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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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3 **Dental homologies and evolutionary **transformations** in Caviomorpha (Hystricognathi,**  
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5 **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).

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3 Since then, the reassessment of the potential links between North American reithroparamyids  
4 and hystricognaths (Dawson 1977; Korth 1984; Meng 1990), as well as the formalization of the  
5 caviomorph-phiomorph relationships via phylogenetic analyses based on morphological (e.g.,  
6 George 1993; Luckett and Hartenberger 1993; Marivaux *et al.* 2002, 2004) and molecular data  
7 (e.g., Nedbal *et al.* 1996; Huchon *et al.* 2000, 2002, 2007; Huchon and Douzery, 2001;  
8 Montgelard *et al.* 2008; Fabre *et al.* 2012) marked the end of this hotly debated biogeographic  
9 issue. The hypothesis of an African origin for caviomorphs, put forward by Lavocat (and  
10 collaborators), is now a well-accepted consensus within the scientific community. However,  
11 critical factors such as the mode and precise timing of the Afro-South-American dispersal(s), and  
12 the pathways by which this (these) dispersal(s) occurred remain still entirely unknown.  
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26 Over the past decades, many authors have studied dental homologies and evolutionary  
27 patterns in caviomorphs (e.g., Jaeger 1989; Vucetich and Verzi 1994; Verzi *et al.* 2018), notably  
28 in erethizontoids (e.g., Candela 1999, 2002) and in octodontoids (e.g., Carvalho and Salles 2004;  
29 Candela and Rasia 2012; Candela 2015; Verzi *et al.* 2014, 2016, 2017, 2018). The debates  
30 regarding the dental homologies in caviomorphs **have** then shifted to other structures, such as the  
31 mesial cristids of lower teeth (Candela 2002; Carvalho and Salles 2004; Candela and Rasia 2012;  
32 Candela 2015; Verzi *et al.* 2014, 2016, 2017, 2018).  
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42 Despite the modern and Neogene high diversity of caviomorphs, the early evolutionary history  
43 of these rodents has long remained obscure. Until recently, most of the Paleogene caviomorph  
44 assemblages were primarily concentrated at middle (Bolivia, Brazil, Chili, southern Peru, and  
45 Uruguay) and high (Argentina) latitudes of South America (15/19; see Boivin *et al.* 2017b and  
46 citations therein). By contrast, lower latitudes have long remained poorly documented (Santa  
47 Rosa and Lircay, Peru; Foz do Breu and Cachoeira São Salvador, Brazil; Hartenberger *et al.*  
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3 1984; Frailey and Campbell 2004; Ribeiro et al. 2013, Kerber *et al.* 2017). During the last  
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5 decade, the continuing field efforts in Peruvian Amazonia (Contamana and Tarapoto areas) have  
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7 led to the discovery of about twenty Paleogene localities yielding many fossils of caviomorphs  
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9 (mainly dental remains; Antoine *et al.* 2016; Boivin *et al.* 2017a, b, 2018). They document three  
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11 South American Land Mammal Ages (SALMA): Barrancan (late Middle Eocene; Contamana),  
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13 Tinguirirican (Early Oligocene; Tarapoto, Shapaja section) and Deseadan (Late Oligocene;  
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15 Contamana). The late Middle Eocene localities have so far yielded the oldest known  
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17 representatives of the group in South America (Antoine *et al.* 2012; Boivin *et al.* 2017a). The  
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19 studies of these fossils have revealed a rich specific diversity, most of the species being new for  
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21 science (Antoine *et al.* 2012; Boivin 2017; Boivin *et al.* 2017a, b, 2018). These ancient fossils  
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23 have provided unusual dental morphologies for caviomorphs, the descriptions and detailed  
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25 comparisons of which have led us to formulate new hypotheses regarding some structural  
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27 homologies, and also to further our understanding regarding some aspects of their evolutionary  
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29 trends. All these observations were at the origin of an updated dental nomenclature, which was  
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31 proposed in Boivin *et al.*, 2017a, b, 2018). In this paper, we propose a detailed overview of the  
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33 dental homology and evolutionary transformation hypotheses that we have formulated in light of  
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35 the dental material from the Paleogene rodent-bearing localities of Contamana and  
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37 Tarapoto/Shapaja. We provide here an exhaustive morphological analysis of the fossil cheek teeth  
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39 from these localities, and compare these rodents from Peruvian Amazonia to other extinct New  
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41 and Old World hystricognaths as well as to extant caviomorphs.  
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## 52 **Material and methods**

### 53 *Material*

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

### 34 ***Dental nomenclature***

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

- 38 - Wood and Wilson (1936), Lavocat (1976), Candela (1999, 2002), Marivaux *et al.* (2002,  
39 2004) and Antoine *et al.* (2012) for the cusps, crests and cristids;
- 40 - Stirton (1935), Black and Wood (1956), Fields (1957), Candela (1999), Antoine *et al.*  
41 (2012) and Marivaux *et al.* (2014, 2017a, b) for the flexi(-ds), fossett(-ids)es and stri(-ds).

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49 Compared with these authors, several modifications regarding the designation of some cusp(-id)s,  
50 loph(-id)s, and flexi(-ds) are the results of our own observations and interpretations of the  
51 material we have studied and used for comparisons. These modifications, based on distinct

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3 homology hypotheses, are abundantly discussed here, and were considered for the selection of  
4 characters and character states used by Boivin (2017) and Boivin et al. (submitted) for their large  
5 scale cladistic analysis of caviomorph rodents. Some of these characters and character states have  
6 already been introduced by Boivin and Marivaux in Boivin *et al.* (2017a, b, 2018), and used by  
7 Marivaux *et al.* (2017a) at a wide taxonomic scale (i.e., for Old World hystricognaths). Upper  
8 case letters are used here for the upper dentition (DP: for **deciduous** premolar, P: for premolar, M:  
9 for molar) and lower case letters for the lower dentition (dp: for **deciduous** premolar, p: for  
10 premolar, m: for molar).  
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### 25 ***Criteria for homologies***

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

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

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21 **GSP**: Yale-Geological Survey of Pakistan; **Z5R**: Zallah 5 Rodent Locality.  
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## 27 **Historical review and current state of caviomorph dental structures (homologies and** 28 29 **nomenclature)**

### 30 31 32 *Upper teeth*

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35 Stirton (1935), then Wood and Wilson (1936) were the first to propose/formalize a nomenclature  
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37 of cusps, crests, cristids and flexi(-ids), applicable to the cheek tooth morphology of rodents, a  
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39 nomenclature which was consistent with the tribosphenic plan characteristic of Theria, as defined  
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41 by Simpson (1936) based on Osborn (1907). Throughout the description of *Platypittamys*  
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43 (Scarritt Pockett, Argentina; Deseadan), Wood (1949) applied the Wood and **Wilson nomenclature**  
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45 to caviomorphs. Their proposition was subsequently completed and formalized by Wood and  
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47 Patterson (1959), and later by Patterson and Wood (1982). For tetralophodont teeth, these authors  
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49 recognized successively on a mesiodistal axis, an antero-, meta-, hypo- and posterolophid on  
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51 lower teeth, and an antero-, proto-, meta- and posteroloph on upper teeth. According to these  
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3 authors, the tetralophodonty of upper molars was likely the ancestral condition in caviomorphs,  
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5 and the pentalophodonty was developed secondarily in some groups, by the addition of a neoloph  
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7 situated between the metaloph (then constituting the third loph) and the posteroloph (the fifth  
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9 loph; Figure 3(A)). The pentalophodonty of lower molars (as well as for dp4s and p4s) was also  
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11 interpreted with the addition of a neolophid (Figures 4(A) and 5(A)).  
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17 After studying the fossil rodents from Salla (Bolivia; Deseadan), Hoffstetter and Lavocat  
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19 (1970) and Lavocat (1976) proposed, however, another interpretation of the crest homologies for  
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21 describing the pentalophodonty of upper molars, a view which was compatible with that of  
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23 Schaub (1953) (Figure 3(B)). For these authors, the configuration of the teeth would be similar to  
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25 that found in the Theridomyidae and Old World hystricognaths (*Phiomorpha sensu* Lavocat  
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27 1967): the third crest would be a mesoloph (that can be linked to a transversal crest stemming  
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29 from the anterior arm of the hypocone; Lavocat 1976, figure 4, p. 71) labially connected to a  
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31 mesostyle, and the fourth crest would be a metaloph labially connected to the metacone (Figure  
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33 3(B)). They interpreted the tetralophodonty of caviomorphs as a simplification (i.e., loss of the  
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35 metaloph) from a pentalophodont ancestral state. They provided several arguments in favor of  
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37 this hypothesis:  
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- 42 - in addition to the formerly known pentalophodont taxa *Protosteiromys* (Cabeza Blanca  
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44 and La Flecha, Argentina; Deseadan; Wood and Patterson 1959), the fact that three new  
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46 genera from Salla (*Branisamys*, *Incamys*, and *Sallamys*) also exhibited a pentalophodont  
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48 pattern of upper molars, revealed that the pentalophodonty was rather common among  
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50 early caviomorphs (known in the 1970s) **and likely primitive**;  
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- 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-

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3 metacone complex, the latter topology being more consistent with the Lavocat's hypothesis of  
4 homologies (Lavocat 1976). Jaeger (1989) and Vucetich and Verzi (1994) followed Lavocat's  
5 view but diverged regarding the pattern of simplification leading to a tetralophodonty from a  
6 pentalophodont scheme. Based primarily on Salla rodents, Jaeger (1989) interpreted the third  
7 crest of tetralophodont upper molars of *Sallamys* as the result of a fusion between the metaloph  
8 and the mesoloph. In this context, the latter was not considered to be the homologous structure  
9 as that observed in Old World hystrognaths. These crests, although occupying an analogous  
10 position would be developed independently in each group as a result. Vucetich and Verzi (1994)  
11 also analyzed the Salla rodent fauna in performing a more extensive comparative analysis, and  
12 considering many other extinct and extant taxa. According to them, the transformation from a  
13 pentalophodont to a tetralophodont pattern would also include the fusion of the metaloph with  
14 another crest, but the latter would be the posteroloph instead of the mesoloph. These authors  
15 recognized that a fusion between the mesoloph and the metaloph is possible, like on the M2 of  
16 the *Branisamys* holotype (MNHN SAL 102, Lavocat 1976: plate 2.4). Nevertheless, this fusion  
17 would be particular in *Branisamys*, generating a part of the intraspecific variation observed in this  
18 taxon. Bryant and McKenna (1995) also advocated that the pentalophodonty of upper molars is  
19 the ancestral condition of caviomorphs, but in considering that the third crest of Old World  
20 hystrognaths and caviomorphs is neither a mesoloph nor a metaloph, but rather a mesolophule  
21 (Figure 3©). This structure was originally defined by Flynn *et al.* (1986) in Baluchimyinae  
22 (*Chapattimyidae sensu Flynn et al. 1986*; *Hystricognathi incertae sedis sensu Marivaux et al.*  
23 2002) as being the crest originating from the metaconule and running towards the labial edge of  
24 the tooth (Flynn *et al.* 1986; Marivaux 2000; Marivaux *et al.* 2000, 2002, 2004; Marivaux and  
25 Welcomme 2003). In studying the morphology of the upper molars of fossil and modern  
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3 erethizontoids, Candela (1999) showed that the third crest is either continuous or discontinuous in  
4 this superfamily. When discontinuous, this crest is formed by a lingual portion linked to a  
5 metaconule (corresponding to a mesolophule) and a neoformed labial portion stemming from the  
6 mesostyle (Figure 3(D)). Given these observations, Candela (1999) proposed a pre-  
7 pentalophodont step as the ancestral condition in erethizontoids, a pattern in which the metaloph  
8 is still connected to the hypocone. Subsequently, this connection would be lost, and the metaloph  
9 would be linked to the posteroloph. A continuous third crest would be formed by the fusion of the  
10 mesolophule with the neocrest of the mesostyle.  
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24 Over the past three decades, the hypothesis of an African origin of caviomorphs, closely  
25 related to the 'phiomorphs', has gained strong support. The phiomorph-caviomorph relationship  
26 derives from a corpus of morpho-anatomical and genetic data (see Introduction), other than the  
27 dental morphology only. Such a strongly supported phylogenetic relationship between Old and  
28 New World hystricognaths then supports Lavocat's dental homology hypothesis, which has now  
29 reached a well-accepted consensus, although some authors have continued to follow the  
30 nomenclature proposed by Wood (Carvalho and Salles 2004; Frailey and Campbell 2004). Since  
31 the 1990s, the discussions have progressively focused on the homology of the third crest on upper  
32 molars, considered as either a mesoloph or a mesolophule (see above). Marivaux (2000) studied  
33 the early radiation of Paleogene rodents via a phylogenetic approach, in order to better  
34 understand the patterns of dental transformations through time, and to identify homoplastic  
35 structures. In related papers, Marivaux *et al.* (2002, 2004) proposed a general dental terminology  
36 applicable to the whole group (at least to their Paleogene representatives and more recent forms  
37 moderately derived from a dental point of view). In this nomenclature, the third crest of upper  
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3 molars can be formed by (1) a lingual part, the mesolophule (*sensu* Flynn *et al.* 1986) that is  
4  
5 connected to the metaconule (conule that can disappear in some groups like caviomorphs and  
6  
7 advanced ‘phiomorphs’), and (2) a labial part, named mesoloph, originating from the mesostyle  
8  
9 and running lingually (Figure 3(E)). This nomenclature was consistent with that proposed by  
10  
11 Candela (1999). However, Marivaux *et al.* (2004) recognized only a mesolophule as the third  
12  
13 crest in the sampled Paleogene Ctenohystrica (caviomorphs included, but limited to few  
14  
15 Deseadean forms; the Afro-Asian hystricognaths being also less known and documented at that  
16  
17 time), the mesoloph being observed only in some Ischyromyiformes (Anomaluroidea,  
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19 Zegdomyidae, Eutypomyidae, Gliridae, Sciuravidae, and Theridomyidae). This terminology has  
20  
21 been applied by Marivaux for the original description of caviomorphs from CTA-27, which are  
22  
23 among the most ancient representatives of the **group known** thus far (Barrancan; Antoine *et al.*  
24  
25 2012; Figure 3(F)). The dental morphology of some of these rodents (*Cachiyacuy* and  
26  
27 *Canaanimys*), characterized by pentalophodont upper molars, is very similar to that of Old World  
28  
29 hystricognaths and especially to some Paleogene African forms. The discovery of these early  
30  
31 caviomorph taxa from the late Middle Eocene of Peruvian Amazonia has provided key elements,  
32  
33 which have strengthened **support for Lavocat’s** hypotheses regarding caviomorph origin and  
34  
35 dental evolutionary patterns (i.e., African origin of caviomorphs and ancestral pentalophodont  
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37 pattern of upper molars in this group; Hoffstetter and Lavocat 1970; Lavocat 1976).  
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### 47 ***Lower teeth***

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49 Although less controversial than for upper teeth, the structural homologies on lower teeth have  
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51 often been questioned, notably regarding the identification of the mesial cristids. According to  
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53 Candela (2000), based on Wood and Wilson (1936), the second cristid of lower molars in  
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3 erethizontids would be a metalophulid II or a mesolophid, depending on the connected cuspids  
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5 (protoconid-metaconid or mesoconid-mesostylid, respectively; Figure 4(B)). Candela (2002)  
6  
7 studied the dp4 morphology of extinct and extant erethizontids and compared it with that of dp4s  
8  
9 of some fossil Old World hystricognaths (i.e., *Baluchimys*, *Gaudeamus*, *Lindsaya*, *Phiomys*, and  
10  
11 *Tsaganomys*). The morphologies being very similar, she concluded that they are probably  
12  
13 homologous, and that the ancestral pattern of erethizontid dp4s (and probably, more generally, of  
14  
15 hystricognaths dp4s) is pentalophodont, contrary to Wood and Patterson (1959). On lower teeth,  
16  
17 based on Wood and Wilson (1936), she recognized successively an anterolophid, metalophulid II,  
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19 mesolophid, hypolophid and posterolophid (Figure 5(B1)). The tetralophodont scheme would be  
20  
21 developed subsequently in *Hypsosteiomys* and some specimens of *Erethizon dorsatum* by the  
22  
23 loss of the mesolophid (Figure 5(B2)). The hexalophodont pattern of some erethizontids (i.e.,  
24  
25 *Eosteiomys homogenidens*, *E. dorsatum*, *Steiromys detentus*, *S. duplicatus*, and *Coendou*  
26  
27 *prehensilis*) would be also achieved from the pentalophodont ancestral configuration, by the  
28  
29 addition of a neolophid between the anterolophid and the metalophulid II (Figure 5(B1)). Candela  
30  
31 (2002) identified the same hexalophodont morphology on one dp4 of *Branisamys* (UM GN 014;  
32  
33 Hartenberger 1975; Patterson and Wood 1982), a taxon from Salla initially described as a  
34  
35 dasyproctid cavioid (Lavocat 1976). Based on this observation, as well as on other cranial and  
36  
37 dental features characterizing erethizontids, Candela (2002) advocated a potential affiliation of  
38  
39 *Branisamys* to the New World porcupines.

