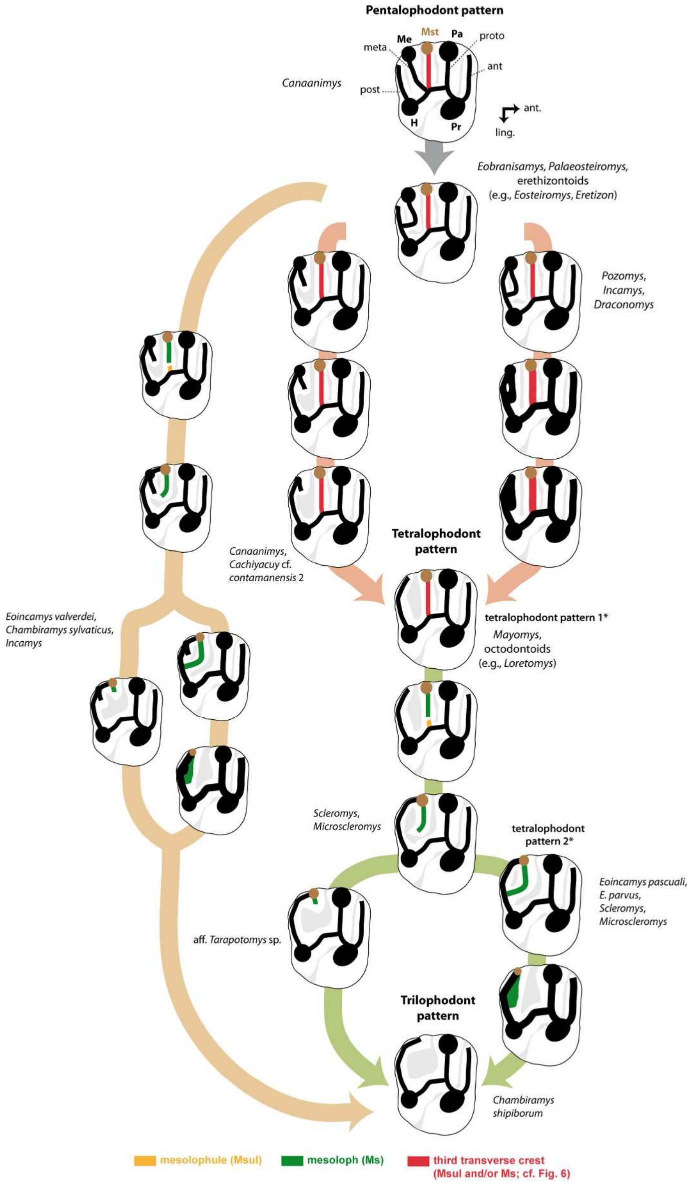

Figure 8. Simplified occlusal schematic line drawings of upper molars illustrating the hypotheses of transformations from a pentalophodont pattern to a tetralophodont pattern, from a tetralophodont pattern to a trilophodont pattern, and from a pentalophodont pattern to a trilophodont pattern. These schematic line drawings focus exclusively on the transformations occurring in the distolabial area of upper molars the cited taxa are example. * sensu (Vucetich and Verzi 1994). Abbreviations: ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Me, metacone; meta, metaloph; Mst, mesostyle; Pa, paracone; post, posteroloph; Pr, protocone; proto, (labial) protoloph.

172x231mm (300 x 300 DPI)

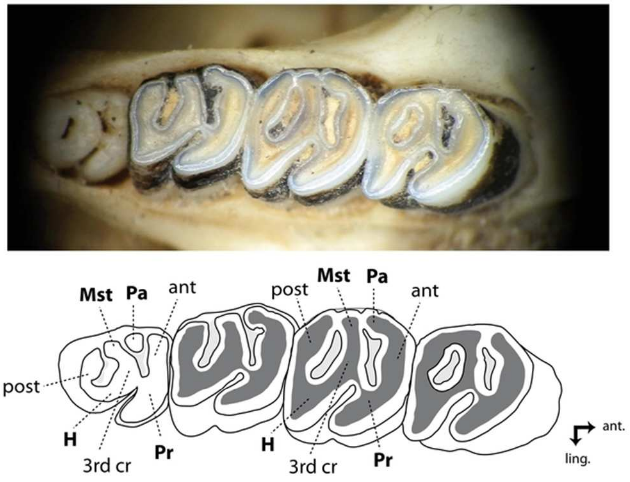

Figure 9. Photograph and interpretative schematic line drawing of the occlusal structures of the upper jaw (P4–M3) of MLP 16 VII0211, attributed to Euryzygomatomys. Abbreviations: 3rd cr, third transverse crest; ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Mst, mesostyle; Pa, paracone; post, posteroloph; Pr, protocone.

86x43mm (300 x 300 DPI)

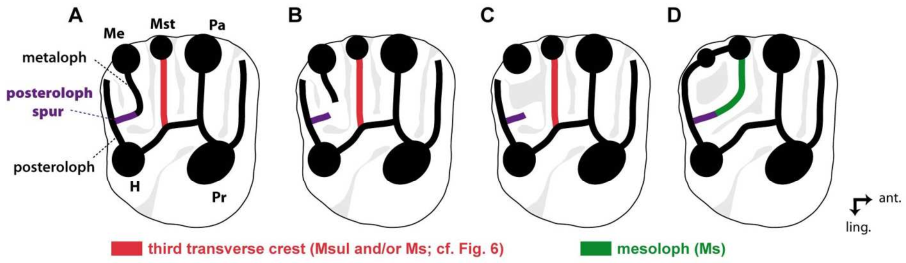

Figure 10. The posteroloph spur of upper teeth. The schematic line drawings focus exclusively on this structure (on upper molars here) and on the distolabial crests with which it can be connected. Abbreviations: ant. anterior; H, hypocone; ling. lingual; Me, metacone; Mst, mesostyle; Pa, paracone; Pr, protocone.