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42 The nomenclatures used so far for the studies on hystricognaths (and more generally other  
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44 rodent groups) **have** often been **inconsistent** across authors. This lack of uniformity (standard  
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46 usage) has somewhat engendered **a** degree of confusion in the terminology: e.g.,  
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3 cingulum/anterior cingulid, anterolophid, paracristid/paralophid, metalophid, metalophid I,  
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5 protolophid/protocristid, metalophid II, metalophulid I, metalophulid II, and posterior arm of the  
6  
7 protoconid (e.g., Wood 1968; Dawson 1984; Flynn *et al.* 1986; Korth 1994; Kumar *et al.* 1997;  
8  
9 Wang 1997; Meng and Wyss 2001). The nomenclature proposed by Marivaux *et al.* (2004),  
10  
11 modified from that of Wood and Wilson (1936), allowed, to some extent, for a first step of  
12  
13 clarification of these issues, notably on the homologous structures used for discriminating the  
14  
15 anterior cristids of lower molars. Following this terminology, basal rodentiaforms display a  
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17 trigonid with a paralophid/paracristid linking the protoconid to the reduced paraconid, as well as  
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19 a metalophulid II (protolophid/protocristid = long posterior arm of protoconid) connecting the  
20  
21 protoconid to the metaconid (e.g., *Tribosphenomys*). The paraconid is subsequently lost and the  
22  
23 paralophid joins lingually the metaconid, then becoming a metalophulid I (e.g., *Archetypomys*,  
24  
25 *Cocomys*). A low anterior cingulid can be present in some “ctenodactyloids” and  
26  
27 “ischyromyoids”. In the latter group, this cingulid iteratively developed to reach a lophid status,  
28  
29 becoming the anterolophid, and in some cases replacing the metalophulid I, which is lost in some  
30  
31 forms (for a synthesis, see Marivaux *et al.* 2004, p. 120). In this context, Marivaux *et al.*  
32  
33 identified on caviomorph lower molars a metalophulid I, a metalophulid II, a hypolophid, and a  
34  
35 posterolophid (Figure 4(C)). According these authors, these same cristids are present on dp4s,  
36  
37 and a mesolophid can be additionally developed between the metalophulid II and the hypolophid  
38  
39 (Figure 5(C)). This terminology was used by Antoine *et al.* (2012). Candela and Rasia (2012)  
40  
41 extended this nomenclature to dp4s and lower molars of echimyids (the more diversified  
42  
43 octodontoid group) and questioned previous terminologies of Patterson and Wood (1982; Figures  
44  
45 4(A) and 5(A)) and Carvalho and Salles (2004; Figures 4(A) and (D), 5(A) and (D)) based on  
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47 cladistic assessments (Figures 4(E) and 5(E)). Following their results, the tetralophodonty would  
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3 be the ancestral condition of lower molars in echimyids, the pentalophodonty and trilophodonty  
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5 (which appears at least three times independently) would be derived. Candela and Rasia (2012)  
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7 shared, however, the view of Patterson and Wood (1982) and Carvalho and Salles (2004) in the  
8  
9 interpretation of the second cristid of pentalophodont lower molars (in *Hoplomys*), which would  
10  
11 be a neoformed structure called neolophid (Figure 4(E1)). As for erethizontids (Candela 2002),  
12  
13 the pentalophodonty would be the plesiomorph condition for echimyid dp4s, and the  
14  
15 tetralophodonty would be the apomorph state. Lastly, these authors interpreted the “crest C” of  
16  
17 dp4s and lower molars of some echimyids (i.e., *Clydomys*, *Euryzygomatomys*, *Lonchothrix*,  
18  
19 *Mesomys*, *Proechimys*, *Therisomysops*, or *Trinomys*) as being a metalophulid II, more or less long  
20  
21 and curved (Figures 4(E2) and 5(E2)). This cristid was originally defined by Carvalho and Salles  
22  
23 (2004) as a metalophid merged with a neolophid (Figures 4(D) and 5(D)). Recently, Verzi *et al.*  
24  
25 (2014, 2016, 2017) have considered the second cristid of lower molars in some octodontoids as a  
26  
27 mesolophid (*Myocastor*, *Acaremys* in Verzi *et al.* [2014, figure 5(D), p. 763]; *Acaremys* and gen.  
28  
29 *et sp. nov.* in Verzi *et al.* [2017, figure 5(B) and (F), p. 418]) or a combination of a metalophulid  
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31 II with a mesolophid (e.g., *Proechimys*, *Myocastor*, *Acarechimys* in Verzi *et al.* [2016, figures 1–  
32  
33 3, p. 96–98]; and potentially *Acarechimys*, *Plesiicarechimys*, and *Protacaremys* in Verzi *et al.*  
34  
35 [2017, figures 4(C), (F) and (G), p. 417]; Figure 4(F1)). In the case of the lower molars of  
36  
37 *Hoplomys*, Verzi *et al.* (2016) have interpreted the second cristid (“crest C”/neolophid *sensu*  
38  
39 Carvalho and Salles [2004] and Candela and Rasia [2012], respectively) as a metalophulid II, and  
40  
41 the third cristid (metalophulid II *sensu* Candela and Rasia [2012]) as a mesolophid (Figure  
42  
43 4(F2)). Following Arnal (2012) and Candela and Rasia (2012), Candela (2015) questioned the  
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45 hypothesis advanced by Verzi *et al.* (2014, and subsequently Verzi *et al.* 2016, 2017). According  
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47 to Candela (2015), in all octodontoids, the second cristid of lower molars would correspond to a  
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3 metalophulid II with notable variation in orientation, size and shape, but not to a mesolophid.  
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5 Recently, Verzi *et al.* (2018), analyzing dp4s of caviomorphs of the four superfamilies and  
6  
7 ancient representatives of New and Old World hystricognaths, have considered that a  
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9 hexalophodont scheme is the ancestral condition for this locus in caviomorphs. This scheme  
10  
11 would be characterized by an anterolophid, metalophulid I, metalophulid II, mesolophid,  
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13 hypolophid and posterolophid (Figure 5(F)). From this ancestral condition, more simple patterns  
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15 would derive with firstly the loss of the metalophulid I.  
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## 22 **Results**

### 23 *Upper teeth*

#### 24 *The third transverse crest*

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28 Marivaux (2000) and Marivaux *et al.* (2002, 2004) have highlighted the third crest of the upper  
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30 molars, which can comprise a lingual part, the mesolophule stemming from the metaconule  
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32 (conule that can disappear in caviomorphs), and a labial part, the mesoloph originating from the  
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34 mesostyle. Based on the available taxonomic sample, it was shown that the mesoloph is present  
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36 more specially in some Ischyromyiformes (*sensu* Marivaux *et al.* 2004), and that the third crest of  
37  
38 the upper molars in Ctenohystrica (including caviomorphs [but limited to *Incamys*, *Branisamys*,  
39  
40 *Sallamys*, and *Platypittamys*]) corresponds only to a mesolophule (see section ‘**Historical review**  
41  
42 **and current state of caviomorph dental structures**’). However, the New World hystricognaths  
43  
44 included in the analysis **were** limited and **inufficient** to appreciate **variability** of the third crest  
45  
46 configuration (works otherwise focused on Old World hystricognaths). In parallel, Candela  
47  
48 (1999) observed that the third crest of erethizontid upper molars can be discontinuous, and in this  
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50 case, in addition to a mesolophule, there is a labial crest neformed from the mesostyle.  
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3 Following the nomenclature proposed by Marivaux *et al.* (2004), this labial crest is an equivalent  
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5 of the mesoloph.  
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10 On several upper teeth of early caviomorphs from the Eocene of Contamana (e.g., MUSM  
11 1873, 2801, 2819, 2832), the third crest is clearly discontinuous and formed by two portions: a  
12 mesoloph and a mesolophule (Figure 6). The study of the **entire** fossil material from Contamana  
13 and Tarapoto/Shapaja has revealed that the third crest morphology is very **variable** (Boivin *et al.*  
14 2017a, b, 2018). Indeed, it can be composed of the mesoloph and mesolophule, connected either  
15 with each other (Figure 6(A)) or not (Figure 6(B)). It can also be only formed by the mesolophule  
16 (e.g., general case of upper molars of *Mayomys*; Figure 6(C) and (D)) or only by the mesoloph  
17 (e.g., general case of upper molars of three species of *Eoincamys* from Tarapoto/Shapaja; Figure  
18 6(E) and (F)) (Boivin *et al.* 2018). Besides, the mesoloph and mesolophule are also strongly  
19 variable in terms of length (Figure 6(A–F)), orientation and connections with other elements (i.e.,  
20 with the mesostyle, anterior arm of the hypocone, metaloph, or posteroloph). The third crest  
21 composition is sometimes hardly interpretable, notably when (1) this crest is fully transverse  
22 from the mesostyle to anterior arm of hypocone without discontinuity or mesiodistal **pinch-point**  
23 (Figure 6(G)), or (2) it displays several discontinuities or mesiodistal pitch-points (Figure 6(H)).  
24 When no interpretation/distinction can be made, the term “third transverse crest” is then used. In  
25 addition to erethizontoids (Candela, 1999), other fossil and modern caviomorphs, such as species  
26 of Santa Rosa, those of Salla, but also *Australoprocta*, *Garridomys*, *Eoviscaccia*, *Willidewu*,  
27 *Protadelphomys*, *Proechimys*, or *Mesomys* display upper molars with a mesoloph, accompanied  
28 or not by a mesolophule (Lavocat 1976; Patterson and Wood 1982; Vucetich and Bond 1984;  
29 Vucetich and Verzi 1991; Kramarz 1998, 2001a; Frailey and Campbell 2004; Kramarz *et al.*  
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3 2013). In this context, the observations made by Candela (1999) on erethizontoid upper molars  
4 must be generalized to the whole caviomorph group and for all upper loci (i.e., P4, DP4, and M1–  
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6 3).  
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### 10 11 12 *Terminology of flexi* 13

14 The flexus nomenclature of upper teeth used in Boivin *et al.* (2017a,b) follows that of Candela  
15 (1999). For pentalophodont teeth, this nomenclature recognizes, labially a paraflexus,  
16 mesoflexus, metaflexus and posteroflexus, and lingually the hypoflexus. Nevertheless, it is not  
17 consistent with the original definitions of the metaflexus and mesoflexus proposed by Black and  
18 Wood (1956). According to these authors, the metaflexus is **distal to** the mesoflexus and should  
19 be the posteroflexus *sensu* Candela (1999). The third crest being a secondary formation with  
20 respect to the ancestral pattern of rodents (see Marivaux *et al.* 2017a, b), the mesoflexus *sensu*  
21 Black and Wood (1956) **corresponds** to the mesoflexus **plus** metaflexus *sensu* Candela (1999). In  
22 Boivin *et al.* (2018), we proposed a new terminology in order to distinguish both flexi separated  
23 by the third crest: the mesial mesoflexus (mesoflexus *sensu* Candela 1999) and the distal  
24 mesoflexus (metaflexus *sensu* Candela 1999) (Figure 7).  
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### 42 *Pentalophodont, tetralophodont and trilophodont patterns* 43

44 Old and New World fossil evidence and phylogenetic inference (e.g., Marivaux et al. 2002,  
45 2004; Antoine et al. 2012; Sallam and Seiffert, 2016; Boivin 2017; Boivin et al. 2017a,  
46 submitted) substantiate **the hypothesis that** the ancestral occlusal pattern of caviomorph upper  
47 molars is composed of five transverse crests (see section '**Historical review and current state of**  
48 **caviomorph dental structures**'). As for the upper molars, the ancestral condition of P4s and DP4s  
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3 is also considered as a pentalophodont scheme. However, on the basis of the phylogenetic results  
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5 of Boivin (2017) and Boivin *et al.* (submitted), the characters corresponding to the  
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7 presence/absence of the metaloph on P4s and DP4s (see coding of the characters 68 and 115 in  
8  
9 Boivin 2017 and Boivin *et al.* submitted) have an ambiguous distribution in the basal branches of  
10  
11 caviomorphs. These ambiguities can be explained by an important polymorphism of these  
12  
13 characters in stem-caviomorphs (e.g., *Cachiyacuy contamanensis* or *Tarapotomys subandinus*)  
14  
15 and their non-coding for some taxa without documented P4 and/or DP4. According to the  
16  
17 nomenclature developed and adopted in this paper (Figures 1 and 2; see the paragraph ‘The third  
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19 transverse crest’ above), an anteroloph, protoloph, third transverse crest (mesoloph and/or  
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21 mesolophule), metaloph and posteroloph can therefore be distinguished on pentalophodont upper  
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26 teeth.