173x47mm (300 x 300 DPI)

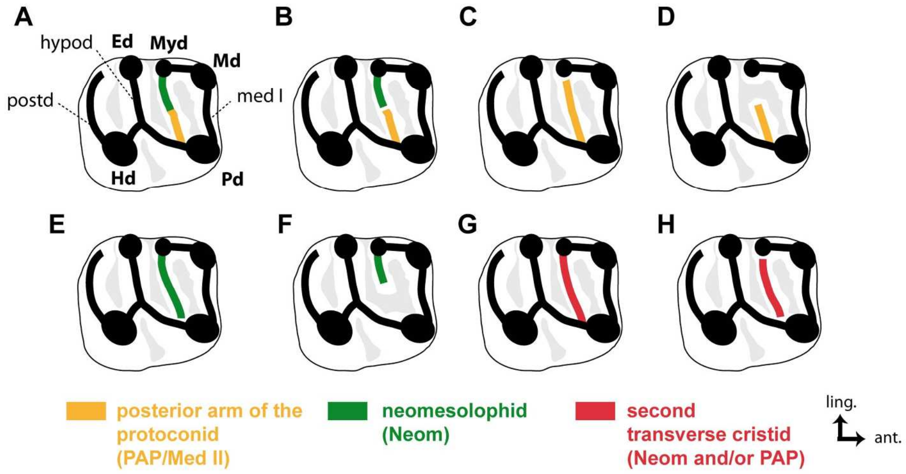

Figure 11. Composition of the second transverse cristid of lower molars. (A) posterior arm of the protoconid and neomesolophid connected; (B) posterior arm of the protoconid and neomesolophid unconnected; (C) without neomesolophid, long posterior arm of the protoconid; (D) without neomesolophid, short posterior arm of the protoconid; (E) without posterior arm of the protoconid, long neomesolophid; (F) without posterior arm of the protoconid, short neomesolophid; (G, H) indeterminate (posterior arm of the protoconid and/or neomesolophid). The schematic line drawings focus exclusively on the second transverse cristid. Abbreviations: ant. anterior; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; med I, metalophulid I ; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

172x86mm (300 x 300 DPI)

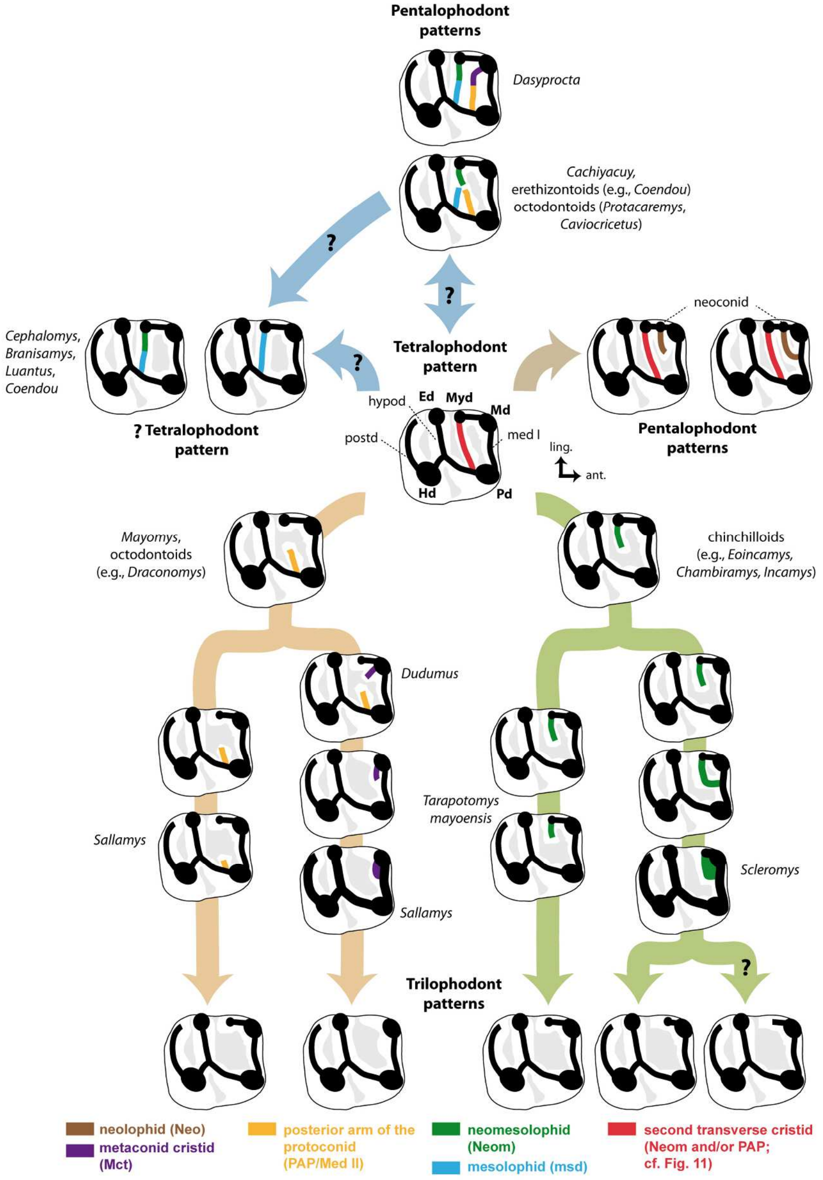

Figure 12. Simplified occlusal schematic line drawings illustrating the hypotheses of transformations of pentalophodont, tetralophodont and trilophodont patterns on lower molars. The ancestral scheme remains ambiguous (scheme pentalophodont or tetralophodont). The schematic line drawings focus exclusively on the transformations observed on the mesial area of lower molars the cited taxa are example. Abbreviations: ant. anterior; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; med I, metalophulid I ; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

172x231mm (300 x 300 DPI)

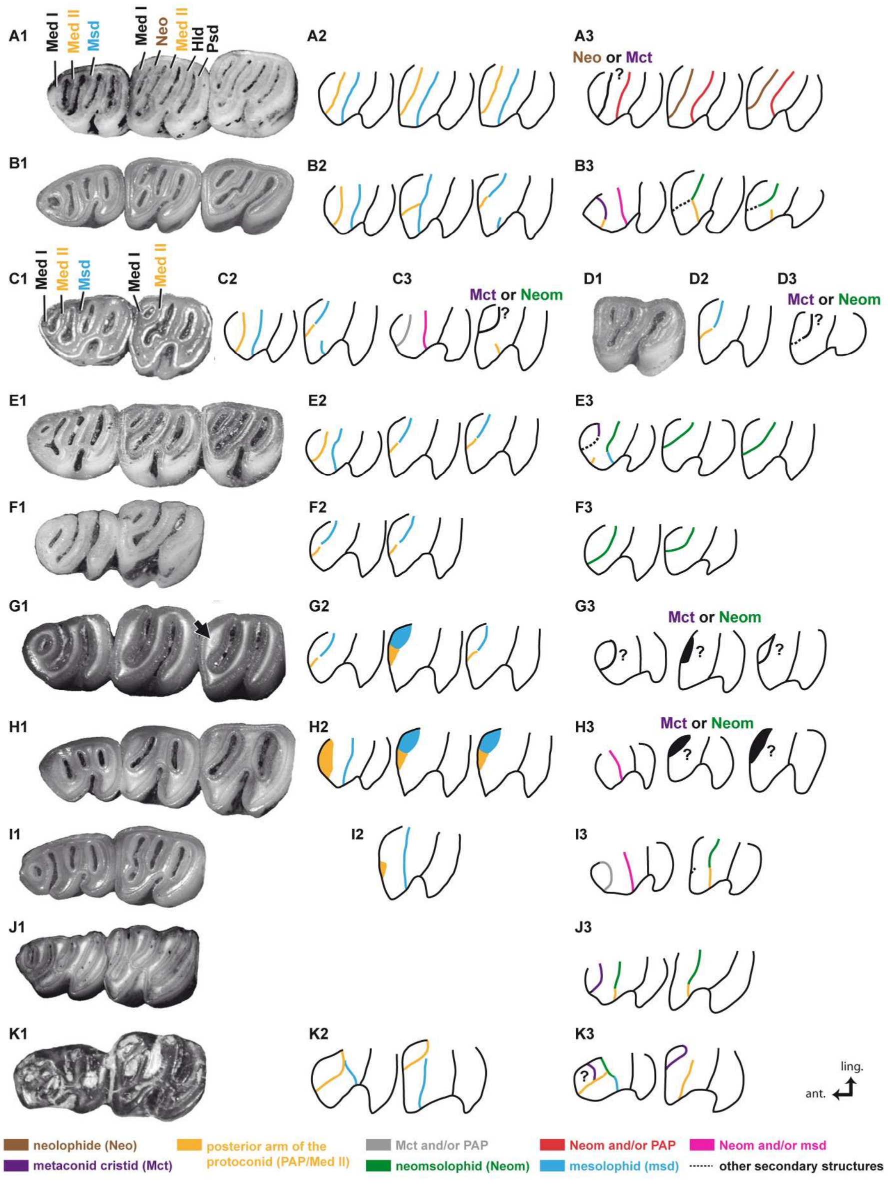

Figure 13. Photographs/drawings (1) and interpretative schematic line drawings of occlusal morphologies according to Verzi et al. (2016) (2) and this study (3) of transverse cristids on lower teeth (dp4–m3s) in several octodontoid taxa. (A) Hoplomys gymnurus USP 2001; (B, I, Proechimys cuvieri MN-UFRJ 20313; (C) Lonchothrix emiliae MN-UFRJ 4856; (D) Proechimys roberti MVZ 197578; (E) Mesomys hispidus MVZ 190653; (F) Trinomys dimidiatus MN-UFRJ 62275; (G) Trinomys elegans MN-UFRJ 43842; (H) Proechimys poliopus MLP 22.II.00.7; (J) Myocastor coypus MLP 20.XII.89.3; (K) Acarechimys minutus MPM-PV 4223. This figure is based on the figure 1 of Verzi et al. (2016, p. 96) with modifications. Abbreviations: ant. anterior; ling. lingual.

173x232mm (300 x 300 DPI)

Figure 14. Photographs/drawings (1) and interpretative schematic line drawings of occlusal morphologies according to Verzi et al. (2016) (2) and this study (3) of transverse cristids on lower teeth (dp4–m3s) in several octodontoid taxa. (A) Acarechimys minutus MPM-PV 4193; (B) Acaremys (Sciamys principalis) MLP 15–349; (C) Sallamys quispea (based on Shockey et al. 2009, figure 5); (D) Sallamys pascuali UATF-V 5010; (E) Protadelphomys sp. MMP 949-M; (F) Protadelphomys latus MPEF 90–166; (G) Protacaremys prior MPEF 5652; (H) Protacaremys prior MPEF 7557; (I) Prospaniomys priscus MPEF 6447; (J) Caviocricetus lucasi MPEF 5076; (K) Deseadomys arambourgi MLP 93-XI-21-5. This figure is a compilation realised from those of Verzi et al. (2016, figures 1–3, p. 96–98) with modifications. Abbreviations: ant. anterior; ling. lingual.

173x232mm (300 x 300 DPI)

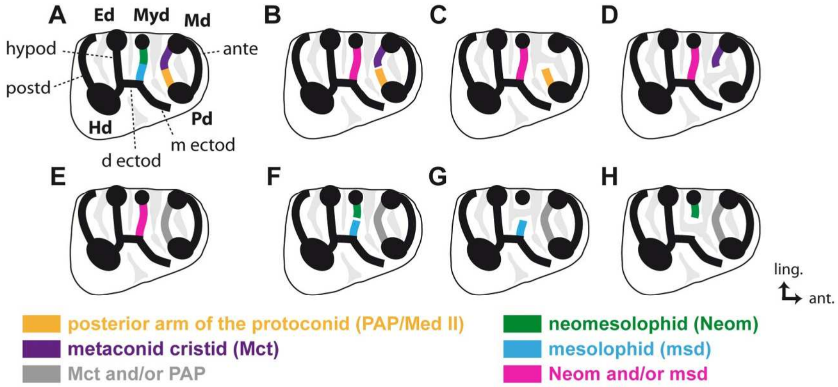

Figure 15. Composition of the second and third transverse cristids of dp4s. (A) posterior arm of the protoconid and metaconid cristid connected, mesolophid and neomesolophid connected; (B) posterior arm of the protoconid and metaconid cristid unconnected; (C) without metaconid cristid; (D) without posterior arm of the protoconid; (E) both cristids indeterminate; (F) mesolophid and neomesolophid unconnected; (G) without neomesolophid; (H) without mesolophid. The schematic line drawings focus exclusively on the second and third transverse cristids. Abbreviations: ant. anterior; ante, anterocristid; d ectod, distal ectolophid; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; m ectod, mesial ectolophid; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

172x70mm (300 x 300 DPI)