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31 In caviomorphs, the tetralophodont pattern, deriving from the pentalophodont ancestral  
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33 scheme (transformation cladistically supported in Boivin 2017 and Boivin *et al.* submitted), is  
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35 frequently developed on upper molars (Figure 8). Several taxa from Contamana (primarily  
36  
37 Eocene localities) and Tarapoto/Shapaja demonstrate of the transformation from a  
38  
39 pentalophodont pattern to a tetralophodont pattern: *Eoespina* sp. from CTA-51, *Cachiyacuy*  
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41 *contamanensis*, *Cachiyacuy kummeli*, *Canaanimys maquiensis* and cf. *Eoespina* sp. from CTA-  
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43 27, *Pozomys ucayaliensis* and *Cachiyacuy* cf. *contamanensis* 2 from CTA-29, *Chambiramys*  
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45 *sylvaticus* from CTA-61 (Late Oligocene), as well as *Eoincamys valverdei* and cf. *Tarapotomys*  
46  
47 sp. from TAR-20 and TAR-21, *Tarapotomys subandinus*, *Tarapotomys mayoensis* and *Mayomys*  
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49 *confluens* from TAR-01 (see Boivin *et al.* 2017a, b, 2018). In these taxa, the metaloph tends to be  
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51 lost: it is reduced and seems to merge with the posteroloph, especially in advanced stages of wear  
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3 (Figure 8). In these taxa, the metacone is usually linked to the posteroloph and tends also to  
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5 merge with the latter (subsumed), thereby forming a posteroloph-metacone-metaloph complex in  
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7 the posterolabial part of the tooth (Figure 8). Nevertheless, the metacone is sometimes still  
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9 distinct and well-defined, as in *Eoincamys valverdei*. Similar observations were previously made  
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11 in other caviomorphs (e.g., *Incamys* or *Draconomys*; Vucetich and Verzi 1994; Vucetich *et al.*  
12  
13 2010a; Verzi *et al.* 2016) that led Vucetich and Verzi (1994) to propose the hypothesis according  
14  
15 to which a tetralophodont pattern would derive from a pentalophodont pattern, notably by the  
16  
17 reduction of the metaloph subsumed within the posteroloph (Figure 8; see section ‘**Historical**  
18  
19 **review and current state of caviomorph dental structures**’). This pattern of occlusal  
20  
21 transformation seems to be the rule in caviomorphs and to have occurred **iteratively during** the  
22  
23 Paleogene. Some specimens (e.g., MUSM 2792–2794 from CTA-27) show a metaloph reduced to  
24  
25 a very short spur nonetheless. Therefore, a loss of the metaloph (by complete reduction not by  
26  
27 incorporation within the posteroloph) cannot be ruled out in some cases (Figure 8). Vucetich and  
28  
29 Verzi (1994, p. 66) also seem to consider as possible complete reduction (= loss) of the metaloph:  
30  
31 ‘*primero, el metalofo se reduce o se fusiona al pósterolofo, dando como resultado el primer*  
32  
33 *patrón tetralofodonte*’. Contrary to some Old World **hystricognaths** such as *Paraphiomys* and  
34  
35 *Thryonomys*, **no** caviomorph seems to develop a tetralophodont pattern as the result of the  
36  
37 reduction of the third crest on upper molars.  
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47 Vucetich and Verzi (1994) defined two main types of tetralophodont patterns on upper molars,  
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49 depending on the morphology of the third crest (mesoloph *sensu* Vucetich and Verzi 1994). The  
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51 first pattern is characterized by a complete third crest stretching from the mesostyle to the  
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53 anterior arm of the hypocone, whereas for the second pattern, this same crest is more reduced and  
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3 is lingually linked to the posteroloph (Figure 8). In the first case, the third crest can be composed  
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5 of a mesoloph and/or a mesolophule, whereas in the second case, it would correspond to a  
6  
7 mesoloph (backwardly curved), the mesolophule being absent (or lost).  
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12 The first scheme is typical of octodontoids but it is also observed in some erethizontoids  
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14 (*Eopululo*, *Hypsosteiromys*, ?*Neosteiromys tordillense*, *Steiromys detentus*, *Neosteiromys*  
15  
16 *bombifrons*, and *Protosteiromys pattersoni*; Vucetich *et al.* 1993, 2010b; Candela 2000, 2004;  
17  
18 Frailey and Campbell 2004; Pérez *et al.* in press) and in several taxa considered here as stem-  
19  
20 caviomorphs (e.g., *Cachiyacuy*, *Canaanimys*, *Eoespina*, *Pozomys*, *Ucayalimys*, *Plesiosteiromys*,  
21  
22 or *Tarapotomys*; see Boivin 2017 and Boivin *et al.* submitted). In octodontoids (e.g.,  
23  
24 *Platypittamys* or *Dudumus*; Wood 1949; Arnal *et al.* 2014), the tetralophodont pattern of upper  
25  
26 molars is associated with four main cusps: the paracone, protocone, hypocone and a cusp situated  
27  
28 **labiodistally, usually joined** to the posteroloph with wear. Owing to its large size (in height and  
29  
30 surface) and its distal position on the occlusal surface, the latter cusp has often – and logically –  
31  
32 been considered as a metacone (e.g., Vucetich and Kramarz 1993; Vucetich and Verzi 1996; Arnal  
33  
34 and Vucetich 2015; Arnal *et al.* 2014). However, in some cases, this distolabial cusp may be a  
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36 **large and displaced** mesostyle. This new nomenclatural assumption is supported by several  
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38 observations:  
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44 - some upper molars of the octodontoid *Protadelphomys* (Vucetich and Bond 1984; Vucetich  
45  
46 *et al.* 1992) **retain** a reduced metaloph associated with a metacone positioned very distally and  
47  
48 slightly lingually, and which appears smaller than the mesostyle;

49 - some octodontoids (e.g., *Galileomys antelucanus*; Vucetich and Kramarz 2003) have on  
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51 some of their upper molars a third transverse crest, which clearly originates from this labiodistal  
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3 cusp. In *Galileomys antelucanus*, the third crest is lingually extended and connected to the  
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5 anterior arm of the hypocone. A short mesolophular spur is sometimes distinct. This morphology  
6  
7 **recalls** the condition found in some taxa such as *Cachiyacuy* and *Eobranisamys javierpradoi*, and  
8  
9 thus can be interpreted as a third crest essentially formed by a long mesoloph stemming from the  
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11 mesostyle. A metacone-metaloph complex is highly doubtful, the metaloph being very rarely  
12  
13 connected to the anterior arm of the hypocone in caviomorphs. A metaloph-anterior arm of the  
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15 hypocone connection is only observed in two ancient caviomorphs (and basal): *Cachiyacuy* and  
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17 *Canaanymys*. Additionally, the metaloph seems to disappear in octodontoids, as observed in  
18  
19 *Plesiacaerchimys* or *Draconomys* (Vucetich and Vieytes 2006; Vucetich *et al.* 2010a);  
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23  
24 - lastly, **the abundant taxon** in TAR-01, *Mayomys confluens*, shows affinities with  
25  
26 octodontoids (Boivin 2017; Boivin *et al.* 2018, submitted). The morphology of its upper molars  
27  
28 appears intermediary (for considered characters), between the ancestral pentalophodont pattern  
29  
30 and the tetralophodont pattern typical of octodontoids. Such a configuration highlights the  
31  
32 understanding regarding the identification of the labiodistal cusp. In *Mayomys*, the tetralophodont  
33  
34 scheme is dominant, with a metaloph sometimes vestigial but absent in most cases. A metacone,  
35  
36 distal to the mesostyle, is clearly distinct on some M3s (MUSM 3462 and 3480; Boivin *et al.*  
37  
38 2018, figure 4S, p. X) and merged with the posteroloph and/or the mesostyle with wear (e.g.,  
39  
40 MUSM 3461; Boivin *et al.* 2018, figure 4N, p. X). On M1–2s, only one labiodistal cusp is  
41  
42 present. It is interpreted as a mesostyle due to, (1) its position moderately close to the paracone;  
43  
44 (2) a third crest (usually a mesolophule) broadly transverse and aligned with this cusp (both  
45  
46 structures can be joint), and (3) the presence of a very extensive distal flexus. The metacone is  
47  
48 subsumed within the posteroloph in most cases. **The** MUSM 3462 M3 has a large and distally  
49  
50 displaced mesostyle, with a labiodistal-linguomesial obliquity of the third crest, and a marked  
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3 expansion of the distal flexus, which are typical features of octodontoids (e.g., *Caviocricetus*,  
4  
5 *Dudumus*).

6  
7 However, it is worth noting that on some specimens of *Sallamys pascuali* from Salla  
8 (MNHN-Bol-V-004256, -007382, -007589, -007823, and -011054), the mesostyle appears  
9  
10 associated (i.e., very closely situated or twinned) to a distal cusp, interpretable as a metacone. On  
11  
12 these specimens, the mesostyle can be larger than the metacone (MNHN-Bol-V-007589), but the  
13  
14 reverse is also observed (MNHN-Bol-V-007382 and -011054). Hence, **total** loss of the metacone  
15  
16 may not have occurred in all octodontoids. A fusion between the mesostyle and the metacone **is**  
17  
18 also possible (as in the erethizontoid *Erethizon* and *Coendou*; Boivin 2017 and Boivin et al.  
19  
20 **submitted**), and as such the hypothesis of loss of the mesostyle instead of the metacone cannot be  
21  
22 completely excluded in this superfamily.  
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31 The second scheme of tetralophodonty defined by Vucetich and Verzi (1994) would be a  
32  
33 characteristic of chinchilloids. Indeed, this morphology is developed in several fossil  
34  
35 chinchilloids (e.g., *Scleromys angustus*, *Eoviscaccia australis*, and *Garridomys curunuquem*;  
36  
37 Ameghino 1887; Kramarz 2001a; Kramarz et al. 2013), taxa originally described as dasyproctids  
38  
39 but which would show closer affinities with chinchilloids (e.g., *Microscleromys cribriphilus*,  
40  
41 *Eoincamys pascuali*, and *Eoincamys parvus*; Walton 1997; Frailey and Campbell 2004; Boivin et  
42  
43 al. 2018), **and** in the octodontoid *Protadelphomys latus* (Vucetich and Bond 1984). Such a case of  
44  
45 **tetralophodonty** also tends to be developed in other taxa such as: the chinchilloid *Eoincamys*  
46  
47 *ameghinoi*, *Eoincamys valverdei*, *Chambiramys sylvaticus*, *Incamys bolivianus*, *Maquiamys*  
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49 *praecursor*, *Scleromys quadrangulatus* and *Microscleromys paradoxalis*, and the octodontoid  
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51 *Sallamys pascuali* (Lavocat 1976; Patterson and Wood 1982; Walton 1997; Frailey and Campbell  
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3 2004; Kramarz 2006a; Boivin 2017; Boivin *et al.* 2017b, 2018, submitted). In these species, the  
4 mesoloph is reduced and it loses its connection(s) with the anterior arm of the hypocone or the  
5 mesolophule (which is strongly reduced or absent), its lingual part is oriented toward the  
6 posteroloph and, in some cases, connects to the latter. In some of these taxa (*E. valverdei*, *C.*  
7 *sylvaticus*, *I. bolivianus*, *S. pascuali*, and *P. latus*), a short metaloph can be still present. With  
8 wear, the mesoloph and mesostyle tend to be subsumed within the posteroloph (and the metaloph,  
9 if it is still present), thus forming a large distolabial complex/platform as observed on upper  
10 molars of *S. pascuali*, *E. valverdei*, and species of *Scleromys*. This complex is suspected on M1–  
11 2s of *Willidewu*, which have three transverse crests including a very thick posteroloph (Vucetich  
12 and Verzi 1991, 1994). This configuration being very similar to that observed for the metaloph,  
13 Vucetich and Verzi (1994) and Verzi *et al.* (2016) have proposed that the transformation from a  
14 tetralophodont pattern to a trilophodont pattern can be explained by the loss of a crest (i.e.,  
15 mesoloph *sensu* Vucetich and Verzi 1994; mesolophule *sensu* Verzi *et al.* 2016; called third  
16 transverse crest here) merging with the posteroloph. This transformation allows explaining the  
17 dental pattern of upper molars of *Chambiramys shipiborum* from CTA-32 (Late Oligocene).  
18 Indeed, this taxon displays trilophodont upper molars, with a mesostyle distally displaced and  
19 strongly linked to the posteroloph and structures associated to the posteroloph, which are likely  
20 the relicts of the third crest or its connection with the posteroloph (on MUSM 2849 and 2852;  
21 Boivin *et al.* 2017b, figure 4B, C, p. 77). With wear (MUSM 2851; Boivin *et al.* 2017b, figure  
22 4D, p. 77), all of these structures merge and form a large complex (i.e., platform).

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50 The observations made here, supported by phylogenetic results of Boivin (2017) and Boivin  
51 *et al.* (submitted) and consistent with the proposition of Vucetich and Verzi (1994), allow to  
52 explain the transformation from a pentalophodont pattern to a tetralophodont pattern: the  
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3 metaloph would merge with the posteroloph or it would **be lost**. Concerning the transformation  
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5 from a tetralophodont pattern to a trilophodont pattern, in this case it is the third crest (mesoloph  
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7 *sensu* Vucetich and Verzi 1994; mesolophule *sensu* Verzi *et al.* 2016) which would merge *in fine*  
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9 with the posteroloph or would disappear, the metaloph being already absent or subsumed  
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11 (indistinct) within the posteroloph (Figure 8). Nevertheless, these transformations do not  
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13 necessarily occur in an ordered fashion (i.e., a trilophodont scheme deriving from a  
14  
15 tetralophodont scheme, itself deriving from the pentalophodont scheme). As a matter of fact,  
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17 some taxa, such as *E. valverdei*, still have a metaloph in addition to the reduced third crest, all of  
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19 these structures tending to merge with the posteroloph. These taxa would then illustrate a direct  
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21 transformation from a pentalophodont to a trilophodont pattern (Figure 8).  
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29 Interestingly, in the extant octodontoid *Euryzygomatomys*, the trilophodonty of upper molars  
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31 seems not to follow a scheme of occlusal transformations presented above. Indeed, its  
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33 trilophodont pattern would be linked to the loss of the labial protoloph instead of the third crest  
34  
35 (always present). The slightly worn teeth of a specimen attributed to this taxon (MLP 16 VII0211;  
36  
37 Figure 9) are characterized by an isolated cusp, positioned to the labial extremity of the first  
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39 transverse crest (i.e., anteroloph), and another labial cusp connected to the apparent second crest.  
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41 With dental wear, the first cusp tends to be connected to the anteroloph. It can be interpreted as a  
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43 paracone. In that context, the cusp directly posterior to this paracone would then be a mesostyle,  
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45 and the crest linked to this style would be the third transverse crest (mesoloph/mesolophule),  
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47 thereby forming a transverse crest in second position. However, the possibility exists that this  
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49 isolated buccal cusp is rather a neof ormation, which would invalidate our interpretation regarding  
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51 the trilophodonty **of** this taxon.  
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### *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*, *Palaeosteiomys amazonensis*, *Eoincamys valverdei*, *Eoincamys parvus*, cf. *Tarapotomys* sp. of TAR-20 and TAR-21, *Tarapotomys subandinus*, *Tarapotomys mayoensis*, *Kichkasteiomys 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 neof ormation 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 although 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*

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

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5 In most caviomorphs, the second transverse cristid of lower molars would correspond to a  
6  
7 posterior arm of the protoconid (= metalophulid II; Candela 2000, 2015; Marivaux 2000;  
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9 Marivaux *et al.* 2002, 2004; Arnal and Vucetich 2011, 2015; Antoine *et al.* 2012; Arnal, 2012;  
10  
11 Candela and Rasia 2012; Kramarz *et al.* 2013; Arnal *et al.* 2014; see section ‘**Historical review**  
12  
13 **and current state of caviomorph dental structures**’). Some authors recognize that a mesolophid  
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15 can form the second cristid instead of a metalophulid II (in erethizontoids; Candela 2000) or in  
16  
17 association with the metalophulid II (in octodontoids; Verzi *et al.* 2014, 2016, 2017). However,  
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19 there are competing interpretations regarding that second cristid, notably in octodontoids. Indeed,  
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21 contrary to the opinion of Verzi *et al.* (2014, 2016, 2017), Arnal (2012), Candela and Rasia (2012)  
22  
23 and Candela (2015) consider that in octodontoids, the second cristid of lower molars is not a  
24  
25 mesolophid but a metalophulid II **that varies** in orientation and length (see section ‘**Historical**  
26  
27 **review and current state of caviomorph dental structures**’).  
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34 Like the third crest of upper teeth, the configuration of the second transverse cristid is highly  
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36 variable on lower molars and p4s of taxa from Contamana and Tarapoto/Shapaja, especially in  
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38 *Cachiyacuy contamanensis* (CTA-27). In the latter, the second transverse cristid of lower molars  
39  
40 is usually formed by two portions of fluctuating length and orientation: (1) a labial portion  
41  
42 stemming from the protoconid (the posterior arm of the protoconid), and (2) a lingual portion  
43  
44 originating from the mesostylid (Figure 11(A) and (B)). The latter, not previously identified, has  
45  
46 been recently called a neomesolophid in Boivin *et al.* (2017a, b, 2018). It is worth noting that the  
47  
48 posterior arm of the protoconid and the neomesolophid can be connected together (Figure 11(A))  
49  
50 or disconnected (Figure 11(B)), and in some cases, only the posterior arm of the protoconid  
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52 (Figure 11(C) and (D)) or the neomesolophid (Figure 11(E) and (F)) forms the second cristid (see  
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3 Boivin *et al.* 2017a, figure 8, p. 21). A posterior arm of the protoconid and neomesolophid are  
4 also recognisable on p4s of *C. contamanensis* (Boivin *et al.* 2017a, figure 7, p. 20). As for the  
5 third crest of upper teeth, it is sometimes difficult to determine the composition of the second  
6 cristid of lower teeth (Figure 11(G) and (H)). The other taxa described from Contamana and  
7 Tarapoto/Shapaja have lower molars that differ regarding the development of these two cristids:  
8 both cristids are present (e.g., *Cachiyacuy kummeli*, *Canaanimys maquiensis*, *Palaeosteiomys*  
9 *amazonensis*, cf. *Tarapotomys* sp. of TAR-20 and TAR-21, and *Tarapotomys mayoensis*), only the  
10 neomesolophid is developed (e.g., *Chambiramys sylvaticus*, *Eoincamys* cf. *pascuali* of TAR-01,  
11 *Tarapotomys subandinus*, and *Tarapotomys mayoensis*), only the posterior arm of the protoconid  
12 is developed (e.g., *Mayomys confluens*), or neither cristid is present (*Chambiramys shipiborum*  
13 and *Tarapotomys mayoensis*) (see Boivin *et al.* 2017a, b, 2018). Other fossil and modern  
14 caviomorphs, such as species of Santa Rosa, those of Salla, *Hypsosteiomys*, *Steiromys*,  
15 *Australoprocta*, *Garridomys*, *Scleromys*, *Drytomomys*, *Prostichomys*, *Erethizon*, *Myocastor*,  
16 *Proechimys* or *Mesomys* (Fields 1957; Lavocat 1976; Patterson and Wood 1982; Kramarz 1998,  
17 2001b, 2006a; Candela 2000; Frailey and Campbell 2004; Kramarz *et al.* 2013), clearly have a  
18 neomesolophid, which is associated or not with a posterior arm of the protoconid. The “crest C”  
19 defined by Carvalho and Salles (2004) on lower molars of some echimyids (e.g., *Clydomys*,  
20 *Euryzygomatomys*, *Lonchothrix*, and *Mesomys*) was interpreted by Candela and Rasia (2012) as  
21 being a metalophulid II, which would have lost its connection with the protoconid, and developed  
22 a link with the metalophulid I (see section ‘Historical review and current state of caviomorph  
23 dental structures’). Nevertheless, this cristid would correspond most likely to a neomesolophid,  
24 with the labial extremity connected to the metalophulid I.



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3 Several p4s and lower molars of *C. contamanensis* (CTA-27, late Middle Eocene; MUSM  
4 1879, 1914, 1915, 2676–2678, 2689, 2692, 2701, 2708, and 2714; Antoine et al. 2012; Boivin et  
5 al. 2017a) show additional and unusual structures (cristids and/or cuspid) between the second  
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10 transverse cristid and the hypolophid. Some of these structures are developed from the  
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12 hypolophid, and as such, are considered as neoformations. Otherwise, it is difficult to establish  
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14 criteria of homology for these structures, notably those stemming from the ectolophid, which can  
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16 be interpreted either as neoformations or as residual parts of an ancestral mesolophid (Boivin *et*  
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18 *al.* 2017a; Figure 12). Among all p4s and lower molars attributed to *C. contamanensis*, only one  
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20 specimen (the MUSM 2678 p4) displays one of these additional cristids stemming from a cuspid  
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22 situated at the level of the ectolophid, and that could be interpreted as a mesoconid. Some lower  
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24 molars seem to bear a mesoconid-like cuspid, but without supernumerary cristid associated with  
25  
26 it. **These structures are** not found in other taxa from Contamana or Tarapoto/Shapaja. The  
27  
28 mesolophid **is commonly** developed but very variable and slender in some ‘baluchimyines’  
29  
30 and ‘phiomorphs’ of the Old World from the Eocene to the Oligocene: *Bugtimys*, *Hodsahibia*,  
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32 ‘*Acritophiomys*’, *Phiomys*, ‘*Waslamys*’, and *Gaudeamus hylaeus* (see Marivaux and Welcomme  
33  
34 2003; Jaeger et al. 2010; Sallam et al. 2009, 2011, 2012). Otherwise, the mesolophid is present  
35  
36 and well developed in many groups of Ischyromyiformes (e.g., Anomaluroidea, Theridomorpha  
37  
38 and Cricetidae; see Marivaux *et al.* 2004, 2017b). It is therefore possible that basal caviomorphs  
39  
40 (including *C. contamanensis*) inherited this structure from their African common ancestor. It is  
41  
42 usually considered that the ancestral pattern of caviomorph lower molars is tetralophodont (e.g.,  
43  
44 metalophid I, second cristid, hypolophid, and posterolophid). But, considering that earliest  
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46 caviomorphs would have **inherited a** mesolophid from their African hystricognath ancestor (and  
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48 not developed this structure **independently**), the possibility exists that a pentalophodont pattern  
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3 characterized earliest caviomorphs. This ancestral pattern would have been rapidly supplanted by  
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5 the tetralophodont scheme (i.e., without mesolophid; Figure 12).  
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10 It is worth noting that the modern caviomorph *Dasyprocta* can have pentalophodont lower  
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12 molars (Figure 12) characterized by:  
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- 14 - a second transverse cristid clearly formed by a posterior arm of the protoconid and  
15  
16 another cristid stemming from the metaconid (metaconid cristid or metaconid spur, see  
17  
18 below);  
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- 20 - a third **cristid between** the second transverse cristid and the hypolophid. It is composed of  
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22 a lingual part corresponding potentially to a neomesolophid, and a labial part stemming  
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24 from the ectolophid, which can be interpreted as a mesolophid.  
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31 In other taxa observed and compared to the material of Contamana and Tarapoto/Shapaja in  
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33 the context of this study (*Coendou*, *Branisamys*, *Cephalomys*, and *Luantus*), the second  
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35 transverse cristid can be distally displaced on lower molars, and notably on m3s. The second  
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37 cristid is then close to the hypolophid and would correspond to a mesolophid (at least for its  
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39 labial part, sometimes connected to a neomesolophid; Figure 12). In addition, some specimens of  
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41 extant erethizontoids (MNHN MO-1909-241 and MNHN MO-1909-242, originally assigned to  
42  
43 *Sphiggurus insidiosus* and probably attributable to *Coendou insidiosus* following the synonymy  
44  
45 proposed by Voss 2011) have pentalophodont lower molars, characterized by the simultaneous  
46  
47 presence of a posterior arm of the protoconid and a mesolophid (Figure 12). The presence of a  
48  
49 mesolophid in erethizontoids had previously been indicated by Candela (2000). Verzi *et al.*  
50  
51 (2014, 2016, 2017) consider that the second cristid of lower molars of some octodontoids is a  
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3 mesolophid or the association of a metalophulid II with a mesolophid. As noted by Verzi *et al.*  
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5 (2016, figure 3, p. 98), a very short mesolophid can be developed posteriorly to the second  
6  
7 transverse cristid in *Protacaremys prior* and *Caviocricetus lucasi* (Figure 14(G) and (J)). In  
8  
9 contrast, in other taxa figured by Verzi *et al.* (2016, figures 1 and 2, p. 96–97; Figures 13, 14), the  
10  
11 second cristid is positioned anteriorly, and it is linked to the protoconid and/or the mesostylid,  
12  
13 and/or the metaconid (see below). Given these connections, **this cristid seems not to correspond**  
14  
15 **to a mesolophid (Figures 13, 14), which** is in agreement with the hypothesis selected by Arnal  
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17 (2012), Candela and Rasia (2012) and Candela (2015).  
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23 Another type of pentalophodonty, different from that previously mentioned for *Dasyprocta*  
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25 and *Shiggurus*, is found on lower molars of the octodontoid *Hoplomys* (Carvalho and Salles  
26  
27 2004; Figure 13(A1, A3)) and several fossil erethizontoids (e.g., *Branisamyopsis australis*,  
28  
29 *Branisamyopsis praesigmoides*, *Steiromys duplicatus*, and *Neosteiromys pattoni*; Candela 2000,  
30  
31 2003, 2004; Kramarz 2004). It corresponds to an addition of a neolophid in the anteroflexid,  
32  
33 situated between the metalophulid I and the second cristid (Patterson and Wood 1982; Candela  
34  
35 2000, 2003, 2004; Carvalho and Salles 2004; Candela and Rasia 2012; Figures 12 and 13(A3)).  
36  
37 This neolophid often originates from a mesiolingual cuspid, which is also neoformed (neoconid),  
38  
39 and situated between the metaconid and the mesostylid. MUSM 2861 is the only lower molar  
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41 from CTA-32 that is assigned to *Palaeosteiromys amazonensis* (Boivin *et al.* 2017b, figure 4L, p.  
42  
43 77). With a neolophid in the anteroflexid, this molar displays a pattern equivalent to that of *B.*  
44  
45 *australis*, *B. praesigmoides*, *S. duplicatus*, *N. pattoni* and *Hoplomys* (Boivin *et al.* 2017b).  
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52 In several caviomorphs (including *Dasyprocta*), a cristid is developed in the anteroflexid of  
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54 lower molars. This cristid is **neither a posterior arm of the protoconid, nor a mesolophid, nor a**  
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3 neomesolophid, and nor to the neolophid aforementioned. It extends labially from the metaconid,  
4 being usually short or very short. It is named here metaconid cristid or metaconid spur (Figures  
5 12 and 13; Boivin 2017; Boivin *et al.* submitted). For most taxa displaying that metaconid cristid,  
6 the development of this structure is very variable. Besides, for a given species, this cristid can be  
7 present or absent (see coding of the character 369 in Boivin 2017 and Boivin *et al.* submitted). It  
8 can be then expected that the development of this structure is convergent among several taxa. It is  
9 frequently found in octodontoids (e.g., *Platypittamys*, *Sallamys*, *Willidewu*, *Acaremys*, *Dudumus*,  
10 and *Galileomys*; Wood 1949; Lavocat 1976; Patterson and Wood 1982; Vucetich and Verzi 1991;  
11 Kramarz 2004; Arnal and Vucetich 2015; Arnal *et al.* 2014). In that group, this metaconid cristid  
12 can be connected to the posterior arm of the protoconid, and in some cases accompanied by other  
13 cristulids stemming from the metalophulid I, the metaconid or even the posterior arm of this  
14 cuspid (when the latter is still present; Figures 13, 14). Verzi *et al.* (2016, 2017) recognized a  
15 metalophulid II and a mesolophid on lower molars of some octodontoids (the two cristids can be  
16 associated to form the second transverse cristid; see above). Nevertheless, given its position,  
17 orientation and connections with other structures, the cristid interpreted by Verzi *et al.* (2016,  
18 figures 1–2, p. 96–98; Figure 13(K); Figure 14(B–H), (J) and (K)) as a metalophulid II seems  
19 more likely a metaconid cristid (in *Acarechimys minutus*, *Acaremys*, *Caviocricetus lucasi*,  
20 *Deseadomys arambourgi*, *Sallamys pascuali*, *Protacaremys prior*, *Protadelphomys* sp., and *P.*  
21 *latus*), and/or a supernumerary cristulid (in *Proechimys cuvieri*, *P. roberti*, *Protadelphomys* sp.,  
22 and *Sallamys quispea*; Figure 13(B), (D) and (I); Figure 14 (C) and (E)). Similarly, the cristid  
23 considered as a mesolophid by Verzi *et al.* (2016, figures 1 and 2, p. 96–97) corresponds more  
24 likely to:

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

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- 2
- 3 - a posterior arm of the protoconid separated from a neomesolophid (m2 of *Proechimys*
- 4 *cuvieri* in Verzi *et al.* (2016, figure 1b', p. 96; Figure 13(B));
- 5
- 6
- 7 - a posterior arm of the protoconid linked to a neomesolophid (in *Myocastor coypus*, m1 of
- 8 *Proechimys cuvieri* in Verzi *et al.* (2016, figure 1b', i', p. 96; Figure 13(B), (I) and (J));
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- 11
- 12 - a posterior arm of the protoconid, separated from a metaconid cristid (in *Acarechimys*
- 13 *minutus*, *Protacaremys prior*, *P. latus*, *Protadelphomys* sp., *Sallamys pascuali*, and *S.*
- 14 *quispea*; Figure 13(K); Figure 14(C–G));
- 15
- 16
- 17 - a posterior arm of the protoconid, connected to a metaconid cristid (*Protacaremys prior*;
- 18 Figure 14(H)).
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24 On lower molars of *Lonchotrix emiliae*, *Proechimys poliopus*, *P. roberti*, *Trinomys elegans*  
 25 figured by Verzi *et al.* (2016), the homology of the cristid situated in second position, stemming  
 26 from the lingual margin of the molars, and which is labially connected to the metalophulid I, is  
 27 somewhat ambiguous. This cristid would correspond either to a neomesolophid or to a metaconid  
 28 cristid (Figure 13(C), (D), (G) and (H)). Verzi *et al.* (2017, figure 4F, G, p. 417) described a  
 29 “lingual extension of the metaconid” on m1s of *Plesiacarechimys* and *Protocaremys*, which  
 30 would not correspond to the metaconid cristid (it is not directly connected to the metaconid), but  
 31 rather to a neoformation.  
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44 Among the Oligocene taxa from Contamana and Tarapoto/Shapaja, several of them show a  
 45 tendency toward a reduction of the second cristid of lower molars: *Chambiramys sylvaticus*,  
 46 *Eoincamys* cf. *pascuali*, *Tarapotomys subandinus*, *Tarapotomys mayoensis* and *Mayomys*  
 47 *confluens* (Boivin *et al.* 2017b, 2018). In caviomorphs, this reduction seems to have occurred  
 48 convergently several times, and two usual types of patterns can then be distinguished (Figure 12):  
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3 - in the first, the posterior arm of the protoconid tends to disappear and the neomesolophid  
4 to be reduced (e.g., *Tarapotomys subandinus*, *T. mayoensis*, *Chambiramys sylvaticus*,  
5 *Eoincamys*, *Incamys*, *Garridomys*, and *Eoviscaccia*; Lavocat 1976; Patterson and Wood  
6 1982; Kramarz 2001a; Frailey and Campbell 2004; Kramarz *et al.* 2013; Boivin *et al.*  
7 2017b, 2018);  
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14 - in the second, the neomesolophid tends to disappear and the posterior arm of the  
15 protoconid (or ?mesolophid) to be reduced (e.g., *Luantus*, *Mayomys*, *Draconomys*,  
16 *Leucokephalos*, and *Xylechimys*; Patterson and Pascual 1968; Kramarz 2006b; Vucetich *et*  
17 *al.* 2010a, 2015; Boivin *et al.* 2018).