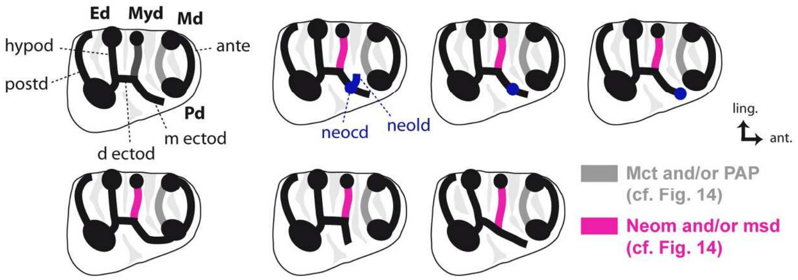

Figure 16. The ectolophids of dp4s. The schematic line drawings focus exclusively on these structures. Abbreviations: ant. anterior; ante, anterocristid; d ectod, distal ectolophid; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; m ectod, mesial ectolophid; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

172x50mm (300 x 300 DPI)

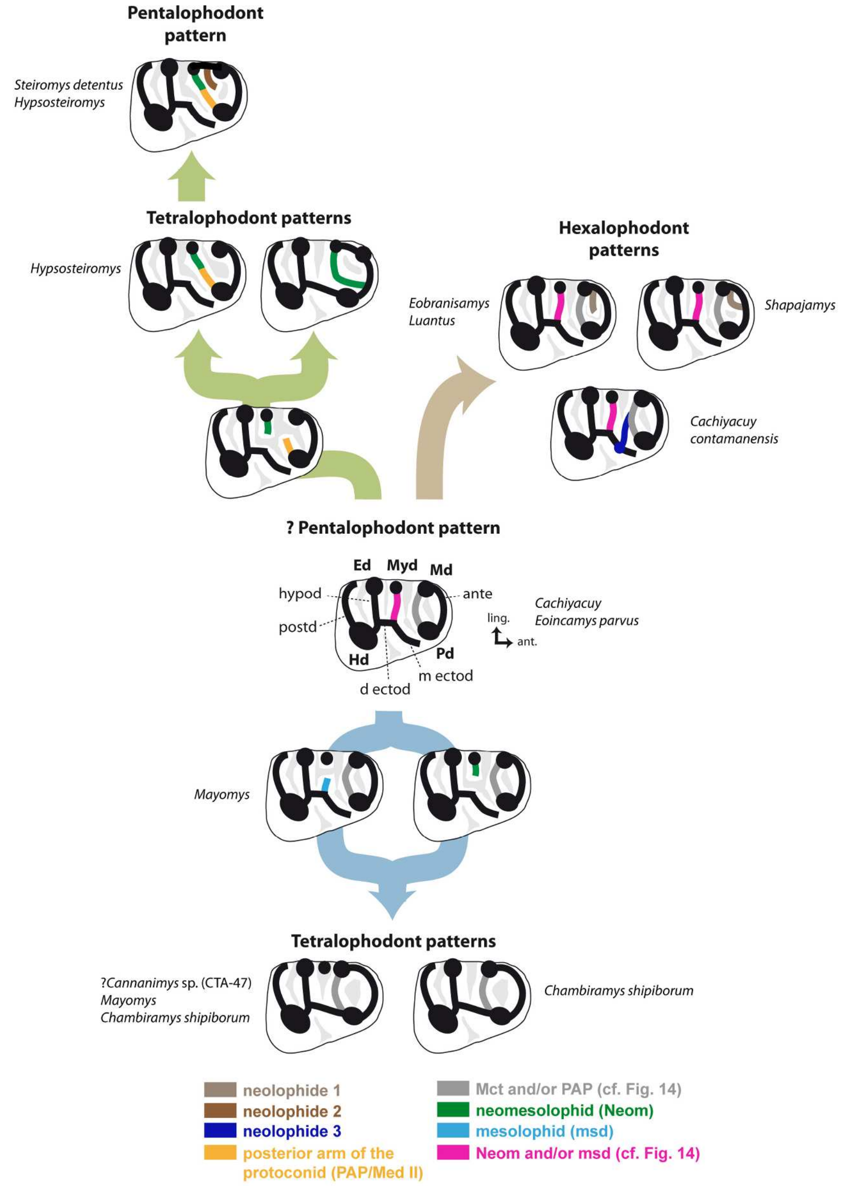

Figure 17. Simplified occlusal schematic line drawings illustrating the hypotheses of transformations of hexalophodont, pentalophodont and tetralophodont patterns of dp4s. The ancestral scheme remains ambiguous (scheme pentalophodont or tetralophodont). These schematic line drawings focused exclusively on transformations of the trigonid of dp4s the cited taxa are example. Abbreviations: ant. anterior; ante, anterocristid; d ectod, distal ectolophid; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; m ectod, mesial ectolophid; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

173x235mm (300 x 300 DPI)

Supplemental Online Material

Caviomorph taxa used for comparisons in this study.

Genre	Species	Locality and/or Formation (Fm.)	Age	Observed material (original or cast)	Primary references
Tribosphenomys	*T. minutus*	Nomogen Fm., China	Late Paleocene		Meng and Wyss 2001; Meng et al. 2007a
Archetypomys	*A. erlianensis*	Huheboerhe-Nuhetingboerhe (AS-1), (Lower Arshanto Fm.), Inner Mongolia	late Early Eocene		Meng et al. 2007b
Cocomys	*C. lingchaensis*	Lingcha Fm., Hengdong County, China	Early Eocene	UM (cast)	Li et al. 1989
Reithroparamys	*R. delicatissimus*	Luman Tongue (Wasatch Fm.), Wyoming, USA	early Early Eocene	UM (cast)	Leidy 1871; Wood 1962
Tamquammys	*T. dispinorum*	Shipigou (Hetaoyuan Fm.), China	middle Middle Eocene		Dawson et al. 1984
	T. wilsoni	Huheboerhe escarpment (IM-1) (Irdin Manha Fm.), Nei Mongol, China	earliest Eocene - earliest Middle Eocene		Dawson et al. 1984
	T. tantillus	Obayla Fm., Kazakhstan	late Early - Middle Eocene		Dawson et al. 1984
Chapattimys	*C. wilsoni*	H-GSP 144, Kala Chitta Range (Kuldana Fm.), Pakistan; Upper Subathu Group, India	early Middle Eocene		Hussain et al. 1978
Birbalomys	*B. sondaari*	H-GSP 144, Kala Chitta Range (Kuldana Fm.), Pakistan; Upper Subathu Group, India	early Middle Eocene	UM (cast)	Hussain et al. 1978
	B. woodi	H-GSP 144, Kala Chitta Range (Kuldana Fm.), Pakistan; Upper Subathu Group, India	early Middle Eocene	UM (cast)	Hussain et al. 1978
Ottomania	*O. proavita*	Süngülü, Lesser Caucasus, Turkey	Eocene/Oligocene boundary interval		De Bruijn et al. 2003
Baluchimys	*B. krabiense*	Bang Mark Lignite Mine, Krabi, Thailand	lastest Eocene		Marivaux et al. 2000
	B. barryi	Y-GSP 417, Bugti Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986
	B. ganeshapher	Y-GSP 417, Bugti Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986
Lindsaya	*L. derabugtiensis*	Y-GSP 417, Bugti Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986
Lophibaluchia	*L. pilbeami*	Y-GSP 417, Bugti Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986
Hodsahibia	*H. azrae*	Y-GSP 417, Bugti Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene	UM (original)	Flynn et al. 1986; Marivaux and Welcomme 2003
	H. gracilis	DBC2, Bugti Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Marivaux and Welcomme 2003
Bugtimys	*B. zafarullahi*	DBC2, Bugti Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene	UM (original)	Marivaux et al. 2002
Talahphiomys	*T. lavocati*	DT-Loc. 2, Bioturbated Unit, Dur At-Talah, Libya	Late Eocene - Early Oligocene		Jaeger et al. 2010
	T. libycus	DT-Loc. 1, Bioturbated Unit, Dur At-Talah, Libya	Late Eocene		Jaeger et al. 2010
"Waslamys"	*"W". attiai*	BQ-2 (Birket Qarun Fm.), Fayum Depression, Egypt	early Late Eocene	UM (cast)	Sallam et al. 2009
Protophiomys	*P. aegyptensis*	BQ-2 (Birket Qarun Fm.), Fayum Depression, Egypt	early Late Eocene	UM (cast)	Sallam et al. 2009
	P. algeriensis	Bir El Ater, Nementcha, Algeria	early Late Eocene	UM (original)	Jaeger et al. 1985
Acritophiomys	*A. bowni*	L-41 (Jebel el Qatrani Fm.), Fayum Depression, Egypt	latest Eocene		Sallam et al. 2012
Birkamys	*B. korai*	L-41 (lowermost Jebel Qatrani Fm.), Fayum Depression, Egypt; + Dakhla DAK-C2	latest Eocene - earliest Oligocene		
Phiomys	*P. hammudai*	DT-Loc. 1, Bioturbated Unit, Dur At-Talah, Libya	Late Eocene	UM (cast)	Jaeger et al. 2010
Metaphiomys	*M. schaubi*	Quarries B, G and E (Jebel Qatrani Fm.), Fayum Depression, Egypt; + Z7I, Zallah Oasis, Libya	Early Oligocene	UM (cast)	Wood 1968; Coster et al. 2015
Gaudeamus	*G. aegypticus*	Quarries A&B and E (Jebel Qatrani Fm.), Fayum Depression, Egypt	Early Oligocene		Wood 1968
	G. aslius	L-41 (lowermost Jebel Qatrani Fm.), Fayum Depression, Egypt; + Dakhla DAK-C2	latest Eocene - earliest Oligocene		Sallam et al. 2011
	G. hylaeus	L-41 (lowermost Jebel Qatrani Fm.), Fayum Depression, Egypt; + Dakhla DAK-C2	latest Eocene - earliest Oligocene		Sallam et al. 2011
Paraphiomys	*P. pigotti*	Rusinga, Kenya	Early Miocene - late Middle Miocene	UM (original)	Lavocat 1973
Thryonomys	*T. swinderianus*		Recent	UM (original)	
CAVIOMOPHA					
Cachiyacuy	*C. contamanensis*	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Boivin et al. 2017a
	C. kummeli	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Boivin et al. 2017a
Canaanimys	*C. maquiensis*	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Boivin et al. 2017a
	Canaanimys sp.	Contamana CTA-47 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Boivin et al. 2017a
Pozomys	*P . ucayaliensis*	Contamana CTA-29 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Boivin et al. 2017a
Eobranisamys	*E . javierpradoi*	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Boivin et al. 2017a
	E. romeropittmanae	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004
	E. riverai	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004
Eosallamys	*E. paulacoutoi*	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004
	E. simpsoni	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004
Eoespina	*E. woodi*	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004
Eosachacui	*E. lavocati*	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004
Tarapotomys	*T. mayoensis*	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
	T. subandinus	TAR-21, TAR-22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
cf. *Tarapotomys*	cf. *Tarapotomys* sp.	TAR-20, TAR-21, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
aff. *Tarapotomys*	aff. *Tarapotomys* sp.	TAR-21, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
Shapajamys	*S. labocensis*	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
Mayomys	*M. confluens*	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
Caviomorpha indet. 4 gen. et sp. indet.	sp. indet.	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a
Llitun	*L. notuca*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
Palaeosteiromys	*P. amazonensis*	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
Plesiosteiromys	*P. newelli*	Contamana CTA-61 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
Ucayalimys	*U. crassidens*	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
Octodontoidea					
Leucokephalos	*L. zeffiae*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
Eodelphomys	*E. almeidacomposi*	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell 2004
Selvamys	*S. paulus*	TAR-22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
Draconomys	*D.verai*	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a
Vallehermosomys	*V. mazzionii*	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a
?Vallehermosomys	*?Vallehermosomys merlinae*	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a
Migraveramus	*M. beatus*	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene		Patterson and Wood 1982
	M. lavocati	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	UM (original)	Pérez et al. 2018