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24 In caviomorphs, several taxa display trilophodont lower molars (e.g., *Tarapotomys*  
25 *mayoensis*, *Chambiramys shipiborum*, *Phoberomys*, *Luantus*, *Sallamys*, *Ethelomys*, and  
26 *Deseadomys*; Wood and Patterson 1959; Lavocat 1976; Patterson and Wood 1982; Kramarz  
27 2006b; Vucetich *et al.* 2015; Rasia and Candela 2017; Boivin *et al.* 2017b, 2018). The  
28 trilophodont pattern is achieved by the loss of the second cristid, and seems to be linked or to  
29 have implied (Figure 12):  
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33 - the fusion of a reduced neomesolophid with the metalophulid I. This fusion is observed for  
34 instance on worn molars of *T. mayoensis*, *Incamys* and *Scleromys*. This structural rearrangement  
35 recalls that observed on upper molars, notably the fusion of the metaloph and third crest with the  
36 posteroloph (see above);  
37

38 - the fusion of the metaconid cristid (or associated cristulids; see previous paragraph) with the  
39 metalophulid I. This fusion occurs on worn molars of *Sallamys*;  
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42 - the complete disappearance of the neomesolophid and/or the posterior arm of the protoconid  
43 (or ?mesolophid; e.g., *T. mayoensis*, *C. shipiborum*, *Luantus*, and *Sallamys*).  
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5 In caviomorphs, p4s develop equivalent structures to those observed on lower molars (i.e.,  
6 posterior arm of the protoconid, mesolophid, neomesolophid, neolophid, and metaconid cristid).  
7  
8 The second transverse cristid can also be reduced or lost on p4s (e.g., *Draconomys*,  
9  
10 *Leucokephalos*, and *Deseadomys*), as well as the metalophulid I (e.g., *Cephalomys arcidens*,  
11  
12 *Asteromys*, *Perimys*, or *Galileomys*; Wood and Patterson 1959; Kramarz 2002, 2004). The  
13  
14 hypolophid, entoconid and posterolophid are merged and form a distal thick cristid on p4s of  
15  
16 some octodontoids (*Platypittamys*, *Deseadomys*, *Galileomys*, *Acaremys*, and *Sciamys*). However,  
17  
18 the fossil taxa being more rarely documented by p4s than lower molars, the evolution of these  
19  
20 different structures on p4s is more difficult to appreciate.  
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### 27 *Nomenclature of the dp4s*

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29 According to Candela (2002) and Candela and Rasia (2012), the ancestral pattern of the dp4s of  
30  
31 echimyids and erethizontids (and more broadly of hystricognaths) is pentalophodont. These  
32  
33 authors recognize on dp4s of these groups: a metalophulid I, a metalophulid II, a mesolophid, a  
34  
35 hypolophid and a posterolophid. In contrast, Verzi *et al.* (2018) consider that a hexalophodont  
36  
37 scheme is the ancestral condition for this locus in caviomorphs. This scheme would be  
38  
39 characterized by the presence of an anterolophid, in addition to the metalophulid I, metalophulid  
40  
41 II, mesolophid, hypolophid and the posterolophid (see section ‘**Historical review and current state**  
42  
43 **of caviomorph dental structures**’).  
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50 Considering the Old and New World hystricognaths, the identification of the mesialmost  
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52 cristid seems to be somewhat **more** complicated than that proposed by Candela (2002), Candela  
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54 and Rasia (2012) and Verzi *et al.* (2018). In some caviomorphs, the anterior cristid on dp4s  
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3 appears to be a metalophulid I, which is formed by the anterior arm of the protoconid and/or the  
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5 anterior arm of the metaconid. In Eocene and Oligocene Old World hystricognaths, the trigonid  
6  
7 of the dp4s is strongly variable and can display an anterior cingulid/anterolophid/anteroconid,  
8  
9 and/or elements of the metalophulid I (which are usually separated and reduced), and/or the  
10  
11 posterior arm of the protoconid/metaconid cristid. In some of these Old World hystricognaths  
12  
13 (e.g., *Baluchimys barryi*, *Lindsaya derbugtiensis*; Flynn *et al.* 1986), there is no direct connection  
14  
15 between the anterior cingulid/anterolophid/anteroconid and the anterior arms of the protoconid  
16  
17 and metaconid, but the latter arms are often oriented toward the anterior  
18  
19 cingulid/anterolophid/anteroconid. In contrast, in some others (*Acritophiomys bowni*, *Birkamys*  
20  
21 *korai*, *Hodsahibia azrae*, *Lophibaluchia*, *Phiomys hammudai*, *Protophiomys aegyptensis*, and  
22  
23 *Protophiomys algeriensis*; Jaeger *et al.* 1985, 2010; Flynn *et al.* 1986; Sallam *et al.* 2009, 2012;  
24  
25 Sallam and Seiffert 2016), the anteroconid (and often its anterior and posterior arms as well)  
26  
27 and/or the anterior cingulid, can be connected to the metalophulid I. So, the anterior cristid on  
28  
29 dp4s in caviomorphs (and in *Gaudeamus* too) could be a more complex structure, composed of a  
30  
31 metalophulid I, an anteroconid, its arms, and of an anterior cingulid/anterolophid. We propose  
32  
33 here to name this mesialmost cristid on caviomorph dp4s an anterocristid.  
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40 Rk1: the specimen GSP 21352 illustrated by Verzi *et al.* (2018, figure 1A, p. 2) and originally  
41  
42 described as a dp4 of *Baluchimys ganeshapher* by Flynn *et al.* (1986, figure 17J, p. 30), does not  
43  
44 correspond in fact to this baluchimyine taxon, but more likely to *Downsimys*, a taxon with  
45  
46 potential anomalurid or even cylindrodontid or bathyergid affinities (see Marivaux 2000;  
47  
48 Marivaux *et al.* 2004, 2017b). In contrast, we consider that GSP 21353 described as a p4 of *B.*  
49  
50 *ganeshapher* by Flynn *et al.* (1986, figure 17I, p. 30), would be rather a dp4. The p4 of *B.*  
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3 *ganeshapher* would be not documented (this assumption was already assumed in former works of  
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5 Marivaux et al. (2002, 2004, etc.).

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7 Rk2: the specimen Z5R-163 illustrated by Verzi *et al.* (2018, figure 1B, p. 2) was originally  
8  
9 described by Coster *et al.* (2012, figure 4N, p. 243) as a dp4 of *Metaphiomys* aff. *schaubi*.  
10  
11 However, according to Marivaux *et al.* (2017a), the specimens attributed to this taxon rather  
12  
13 correspond to a morphology corresponding to *Acritophiomys* (*A. boweni*), a genus also considered  
14  
15 as a junior synonym of *Phiomys*. In this context, the material of *Metaphiomys* aff. *schaubi* from  
16  
17 Zallah (Central Libya; Coster *et al.* 2012) should be rather designated as belonging to a species of  
18  
19 *Phiomys*.  
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26 The dp4s from CTA-27 (late Middle Eocene) attributed to *Cachiyacuy contamanensis* and *C.*  
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28 *kummeli* are pentalophodont, except one, MUSM 1880, attributed to *C. contamanensis*, with  
29  
30 almost hexalophodont scheme (Antoine *et al.* 2012, figure 2k, p. 1322). Except for the  
31  
32 mesialmost cristid (see above), the nomenclature proposed by Candela (2002) and Candela and  
33  
34 Rasia (2012) is applicable on all dp4s. However, some clarifications are appropriate:

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37 - the second transverse cristid does not always correspond to a long posterior arm of the  
38  
39 protoconid (= metalophulid II). Indeed, it can be composed of a posterior arm of the  
40  
41 protoconid plus a short cristid developed from the metaconid (MUSM 1880, 1888, 2663,  
42  
43 2665, and 2673; Boivin *et al.* 2017a; Figure 15(A–E)). This short cristid is the equivalent  
44  
45 of the metaconid cristid or metaconid spur of p4s and lower molars;  
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47  
48 - the mesolophid can be aligned and connected to a lingual cristid stemming from the  
49  
50 mesostylid (MUSM 1880; Figure 15(A) and (E–H)). This lingual cristid is the equivalent  
51  
52 of the neomesolophid of p4s and lower molars;  
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3 - mesial and distal ectolophids can be recognized (Figures 14 and 15). The distal ectolophid  
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5 is longitudinal and links the mesolophid to the hypolophid. The mesial ectolophid is  
6  
7 longitudinally oriented in its anterior part and linguodistally oriented in its posterior part.  
8  
9 It links the protoconid to the mesolophid and the distal ectolophid. On some dp4s of *C.*  
10  
11 *contamanensis* (MUSM 1880, 2464, and 2671), the mesial ectolophid appears composed  
12  
13 of different structures: two cristulids on MUSM 2464 and 2671, and one large cuspid with  
14  
15 anterior and posterior arms on MUSM 1880 (Antoine et al., 2012; Boivin *et al.* 2017a).  
16  
17 This cuspid is connected to a cristid situated between the second cristid and the  
18  
19 mesolophid, and which seems to be composed of two cristulids. This cuspid would be a  
20  
21 mesoconid labially displaced, but it is interpreted here as a neocuspid, as well as the  
22  
23 cristid that is connected to it (neolophid; Figures 16, 17). Indeed, these structures are  
24  
25 developed on only one dp4 of *C. contamanensis* (MUSM 1880). **Paleogene** Old World  
26  
27 hystrognaths do not have structures with equivalent morphology and position (e.g.,  
28  
29 ‘*Acritophiomys*’, *Protophiomys*, *Phiomys*, ‘*Waslamys*’, *Metaphiomys*, *Gaudeamus*; Wood  
30  
31 1968; Sallam *et al.* 2009, 2011, 2012; Jaeger *et al.* 2010; Coster *et al.* 2012; Marivaux *et*  
32  
33 *al.* 2014). Conversely, the mesoconid, at the intersection of the two ectolophids and  
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35 mesolophid, tends to disappear in these taxa.  
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45 As for the p4s and lower molars, the metaconid cristid and neomesolophid are present on  
46  
47 dp4s of other fossil taxa from Contamana (e.g., *Cachiyacuy* cf. *contamanensis* 1 of CTA-51;  
48  
49 Boivin *et al.* 2017a) and Tarapoto/Shapaja (e.g., *Caviomorpha* indet. 1. of TAR-21, *Eoincamys* cf.  
50  
51 *pascuali* of TAR-01, and *Mayomys*; Boivin *et al.* 2018), and elsewhere in South America (e.g.,  
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53 *Branisamys*, *Incamys*, *Drytomomys*, *Eosallamys*, and *Galileomys*; Fields 1957; Patterson and  
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3 Wood 1982; Frailey and Campbell 2004; Kramarz 2004; see coding of the characters 317 and 329  
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5 in Boivin 2017 and Boivin *et al.* submitted). Verzi *et al.* (2017, figure 4A, F, G, p. 417 and figure  
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7 5A, p. 418) have described a “lingual extension of the metaconid” on dp4s, in notably  
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9 *Ameghinomys constans*, *Protocaremys avunculus*, *Plesiacarechimys koenigswaldi* and in  
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11 *Acaremys (Sciamys principalis)*. This would be the metaconid cristid in *Ameghinomys* and  
12  
13 *Protocaremys*, whereas it could be rather a neof ormation in the other taxa (in which it seems to be  
14  
15 not directly connected to the metaconid). As for the lower molars, the “crest C” defined by  
16  
17 Carvalho and Salles (2004) on dp4s of some echimyids (see Candela and Rasia (2012) and  
18  
19 ‘Historical review and current state of caviomorph dental structures’) would correspond more  
20  
21 likely to a neomesolophid with a labial extremity connected to the anterocristid. Within  
22  
23 caviomorphs, the mesial ectolophid of the dp4s has variable morphology (Figure 16): it is more  
24  
25 or less long, mesially connected or not to the protoconid, with or without neocusp id, and it can be  
26  
27 aligned with the third cristid (mesolophid and/or neomesolophid; e.g., Caviomorpha indet. 5 and  
28  
29 Cavioid ea or Chinchilloidea indet. of CTA-29, *Eobranisamys*, *Branisamys*; Patterson and Wood  
30  
31 1982; Frailey and Campbell 2004; Boivin *et al.* 2017a) or with the distal ectolophid and  
32  
33 hypolophid (e.g., *E. cf. pascuali* of TAR-01, *Eoviscaccia*, *Drytomomys*; Fields 1957; Kramarz  
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35 2001a).

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

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3 protoconid, mesolophid, neomesolophid, metaconid cristid, and neolophid) is often ambiguous on  
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5 dp4s of erethizontoids. Moreover, some representatives of this superfamily would develop  
6  
7 another type of **neolophid located** not mesially to the metaconid but distally to this cuspid (see  
8  
9 coding of the character 318 in Boivin 2017 and Boivin *et al.* submitted). For instance, the  
10  
11 specimen MACN A 4160, attributed to *Steiromys detentus*, shows a short neocristulid stemming  
12  
13 from the lingual edge in the anteroflexid. This neocristulid, situated between the anterocristid and  
14  
15 the second cristid, is distally located to the metaconid (Figure 17). The oblique ‘second cristid’  
16  
17 would **correspond to** the posterior arm of the protoconid, which is connected to a neomesolophid  
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19 (i.e., a combination of branches forming the second and third cristids of the pentalophodont  
20  
21 scheme, respectively). The MACN 52-176 dp4 of *Hypsosteiromys* **presents** a similar cristulid to  
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23 that observed in MACN A 4160, which is positioned distally to the metaconid.  
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## 31 **Conclusions**

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34 The exhaustive analysis of the material from Contamana and Tarapoto/Shapaja, and its  
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36 comparisons with other hystricognath specimens (fossil and modern New and Old World  
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38 hystricognaths) further our understanding regarding the homology and the evolutionary patterns  
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40 of the dentary structures in caviomorphs. Our analytical results (1) support and/or allow to  
41  
42 generalize some hypotheses formerly proposed about the occlusal morphology of caviomorph  
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44 cheek teeth **and associated evolutionary transformations** (e.g., Vucetich and Verzi 1994; Candela  
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46 1999, 2002; Candela and Rasia 2012), and (2) propose new hypotheses of dental homologies and  
47  
48 evolutionary trends. In caviomorphs, the third crest of the upper teeth is highly variable and  
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50 would correspond either to a mesoloph (stemming from the mesostyle), or a mesolophule  
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52 (originating from the mesial extremity of the anterior arm of the hypocone [i.e., former position  
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3 of the ancestral metaconule]), or a combination of both. In most early and subsequent  
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5 caviomorphs, the transformation from a pentalophodont pattern to a tetralophodont pattern would  
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7 be explained by the reduction/loss of the metaloph or its merging with the posteroloph, and the  
8  
9 transformation from a tetralophodont pattern to a trilophodont pattern, by the reduction/loss of the  
10  
11 the third crest or its merging with the posteroloph. A direct transformation from a pentalophodont  
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13 pattern to a trilophodont pattern is also observed. On the mesial part of lower teeth, the  
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15 development of distinct cristids can be recognized, depending primarily on their connections with  
16  
17 other structures and secondarily on their position and orientation: metalophulid I (for p4s and  
18  
19 lower molars)/anterocristid (for dp4s), posterior arm of the protoconid, metaconid cristid,  
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21 neomesolophid, mesolophid, and different types of neolophids. Given our **observations on**  
22  
23 ancient fossil specimens, the ancestral pattern of lower molars in caviomorphs was likely  
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25 tetralophodont, and that of dp4s pentalophodont. However, schemes with five and four (even  
26  
27 three) transverse cristids can not be ruled out for the two loci, respectively. The trilophodont  
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29 pattern of lower molars was mostly secondarily achieved by the loss of the second cristid, a loss  
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31 which seems to have occurred distinctly, iteratively and at different times in several superfamilies  
32  
33 (notably chinchilloids vs octodontoids) and **genera**. Caviomorphs show a significant disparity of  
34  
35 occlusal patterns on their cheek teeth throughout their evolutionary history, **which** is the result of  
36  
37 a complex evolution, involving many contemporaneous and non-contemporaneous  
38  
39 convergences and parallelisms for each locus. It would be now interesting to **assess the**  
40  
41 correlative effects of the modifications in the number of loph(-id)s and cusp(id)s with other  
42  
43 characters (dental, but also mandibular and cranial), to determine if they could be key innovations  
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45 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/hyposfossette; 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

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3 protoconid; 11, neomesolophid; 12, second transverse cristid; 13, mesolophid; 14, rest of the  
4 mesolophid?; 15, ectolophid; 16, mesial ectolophid; 17, distal ectolophid; 18, hypolophid; 19,  
5 mesolophid?; 15, ectolophid; 16, mesial ectolophid; 17, distal ectolophid; 18, hypolophid; 19,  
6 anterior arm of the entoconid; 20, posterior arm of the entoconid; 21, anterior arm of the  
7 hypoconid; 22, posterior arm of the hypoconid; 23, anterior outgrowth of the hypoconid; 24,  
8 posterolophid; 25, anteroflexid/anterofossettid; 26, anterostrid; 27, mesoflexid; 28, mesial  
9 mesoflexid; 29, distal mesoflexid; 30, mesostrid; 31, confluence of the anteroflexid with the  
10 mesoflexid; 32, hypoflexid; 33, hypostrid; 34, metaflexid; 35, metastrid; 36, confluence of the  
11 hypoflexid with the metaflexid. Abbreviations: ant., anterior; ling., lingual.

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25 **Figure 3. The hypotheses** regarding the homology of structures on upper molars. (A) Wood and  
26 Patterson (1959), Patterson and Wood (1982) (caviomorphs); (B) Hoffstetter and Lavocat (1970),  
27 Lavocat (1976) (caviomorphs); (C) Bryant and McKenna (1995; ‘phiomorphs’ and caviomorphs);  
28 (D) Candela (1999; erethizontoids); (E) Marivaux *et al.* (2004; general nomenclature for rodents);  
29 (F) Marivaux *et al.* (2004), Antoine *et al.* (2012) (caviomorphs). 1 paracone; 2 protocone; 3  
30 metacone; 4 hypocone; 5 mesostyle; 6 metaconule; 7 anteroloph; 8 protoloph; 9 mesolophule; 10  
31 mesoloph; 11 neocrest *sensu* Candela (1999); 12 metaloph; 13 neoloph *sensu* Wood and Patterson  
32 (1959); 14 posteroloph; 15 paraflexus; 16 hypoflexus; 17 mesoflexus; 18 metaflexus; 19  
33 posteroflexus; 20 neofossette *sensu* Wood and Patterson (1959). Abbreviations: ant., anterior;  
34 ling., lingual.

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

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3 (2004; non-tetralophodont echimyids); (B) Candela (2000; erethizontoids); (C) Marivaux *et al.*  
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5 (2004), Antoine *et al.* (2012) (caviomorphs); (D) Carvalho and Salles (2004; tetralophodont  
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7 echimyids); (E) Candela and Rasia (2010), (E1) non-tetralophodont echimyids, (E2)  
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9 tetralophodont echimyids; (F) Verzi *et al.* (2014, 2016, 2017), (F1) some tetralophodont  
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11 octodontoids, (F2) non-tetralophodont octodontoids. 1 protoconid; 2 metaconid; 3 mesoconid; 4  
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13 entoconid; 5 hypoconid; 6 mesostylid; 7 metalophulid I; 8 anterolophid; 9 neolophid; 10  
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15 metalophulid II; 11 metalophid; 12 crest C (neolophid + metalophid); 13 mesolophid; 14  
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17 hypolophid; 15 posterolophid; 16 anteroflexid; 17 neoflexid; 18 mesoflexid; 19 hypoflexid; 20  
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19 metaflexid. Abbreviations: ant., anterior; ling., lingual.  
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27 **Figure 5. The hypotheses** regarding the homology of structures on dp4s. (A) Wood and Patterson  
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29 (1959; caviomorphs), Patterson and Wood (1982; caviomorphs), Carvalho and Salles (2004; non-  
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31 tetralophodont echimyids); (B) Candela (2002), (B1) non-tetralophodont erethizontoids, (B2)  
32  
33 tetralophodont erethizontoids; (C) Marivaux *et al.* (2004; caviomorphs), Antoine *et al.* (2012;  
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35 caviomorphs), Candela and Rasia (2010; non-tetralophodont echimyids); (D) Carvalho and Salles  
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37 (2004; tetralophodont echimyids); (E) Candela and Rasia (2010), (E1) tetralophodont echimyids  
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39 configuration 1, (E2) tetralophodont echimyids configuration 2; (F) Verzi *et al.* (2018;  
40  
41 caviomorphs). 1 protoconid; 2 metaconid; 3 mesoconid; 4 entoconid; 5 hypoconid; 6 mesostylid;  
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43 7 metalophulid I; 8 anterolophid; 9 neolophid *sensu* Candela (2002); 10 metalophulid II; 11  
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45 neolophid *sensu* Wood and Patterson (1959); 12 metalophid; 13 crest C (neolophid +  
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47 metalophid); 14 mesolophid; 15 hypolophid; 16 posterolophid; 17 anterior cingulid (anterior  
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49 cingulid). Abbreviations: ant., anterior; ling., lingual.  
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6 **Figure 6.** Composition of the third transverse crest of upper teeth. (A) mesolophule and  
7 mesoloph connected; (B) mesolophule and mesoloph unconnected; (C) without mesoloph, long  
8 mesolophule; (D) without mesoloph, short mesolophule; (E) without mesolophule, long  
9 mesoloph; (F) without mesolophule, short mesoloph; (G, H) indeterminate (mesolophule and/or  
10 mesoloph). The schematic line drawings focus exclusively on the third transverse crest of upper  
11 teeth (on upper molars here). Abbreviations: ant. anterior; ant, anteroloph; H, hypocone; ling.  
12 lingual; Me, metacone; meta, metaloph; **Mst**, mesostyle; Pa, paracone; post, posteroloph; Pr,  
13 protocone; proto, (labial) protoloph.  
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28 **Figure 7.** Terminology of flexi on upper teeth. In red, third transverse crest (cf. Figure 6).  
29 Abbreviations: ant. anterior; H, hypocone; ling. lingual; Me, metacone; **Mst**, mesostyle; Pa,  
30 paracone; Pr, protocone.  
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38 **Figure 8.** Simplified occlusal schematic line drawings of upper molars illustrating the hypotheses  
39 of transformations from a pentalophodont pattern to a tetralophodont pattern, from a  
40 tetralophodont pattern to a trilophodont pattern, and from a pentalophodont pattern to a  
41 trilophodont pattern. These schematic line drawings focus exclusively on the transformations  
42 occurring in the distolabial area of upper molars the cited taxa are example. \* *sensu* (Vucetich  
43 and Verzi 1994). Abbreviations: ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Me,  
44 metacone; meta, metaloph; **Mst**, mesostyle; Pa, paracone; post, posteroloph; Pr, protocone; proto,  
45 (labial) protoloph.  
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6 **Figure 9.** Photograph and interpretative schematic line drawing of the occlusal structures of the  
7 upper jaw (P4–M3) of MLP 16 VII0211, attributed to *Euryzygomatomys*. Abbreviations: 3rd cr,  
8 third transverse crest; ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; **Mst**, mesostyle;  
9 Pa, paracone; post, posteroloph; Pr, protocone.  
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19 **Figure 10.** The posteroloph spur of upper teeth. The schematic line drawings focus exclusively  
20 on this structure (on upper molars here) and on the distolabial crests with which it can be  
21 **connected**. Abbreviations: ant. anterior; H, hypocone; ling. lingual; Me, metacone; **Mst**,  
22 mesostyle; Pa, paracone; Pr, protocone.  
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31 **Figure 11. Composition of the** second transverse cristid of lower molars. **(A) posterior arm of the**  
32 **protoconid and neomesolophid connected; (B) posterior arm of the protoconid and**  
33 **neomesolophid unconnected; (C) without neomesolophid, long posterior arm of the protoconid;**  
34 **(D) without neomesolophid, short posterior arm of the protoconid; (E) without posterior arm of**  
35 **the protoconid, long neomesolophid; (F) without posterior arm of the protoconid, short**  
36 **neomesolophid; (G, H) indeterminate (posterior arm of the protoconid and/or neomesolophid).**  
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45 The schematic line drawings focus exclusively on **the second transverse cristid**. Abbreviations:  
46 ant. anterior; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid;  
47 med I, metalophulid I ; Myd, mesostylid; Pd, protoconid; postd, posterolophid.  
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3 **Figure 12.** Simplified occlusal schematic line drawings illustrating the hypotheses of  
4 transformations of pentalophodont, tetralophodont and trilophodont patterns on lower molars.  
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6 transformations of pentalophodont, tetralophodont and trilophodont patterns on lower molars.  
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8 The ancestral scheme remains ambiguous (scheme pentalophodont or tetralophodont). The  
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10 schematic line drawings focus exclusively on the transformations observed on the mesial area of  
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12 lower molars the cited taxa are example. Abbreviations: ant. anterior; Ed, entoconid; Hd,  
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14 hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; med I, metalophulid I ; Myd,  
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16 mesostylid; Pd, protoconid; postd, posterolophid.  
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23 **Figure 13.** Photographs/drawings (1) and interpretative schematic line drawings of occlusal  
24 morphologies according to Verzi *et al.* (2016) (2) and this study (3) of transverse cristids on lower  
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26 teeth (dp4–m3s) in several octodontoid taxa. (A) *Hoplomys gymnurus* USP 2001; (B, I,  
27  
28 *Proechimys cuvieri* MN-UFRJ 20313; (C) *Lonchothrix emiliae* MN-UFRJ 4856; (D) *Proechimys*  
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30 *roberti* MVZ 197578; (E) *Mesomys hispidus* MVZ 190653; (F) *Trinomys dimidiatus* MN-UFRJ  
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32 62275; (G) *Trinomys elegans* MN-UFRJ 43842; (H) *Proechimys poliopus* MLP 22.II.00.7; (J)  
33  
34 *Myocastor coypus* MLP 20.XII.89.3; (K) *Acarechimys minutus* MPM-PV 4223. This figure is  
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36 based on the figure 1 of Verzi *et al.* (2016, p. 96) with modifications. Abbreviations: ant. anterior;  
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38 ling. lingual.  
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47 **Figure 14.** Photographs/drawings (1) and interpretative schematic line drawings of occlusal  
48 morphologies according to Verzi *et al.* (2016) (2) and this study (3) of transverse cristids on lower  
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50 teeth (dp4–m3s) in several octodontoid taxa. (A) *Acarechimys minutus* MPM-PV 4193; (B)  
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52 *Acaremys (Sciamys principalis)* MLP 15–349; (C) *Sallamys quispea* (based on Shockey *et al.*  
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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.

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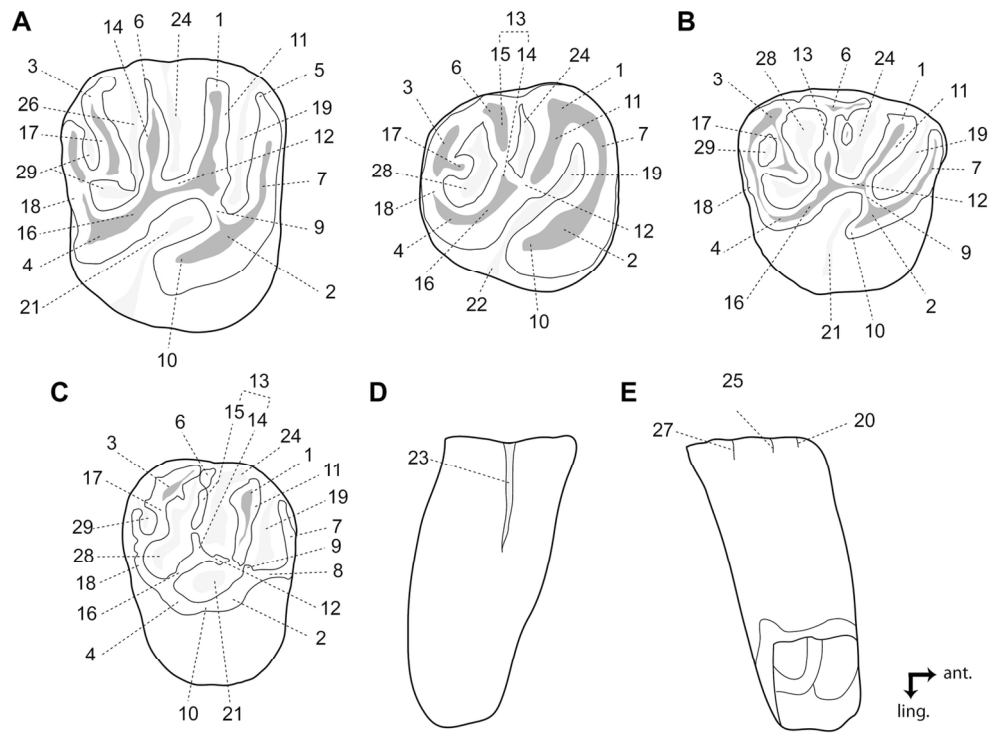


Figure 1. Nomenclature of upper teeth used in this study. (A) occlusal view of upper molar (based of two different specimens); (B) occlusal view of DP4; (C) occlusal view of P4; (D) lingual view of upper tooth; (E) labial view of upper tooth. The nomenclature is based on the dental terminology of different 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.

134x103mm (300 x 300 DPI)

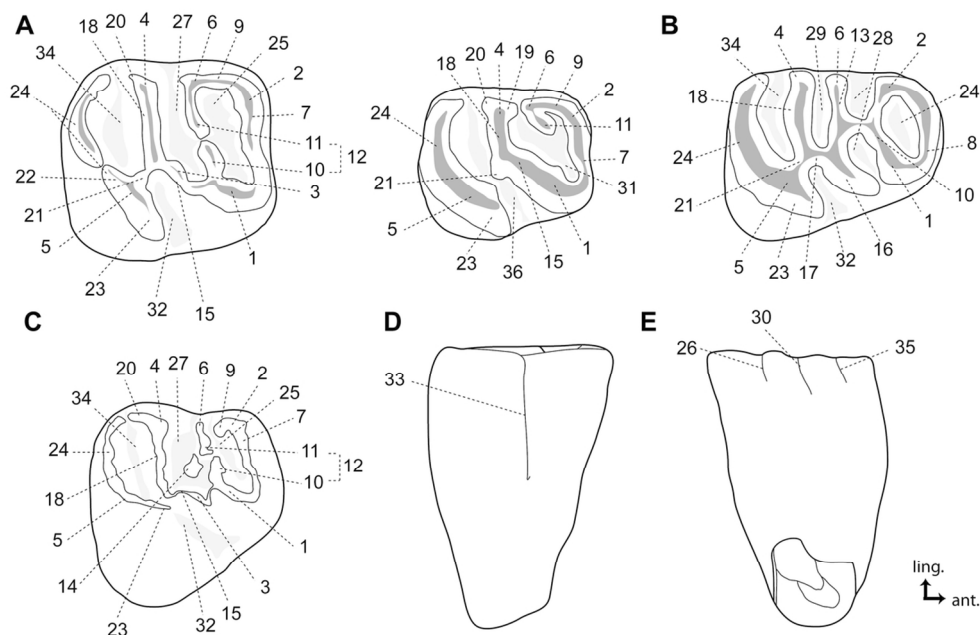


Figure 2. Nomenclature of lower teeth used in this study. (A) occlusal view of lower molar (based of two different specimens); (B) occlusal view of dp4; (C) occlusal view of p4; (D) labial view of lower tooth; (E) lingual view of lower tooth. The nomenclature is based on the dental terminology of different 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, hypopstriid; 34, metaflexid; 35, metastriid; 36, confluence of the hypoflexid with the metaflexid. Abbreviations: ant., anterior; ling., lingual.

113x74mm (300 x 300 DPI)

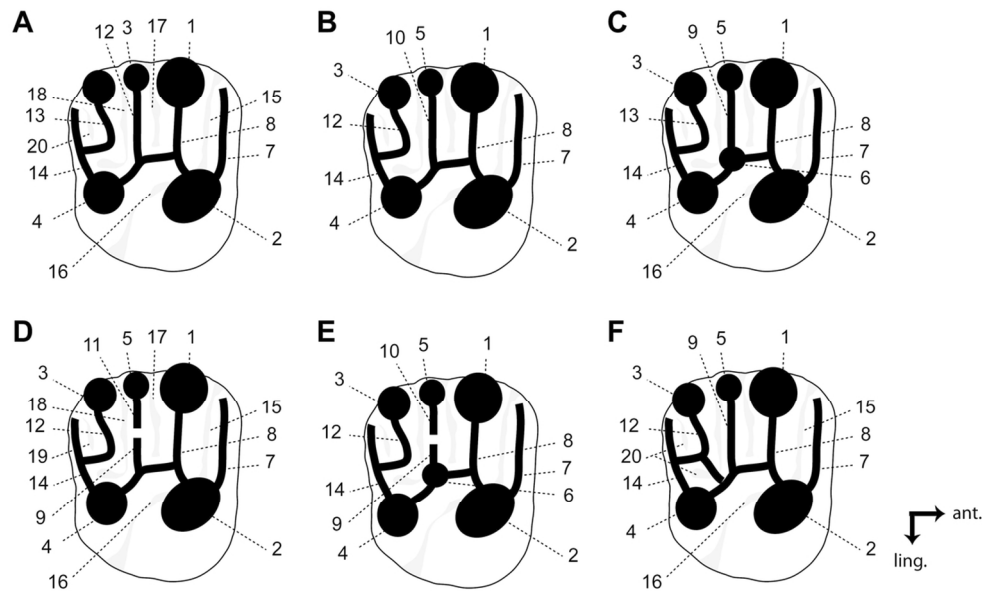


Figure 3. The hypotheses regarding the homology of structures on upper molars. (A) Wood and Patterson (1959), Patterson and Wood (1982) (caviomorphs); (B) Hoffstetter and Lavocat (1970), Lavocat (1976) (caviomorphs); (C) Bryant and McKenna (1995; 'phiomorphs' and caviomorphs); (D) Candela (1999; erethizontoids); (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.