	M. quispea	Cerro Pan de Azúcar (Moquega Fm.), Peru	Late Oligocene	MUSM (original)	Shockey et al. 2009
Sallamys	*S. pascuali*	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Hoffstetter and Lavocat 1970; Lavocat 1976; Patterson and Wood 1982
	S. woodi	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	UM (original)	Pérez et al. 2018
	S. sp.	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	UM (original)	Pérez et al. 2018
?Sallamys	*?Sallamys minutus*	Fazenda Santa Fé (Tremembé Fm. Brazil	late Early Oligocene – Late Oligocene		Vucetich and Ribeiro 2003
	?Sallamys sp.	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	UM (original)	Pérez et al. 2018
Lapazomys	*L. hartenbergeri*	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	UM (original)	Pérez et al. 2018
Paulacoutomys	*P. paulista*	Fazenda Santa Fé (Tremembé Fm.), Brazil	late Early Oligocene – Late Oligocene	MLP (cast)	Vucetich et al. 1993a
Xylechimys	*X. obliquus*	Laguna de los Machos (Sarmiento Fm.), Argentina	Late Oligocene	MLP (original)	Patterson and Pascual 1968
Platypittamys	*P. brachyodon*	Scaritt Pocket (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Wood 1949; Wood and Patterson 1959
Deseadomys	*D. arambourgi*	Cabeza Blanca (Sarmiento Fm.) and La Flecha, Argentina	Late Oligocene	MHNH (original)	Wood and Patterson 1959
Ethelomys	*E. loomisi*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Wood and Patterson 1959; Vucetich et al. 2015
Loretomys	*L. minutus*	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
Acarechimys	*A. leucothea*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015; Arnal et al. 2017
	A. gracilis	Gran Barranca (also collected by Ameghino; Sarmiento Fm.) and Santa Cruz Fm., Argentina	Early Miocene		Ameghino 1902; Vucetich et al. 2010b; Arnal et al. 2017
	A. minutissimus	Pinturas Fm., Santa Cruz and Collón Cura Fm., Argentina; La Venta, Colombia	Early Miocene – Middle Miocene	MLP (original)	Ameghino 1887; Kramarz 2004; Arnal et al. 2017
	A. minutus	Santa Cruz and Collón Cura Fm., Argentina; Quebrada Honda, Bolivia	late Early Miocene – late Middle Miocene	MACN & MLP (original)	Ameghino 1887; Kramarz 2004; Arnal et al. 2017
	A. constans	Santa Cruz Fm., Argentina	late Early Miocene	MLP (original)	Ameghino 1887; Arnal et al. 2017
Galileomys	*G. baios*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
	G. antelucanus	Bryn Gwyn, Gran Barranca (Sarmiento Fm.), Argentina	Early Miocene	MACN & MLP (original)	Vucetich and Kramarz 2003; Vucetich et al. 2010b
	G. eurygnathus	Pinturas Fm. (for the list of localities, see Kramarz, 2004), Argentina	late Early Miocene	MACN (original)	Kramarz 2004
?Protacaremys	*?Protacaremys adilos*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
Protacaremys	*P. prior*	Gran Barranca (also collected by Ameghino; Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Ameghino 1902; Vucetich et al. 2010b
	P. avunculus	Gran Barranca (also collected by Ameghino; Sarmiento Fm.), Argentina	Early Miocene		Ameghino 1902; Vucetich et al. 2010b
	P. denisae	Localities 1 and 5 of the Cañadon del Tordillo (Collón Cura Fm.), Argentina	Middle Miocene	MLP (original)	Vucetich et al. 1993b
Dudumus	*D. ruigomezi*	Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Arnal et al. 2014
Caviocricetus	*C. lucasi*	Bryn Gwyn and Gran Barranca (Sarmiento Fm.), Paso Córdoba (Chinchinales Fm.) and Cerro Bandera (Cerro Bandera Fm.), Argentina	Early Miocene	MACN (original)	Vucetich and Verzi 1996; Vucetich et al. 2010b
Acaremys	*A. murinus*	Sarmiento Fm., Pinturas Fm. and Santa Cruz Fm. (for the list of localities, see Arnal and Vucetich, 2015), Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1887; Arnal and Vucetich 2015
Willidewu	*W. esteparius*	Paso Córdoba (Chinchinales Fm.) and Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene	MLP (original & cast)	Vucetich and Verzi 1991; Vucetich et al. 2010b
Prospaniomys	*P. priscus*	Gran Barranca, Bryn Gwyn?, Sacanana (also collected by Ameghino; Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Ameghino 1902; Vucetich et al. 2010b
	P. cf. *priscus*	Pampa de Gran Gan (Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Arnal and Kramarz 2011
	P. sp. 1	Gran Barranca (Sarmiento Fm.), Argentina	Early Miocene		Vucetich et al. 2010b
'Acaremys'	*A. preminutus*	Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Bordas 1939; Arnal and Vucetich 2015
Pseudoacaremys	*P. kramarzi*	Santa Cruz, River Cliffs, La Cueva, Killik Aik (Santa Cruz Fm.), Argentina	Early Miocene	MACN (original)	Arnal and Vucetich 2015
Prostichomys	*P. bowni*	Gran Barranca (Sarmiento Fm.) and Pinturas Fm. (for the list of localities, see Kramarz, 2001, 2004), Argentina	Early Miocene	MACN (original)	Kramarz 2001a, 2004; Kramarz et al. 2010
Adelphomys	*A. candidus*	Lago Cardiel and Gobernador Gregores (Pinturas Fm.) and Santa Cruz Fm., Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1887; Kramarz 2004
Paradelphomys	*P. fissus*	Gran Brranca (Sarmiento Fm.), Argentina	Early Miocene	MLP (original)	Patterson and Pascual 1968; Vucetich et al. 2010b
Protadelphomys	*P. latus*	Gran Brranca, Bryn Gwyn, Sacanana (Sarmiento Fm.), Argentina	Early Miocene	MLP (original)	Ameghino 1902; Vucetich and Bond 1984; Vucetich et al. 1992, 2010b; Vucetich and Verzi 1994
Plesiacarechimys	*P. koenigswaldi*	Estancia Cerro San Antonio (Collón Cura Fm.), Argentina	Middle Miocene	MLP (original)	Vucetich and Vieytes 2006
Spaniomys	*S. modestus*	Pinturas Fm. (for the list of localities, see Kramarz, 2004) and Santa Cruz Fm., Argentina	late Early Miocene	MACN & MLP (original)	Ameghino 1887; Kramarz 2004; Kay et al. 2012
	S. riparius	Santa Cruz Fm., Argentina; Pampa Castillo (unnamed Fm.), Chile	late Early Miocene	MACN & MLP (original)	Ameghino 1887, 1894; Flynn et al. 2002
Stichomys	*S. regularis*	Santa Cruz Fm., Argentina	late Early Miocene	MACN (original)	Ameghino 1887
Sciamys	*S. principalis*	Santa Cruz Fm., Argentina; Pampa Castillo (unnamed Fm.), Chile	late Early Miocene	MACN & MLP (original)	Ameghino 1887; Arnal and Vucetich 2011; Arnal and Pérez 2013; Flynn et al. 2002
	S. petisensis	El Petiso, Argentina	Middle Miocene		Arnal and Pérez 2013
Ricardomys	*R. longidens*	La Venta (Villavieja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997
Quebradahondomys	*Q. potosiensis*	Quebrada Honda (unnamed Fm.), Bolivia	late Middle Miocene		Croft et al. 2011
Pithanotomys	*P. columnaris*	Monte Hermoso Fm., Argentina	Early ?Pliocene	MACN (original)	
Abrocoma	*A. bennettii*		Recent	MNHN (original)	
Spalacopus	*S. cyanus*		Recent	MNHN (original)	
Octodon	*O. degus*		Recent	UM (original)	
Ctenomys	*C. boliviensis*		Recent	MLP & UM (original)	
Mesocapromys/Mysasteles	*Mesocapromys/Mysasteles* sp.		Recent	UM (original)	
Euryzygomatomys	*E. spinosus*		Recent	MLP & MNHN (original)	
Makalata	*M. didelphoides*		Recent	UM (original)	