113x69mm (300 x 300 DPI)

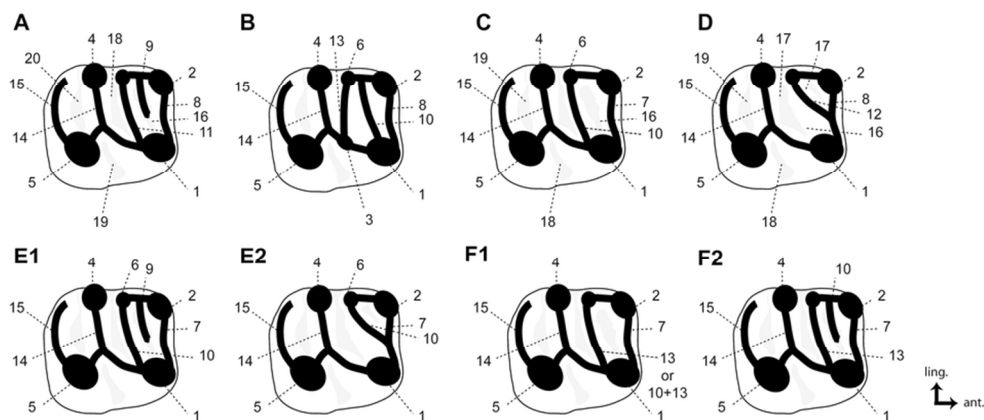


Figure 4. The hypotheses regarding the homology of structures on lower molars. (A) Wood and Patterson (1959; caviomorphs), Patterson and Wood (1982; caviomorphs), Carvalho and Salles (2004; non-tetralophodont echimyids); (B) Candela (2000; erethizontoids); (C) Marivaux et al. (2004), Antoine et al. (2012) (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.

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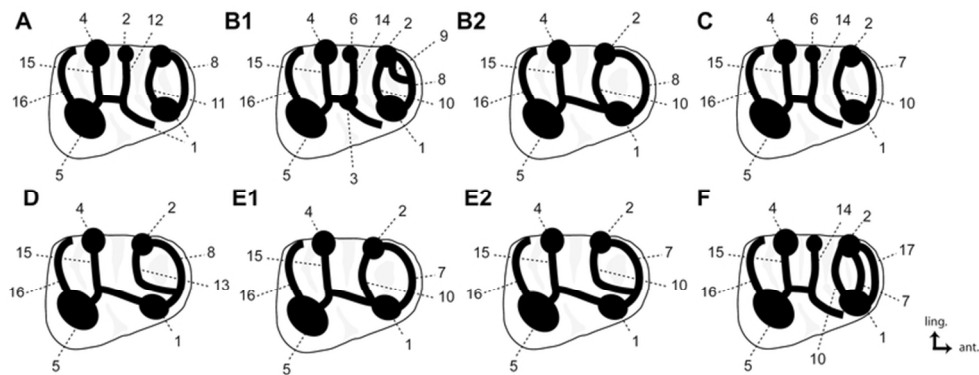


Figure 5. The hypotheses regarding the homology of structures on dp4s. (A) Wood and Patterson (1959; caviomorphs), Patterson and Wood (1982; caviomorphs), Carvalho and Salles (2004; non-tetralophodont echimyids); (B) Candela (2002), (B1) non-tetralophodont erethizontoids, (B2) tetralophodont erethizontoids; (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)

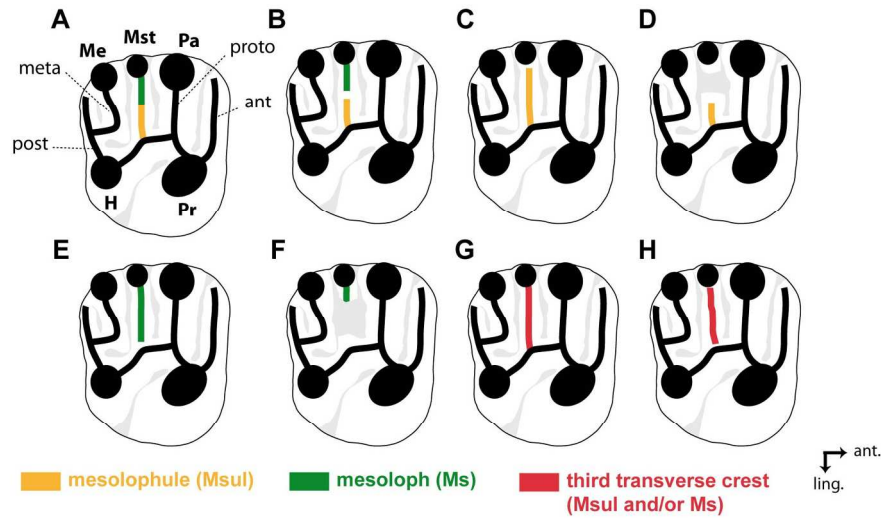


Figure 6. Composition of the third transverse crest of upper teeth. (A) mesolophule and mesoloph connected; (B) mesolophule and mesoloph unconnected; (C) without mesoloph, long mesolophule; (D) without mesoloph, short mesolophule; (E) without mesolophule, long mesoloph; (F) without mesolophule, short 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)

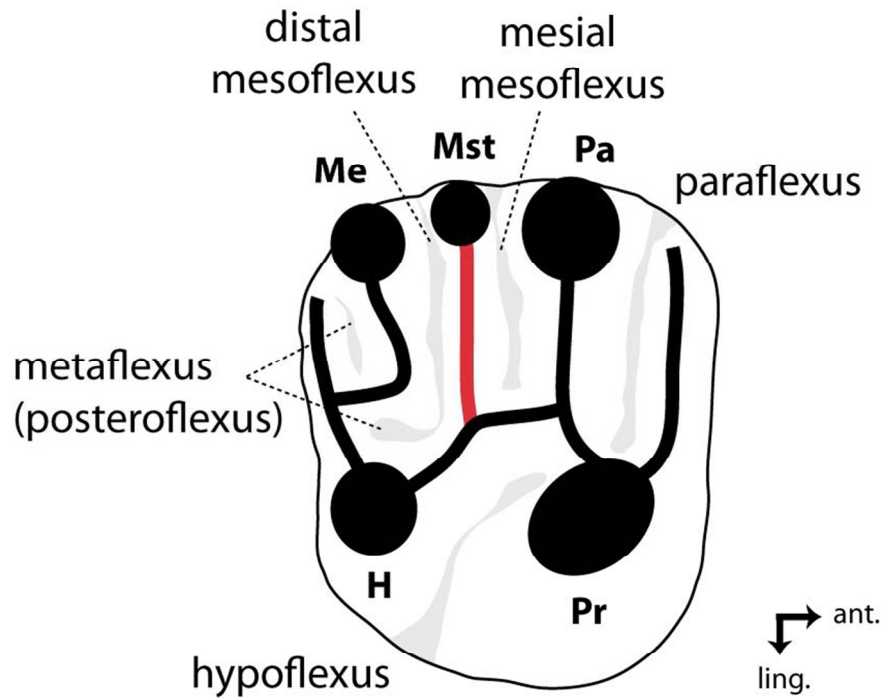


Figure 7. Terminology of flexi on upper teeth. In red, third transverse crest (cf. Figure 6). Abbreviations: ant. anterior; H, hypocone; ling. lingual; Me, metacone; Mst, mesostyle; Pa, paracone; Pr, protocone.

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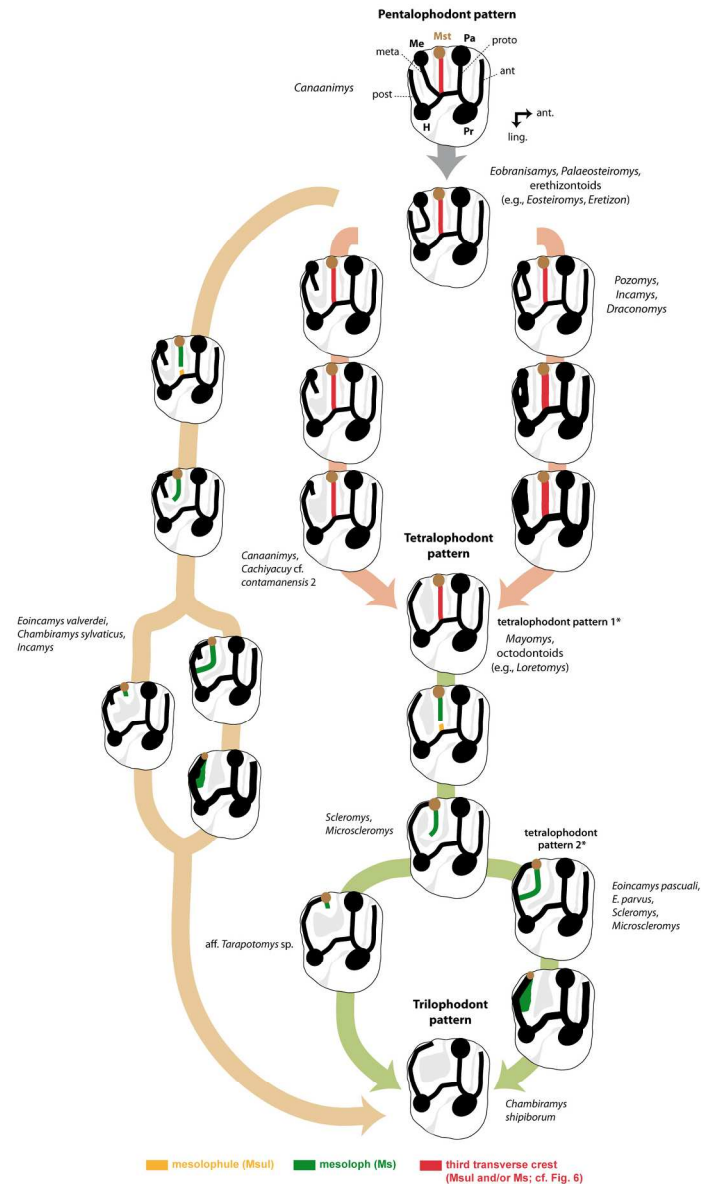


Figure 8. Simplified occlusal schematic line drawings of upper molars illustrating the hypotheses of transformations from a pentalophodont pattern to a tetralophodont pattern, from a tetralophodont pattern to a trilophodont pattern, and from a pentalophodont pattern to a trilophodont pattern. These schematic 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)



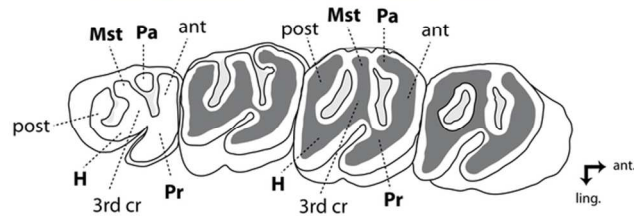
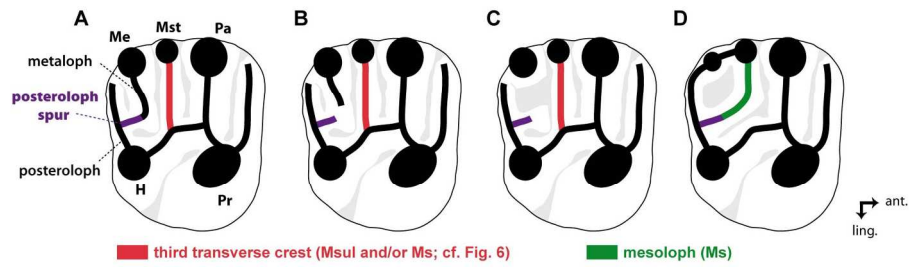


Figure 9. Photograph and interpretative schematic line drawing of the occlusal structures of the upper jaw (P4–M3) of MLP 16 VII0211, attributed to *Euryzygomatomys*. Abbreviations: 3rd cr, third transverse crest; ant. anterior; ant, anteroloph; H, hypocone; ling. lingual; Mst, mesostyle; Pa, paracone;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

86x43mm (300 x 300 DPI)



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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.

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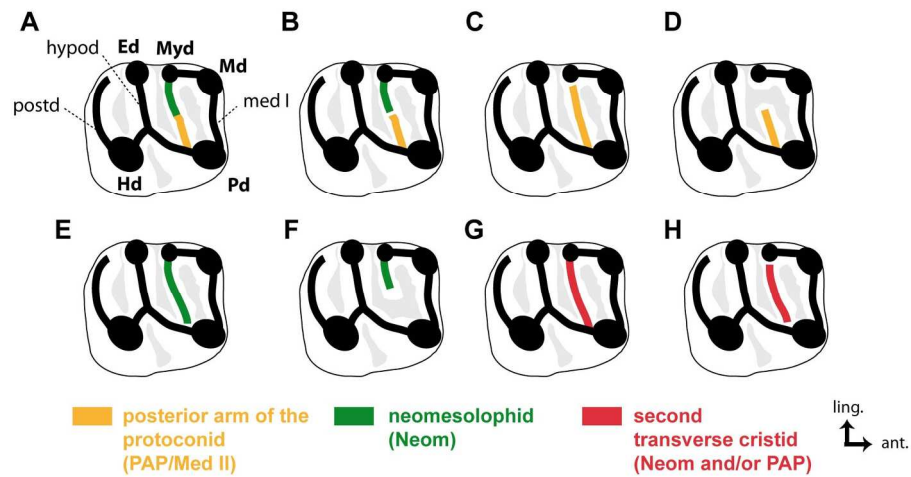


Figure 11. Composition of the second transverse cristid of lower molars. (A) posterior arm of the protoconid and neomesolophid connected; (B) posterior arm of the protoconid and neomesolophid unconnected; (C) without neomesolophid, long posterior arm of the protoconid; (D) without neomesolophid, short 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, metalophid I; Myd, mesostylid; Pd, protoconid; postd, posterolophid.