Genre	Species	Locality and/or Formation (Fm.)	Age	Observed material (original or cast)	Primary references
Echimys	*E. chrysurus*		Recent	UM (original)	
Thrichomys	*T. apereoides*		Recent	MNHN (original)	
Proechimys	*P. cuvieri*		Recent	UM (original)	
Myocastor	*M. coypus*		Recent	UM (original)	
Erethizontoidea					
Eopululo	*E. wigmorei*	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004
Kichkasteiromys	*K. raimondii*	TAR-21, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
Protosteiromys	*P. medianus*	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene	MACN & MHNH (original)	Ameghino 1903; Wood and Patterson 1959
	P. asmodeophilus	La Flecha (Sarmiento Fm.), Argentina	Late Oligocene	MHNH (original)	Wood and Patterson 1959
	P. pattersoni	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Candela 2000; Pérez et al. 2018
Cholamys	*C. tetralophodonta*	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	UM (original)	Pérez et al. 2018
Hypsosteiromys	*H. axiculus*	Bryn Gwyn and Grand Barranca (also collected by Ameghino, Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Ameghino 1902; Candela 2000; Candela and Vucetich 2002; Vucetich et al. 2010b
	H. nectus	Gran Barranca (also collected by Ameghino, Sarmiento Fm.), Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1902; Candela 2000; Candela and Vucetich 2002; Vucetich et al. 2010b
Steiromys	*S. detentus*	Santa Cruz Fm., Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1887; Candela 2000; Candela et al. 2012; Kay et al. 2012
	S. duplicatus	Santa Cruz Fm., Argentina; Pampa Castillo (unnamed Fm.), Chile	Early Miocene	MACN & MLP (original)	Ameghino 1887; Candela 2000; Flynn et al. 2002; Candela et al. 2012; Kay et al. 2012
Parasteiromys	*P. uniformis*	Southern Cliff of Lake Colhué Huapi (Gran Barranca and also collected by Ameghino; Sarmiento Fm.), Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1903, 1904; Candela 1999, 2000; Vucetich et al. 2010b
	P. friantae	Southern Cliff of Lake Colhué Huapi (Gran Barranca; Sarmiento Fm.), Argentina	Early Miocene	MLP (original)	Candela 1999, 2000; Vucetich et al. 2010b
Eosteiromys	*E. homogidens*	Bryn Gwyn and Grand Barranca (also collected by Ameghino, Sarmiento Fm.), Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1902; Candela 2000; Vucetich et al. 2010b
?*Eosteiromys*	?*Eosteiromys* sp. nov.		Early Miocene		Candela 2002
Branisamyopsis	*B. australis*	Southern Cliff of Lake Colhué Huapi (Gran Barranca; Sarmiento Fm.), Argentina	Early Miocene	MLP & MHNH (original)	Candela 2000, 2003; Vucetich et al. 2010b
	B. praesigmoides	Pinturas Fm. (for the list of localities, see Kramarz, 2004), Argentina	Early Miocene	MACN (original)	Kramarz 2004
?*Neosteiromys*	?*Neosteiromys tordillense*	Cańodon de Tordillo (Collón Cura Fm.), Argentina	Middle Miocene		Vucetich et al. 1993b
Microsteiromys	*M. jacobsi*	La Venta (Villavieja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997
	cf. *Microsteiromys* sp.	Madre de Dios MD-67 (unnamedFm.), Peru	Middle Miocene	MIUSM (original)	Antoine et al. 2013
Neosteiromys	*N. pattoni*	Catamarca Province (Andalhuala Fm.), Argentina	late Miocene		Candela 2000, 2004
	N. bombifrons	Andalhuala Fm., Argentina	late Miocene	MACN (original)	Candela 2000, 2004
Coendou	*C. prehensilis*		Recent	MLP & MNHN (original)	Candela 1999
	C. insidiosus		Recent	MLP & MNHN (original)	
Erethizon	*E. dorsatum*		Recent	MNHN (original)	
Chaetomys	*C. subspinosus*		Recent	MHNG (pictures)	Martin 1994
Chinchilloidea					
Eoincamys	*E. ameghinoi*	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell 2004
	E. pascuali	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell 2004
	E. cf. *pascuali*	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
	E. valverdei	TAR-13, TAR-20–22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
	E. parvus	TAR-20–22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
?*Eoincamys*	?*Eoincamys* sp.	TAR-13, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
Loncolicu	*L. tretos*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
Scotamys	*S. antiquus*	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene		Loomis 1914; Wood and Patterson 1959
Incamys	*I. menniorum*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
	I. bolivianus	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Hoffstetter and Lavocat 1970; Lavocat 1976; Patterson and Wood 1982
Chambiramys	*C. shipiborum*	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
	C. sylvaticus	Contamana CTA-61 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
Maquiamys	*M. praecursor*	Contamana CTA-61 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
Eoviscaccia	*E. frassinetii*	Tinguiririca Termas del Flaco (Abanico Fm.), Chile	Early Oligocene		Wyss et al. 1993; Bertrand et al. 2012
	E. boliviana	Lacayani (unnamed Fm.), Bolivia	Oligocene - Miocene boundary	MNHN (original)	Vucetich 1989
	E. australis	Sarmiento Fm., Chichinales Fm. and Cerro Bandera Fm., Argentina (for the list of localities, see Vucetich et al., 2010b)	Early Miocene	MACN (original)	Vucetich 1989; Kramarz 2001b; Vucetich et al. 2010b
Garridomys	*G. curnunuquem*	near Barda Negra (Cerro Bandera Formation), Argentina	Early Miocene		Kramarz et al. 2013
Scleromys	*S. quadrangualtus*	Pinturas Fm. (for the list of localities, see Kramarz, 2006), Argentina	late Early Miocene	MACN & MLP (original)	Kramarz 2006
	S. angustus	Santa Cruz Fm., Argentina	late Early Miocene	MACN (original)	Ameghino 1887
	S. osbornianus	Santa Cruz Fm. and Pinturas Fm., Argentina	late Early Miocene	MACN (original)	Ameghino 1894; Kramarz 2006
Perimys	*P. intermedius*	Pinturas Fm. (for the list of localities, see Kramarz, 2002), Argentina	late Early Miocene		
Drytomomys	*D. aequatorialis*	near the hacienda of Seňor Carrasco (near Nabon), Equador; La Venta (Villavieja Fm.), Colombia	late Middle Miocene		Anthony 1922; Fields 1957; Walton 1997; Candela and Nasif 2006
	D. typicus	Ituzaingo Fm., Argentina	Late Miocene		Ameghino 1889; Candela and Nasif 2006
Microscleromys	*M. paradoxalis*	La Venta (Villavieja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997
	M. cribriphilus	La Venta (Villavieja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997
Potamarchus	*P. murinus*	Solimoes Fm. (for the list of localities, see Kerber et al., 2016), Brazil	Late Miocene		Kerber et al. 2016
Neoepiblema	*N. ambrossetianus*	Niterói locality (Solimoes Fm.), Brazil	Late Miocene	UFAC (original)	Kerber et al. 2017
	N. horridula	Talismã and Cachoeira do Bandeiro localities (Solimoes Fm.), Brazil	Late Miocene	UFAC (original)	Kerber et al. 2017
Chinchilla	*C. lanigera*		Recent	MLP (original)	
Lagidium	*L. viscacia*		Recent	MLP & MNHN (original)	
Lagostomus	*L. maximus*		Recent	MLP & MNHN (original)	
Dinomys	*D. branickii*		Recent	MNHN (original)	
Cavioidea					
Andemys	*A. termasi*	Tinguiririca Termas del Flaco (Abanico Fm.), Chili	Early Oligocene		Bertrand et al. 2012
Chubutomys	*C. simpsoni*	Cabeza Blanca, La Flecha, and Punta Nava (Sarmiento Fm.) and Cerro Pico Truncado, Argentina	Late Oligocene		Wood and Patterson 1959; Pérez et al., 2012, 2018
	C. navaensis	Punta Nava (Sarmiento Fm.), Argentina	Late Oligocene		Pérez et al., 2012
Branisamys	*B. luribayensis*	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Hoffstetter and Lavocat 1970; Lavocat 1976; Patterson and Wood 1982
Australoprocta	*A. fleagei*	Bryn Gwyn, Sacanana (Sarmineto Fm.) and Paso Córdoba (Chinchinales Fm.), Argentina	Early Miocene		Kramarz 1998; Vucetich et al. 2010b
Neoreomys	*N. pinturensis*	Gran Barranca (Sarmiento Fm.) and Carmen Lower and Potezuelo Sumich Norte (Pinturas Fm.), Argentina	Early Miocene		Kramarz 2006; Kramarz et al. 2010
	N. australis	Santa Cruz Fm. and Pinturas Fm. (for the list of localities, see Kramarz 2006), Argentina; Pampa Castillo (unnamed Fm.), Chile	late Early Miocene	MACN & MLP (original)	Ameghino 1887; Flynn et al. 2002; Kramarz 2006; Candela et al. 2012; Kay et al. 2012
Luantus	*L. propheticus*	Pinturas Fm. (for the list of localities, see Kramarz, 2006), Argentina	late Early Miocene		Kramarz 2006
Dasyprocta	*D.* sp.		Recent	MLP & UM (original)	
Cuniculus	*C. paca*		Recent	UM (original)	
	C. taczanowskii		Recent	UM (original)	
Cavia	*C. aperea*		Recent	MLP (original)	
Galea	*G. spixii*		Recent	MNHN (original)	
Dolichotis	*D. patagonum*		Recent	UM (original)	
Hydrochoerus	*H. hydrochaeris*		Recent	MLP & MNHN (original)	
***Incertae sedis* extinct superfamily**					
Litodontomys	*L. chubutomys*	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene		Loomis 1914; Wood and Patterson 1959
Cephalomys	*C. arcidens*	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene	MNHN (original)	Ameghino 1897; Wood and Patterson 1959
	C. plexus	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene		Ameghino 1897; Wood and Patterson 1959
	C. ceciae	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
Asteromys	*A. punctus*	Cabeza Blanca, Laguna de los Machos, and Punta Nava (Sarmiento Fm.), Argentina	Late Oligocene	MACN (original)	Ameghino 1887; Wood and Patterson 1959; Pérez and Vucetich 2012; Pérez et al. 2018
"Asteromys"	*"A." bolivianus*	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Lavocat 1976; Patterson and Wood 1982; Pérez et al. 2018
Banderomys	*B. leanzai*	Cerro Bandera Fm. and La Estrella (Sarmiento Fm.), Argentina	Early Miocene		Kramarz 2005; Busker et al. 2017
Soriamys	*S. gaimanensis*	Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene		Kramarz 2001c; Vucetich et al. 2010b
	S. ganganensis	Pampa de Gan Gan/Sacanana (Sarmiento Fm.), Argentina	Early Miocene		Kramarz 2001c; Vucetich et al. 2010b

Fm., Formation; INGEMMET, Instituto Geológico Minero y Metalúrgico, Lima; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MLP, Museo de Ciencias Naturales de La Plata; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima; MNHN-Bol, Museo Nacional de Historia Natural, La Paz, Bolivia; MNHN, Musée National d'Histoire Naturelle, Paris; UFAC, Laboratorio de Pesquisa Palontologica, Universidad Federal do Acre; UM, Université de Montpellier.

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Supplemental Online Material

Caviomorph taxa used for comparisons in this study.

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