172x86mm (300 x 300 DPI)

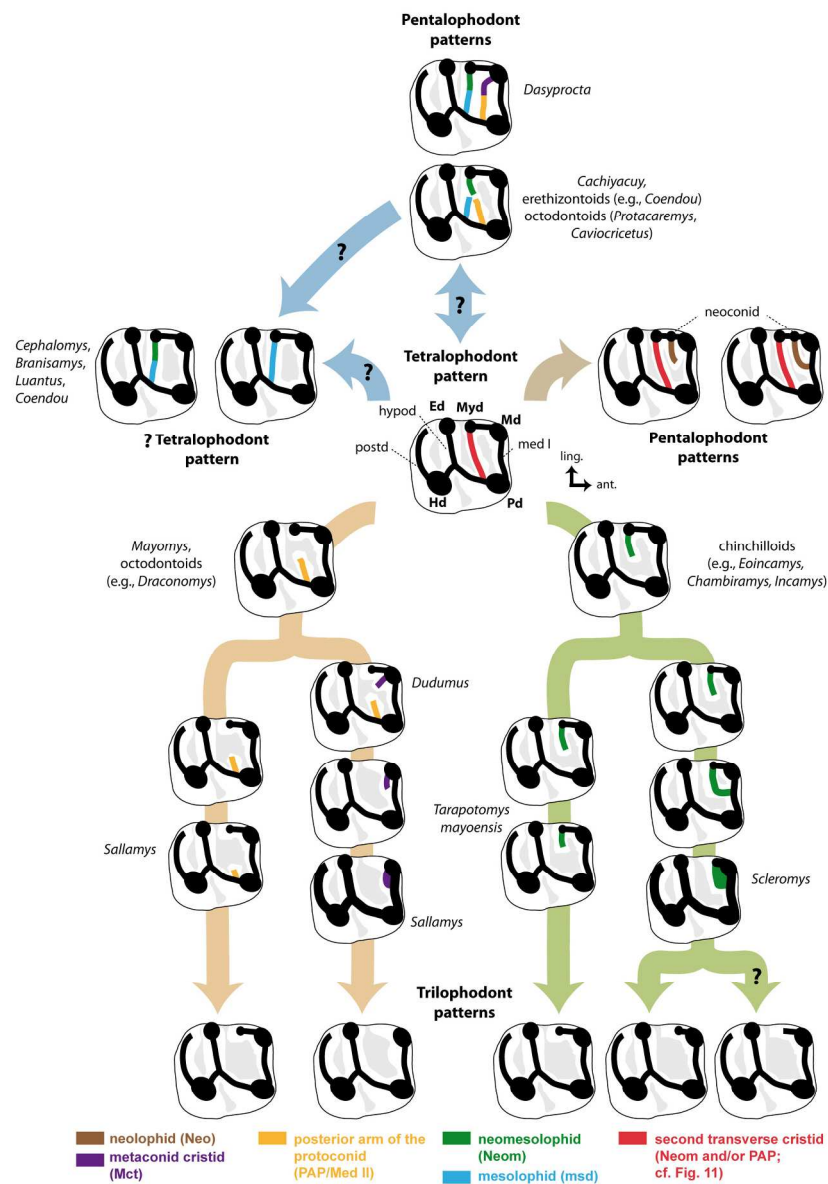


Figure 12. Simplified occlusal schematic line drawings illustrating the hypotheses of transformations of pentalophodont, tetralophodont and trilophodont patterns on lower molars. The ancestral scheme remains ambiguous (scheme pentalophodont or tetralophodont). The schematic line drawings focus exclusively 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)

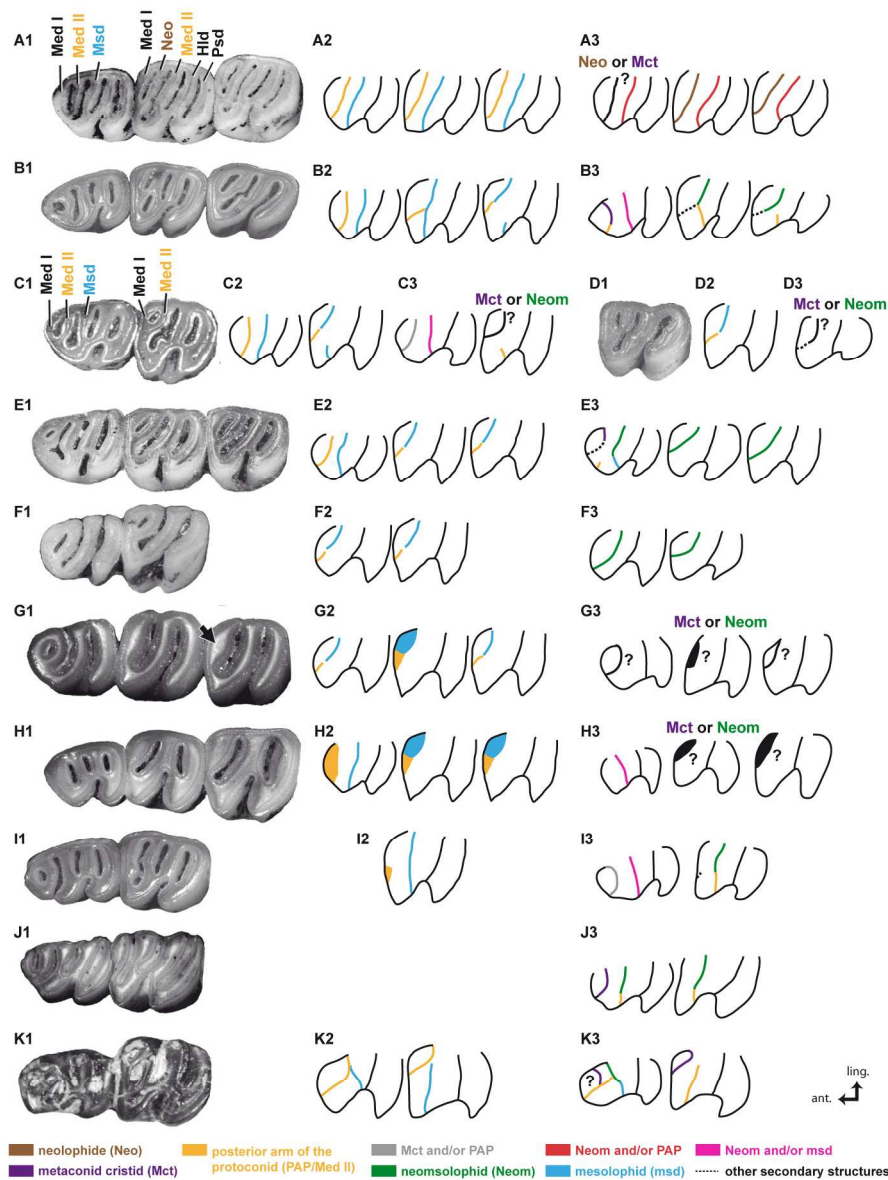


Figure 13. Photographs/drawings (1) and interpretative schematic line drawings of occlusal morphologies according to Verzi et al. (2016) (2) and this study (3) of transverse cristids on lower teeth (dp4–m3s) in several octodontoid taxa. (A) *Hoplomys gymnurus* USP 2001; (B, I, *Proechimys cuvieri* MN-UFRJ 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) *Acarechimyus minutus* MPM-PV 4193; (B) *Acaremys* (*Sciameys 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)



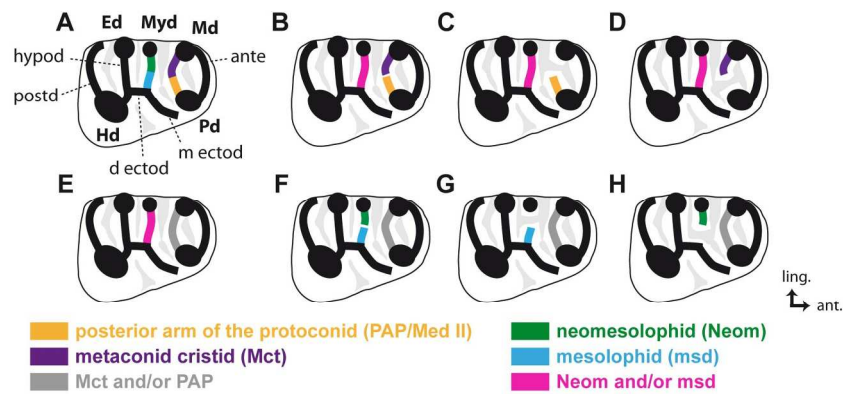


Figure 15. Composition of the second and third transverse cristids of dp4s. (A) posterior arm of the protoconid and metaconid cristid connected, mesolophid and neomesolophid connected; (B) posterior arm of the protoconid and metaconid cristid unconnected; (C) without metaconid cristid; (D) without posterior 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)

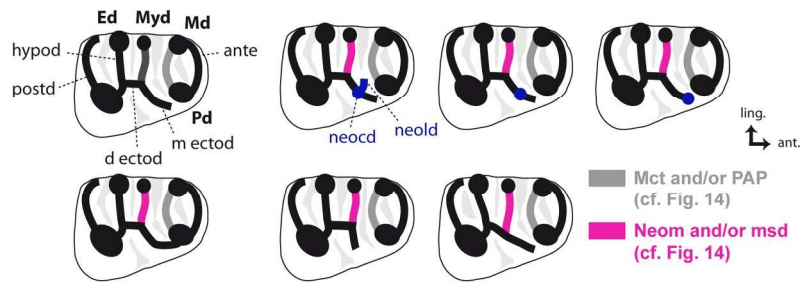


Figure 16. The ectolophids of dp4s. The schematic line drawings focus exclusively on these structures. Abbreviations: ant. anterior; ante, anterocristid; d ectod, distal ectolophid; Ed, entoconid; Hd, hypoconid; hypod, hypolophid; ling. lingual; Md, metaconid; m ectod, mesial ectolophid; Myd, mesostylid;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

172x50mm (300 x 300 DPI)

Peer Review Only



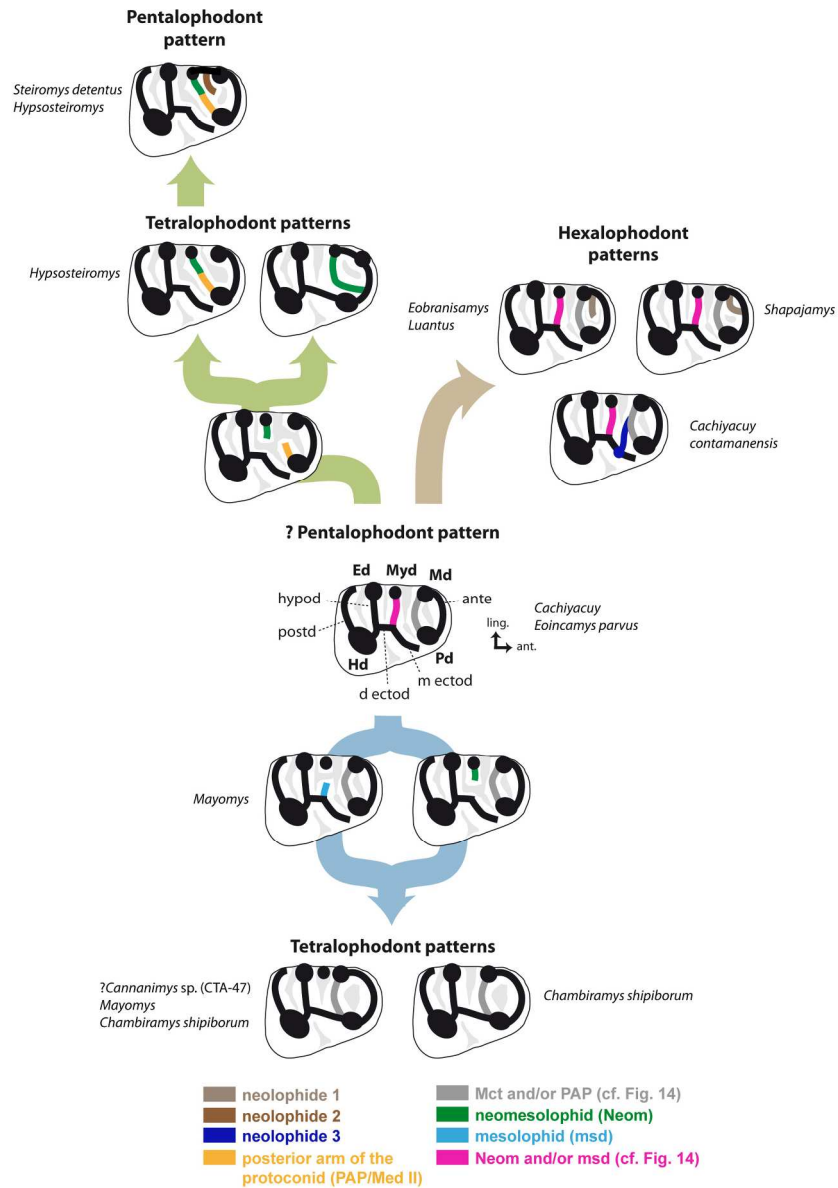


Figure 17. Simplified occlusal schematic line drawings illustrating the hypotheses of transformations of hexalophodont, pentalophodont and tetralophodont patterns of dp4s. The ancestral scheme remains ambiguous (scheme pentalophodont or tetralophodont). These schematic line drawings focused exclusively 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.

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3 **Supplemental Online Material**  
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6 Caviomorph taxa used for comparisons in this study.  
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Genre	Species	Locality and/or Formation (Fm.)	Age	Observed material (original or cast)	Primary references																																																						
<i>Tribosphenomys</i>	<i>T. minutus</i>	Nomogon Fm., China	Late Paleocene		Meng and Wyss 2001; Meng et al. 2007a																																																						
<i>Archetophomys</i>	<i>A. erlianensis</i>	Huibeboerhe-Nuhetingboerhe (AS-1), (Lower Arshanto Fm.), Inner Mongolia	late Early Eocene		Meng et al. 2007b																																																						
<i>Coccyus</i>	<i>C. lingchaensis</i>	Lingcha Fm., Hengdong County, China	Early Eocene	UM (cast)	Li et al. 1989																																																						
<i>Raietophomys</i>	<i>R. delicatissimus</i>	Luman Tongus (Wasatch Fm.), Wyoming, USA	early Early Eocene	UM (cast)	Leidy 1871; Wood 1962																																																						
<i>Tamquammys</i>	<i>T. dispinorium</i>	Shipigou (Hetaoyuan Fm.), China	middle Middle Eocene		Dawson et al. 1984																																																						
	<i>T. wilsoni</i>	Huibeboerhe escarpment (IM-1) (Irdin Manha Fm.), Nei Mongol, China	earliest Eocene - earliest Middle Eocene		Dawson et al. 1984																																																						
	<i>T. tanillius</i>	Obayla Fm., Kazakhstan	late Early - Middle Eocene		Dawson et al. 1984																																																						
<i>Chapatimys</i>	<i>C. wilsoni</i>	H-GSP 144, Kala Chitta Range (Kuldana Fm.), Pakistan; Upper Subathu Group, India	early Middle Eocene		Hussain et al. 1978																																																						
<i>Baluchimys</i>	<i>B. sombani</i>	H-GSP 144, Kala Chitta Range (Kuldana Fm.), Pakistan; Upper Subathu Group, India	early Middle Eocene	UM (cast)	Hussain et al. 1978																																																						
	<i>B. woodi</i>	H-GSP 144, Kala Chitta Range (Kuldana Fm.), Pakistan; Upper Subathu Group, India	early Middle Eocene	UM (cast)	Hussain et al. 1978																																																						
<i>Ottomania</i>	<i>O. proavita</i>	Süngülü, Lesser Caucasus, Turkey	Eocene/Oligocene boundary interval		De Bruijn et al. 2003																																																						
<i>Baluchimys</i>	<i>B. krabiense</i>	Bang Mark Lignite Mine, Krabi, Thailand	latest Eocene		Marivaux et al. 2000																																																						
	<i>B. baryi</i>	Y-GSP 417, Bugli Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986																																																						
	<i>B. ganeshapher</i>	Y-GSP 417, Bugli Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986																																																						
	<i>Lindsaya</i>	Y-GSP 417, Bugli Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986																																																						
<i>Lophibaluchia</i>	<i>L. pilbeami</i>	Y-GSP 417, Bugli Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Flynn et al. 1986																																																						
<i>Hodsahibia</i>	<i>H. azrae</i>	Y-GSP 417, Bugli Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene	UM (original)	Flynn et al. 1986; Marivaux and Welcomme 2003																																																						
	<i>H. gracilis</i>	DBC2, Bugli Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene		Marivaux and Welcomme 2003																																																						
	<i>Buglimys</i>	DBC2, Bugli Hills (Chitarwata Fm.), Balochistan, Pakistan	Early Oligocene	UM (original)	Marivaux et al. 2002																																																						
<i>Taliphomys</i>	<i>T. lavocati</i>	DT-Loc. 2, Bioturbated Unit, Dur Al-Talah, Libya	Late Eocene - Early Oligocene		Jaeger et al. 2010																																																						
	<i>T. libycus</i>	DT-Loc. 1, Bioturbated Unit, Dur Al-Talah, Libya	Late Eocene		Jaeger et al. 2010																																																						
	"W", <i>sittii</i>	BQ-2 (Birket Qarun Fm.), Fayum Depression, Egypt	early Late Eocene	UM (cast)	Sallam et al. 2009																																																						
<i>Protophomys</i>	<i>P. aegyptensis</i>	BQ-2 (Birket Qarun Fm.), Fayum Depression, Egypt	early Late Eocene	UM (cast)	Sallam et al. 2009																																																						
	<i>P. algeriensis</i>	Bir El Ater, Nemetcha, Algeria	early Late Eocene	UM (original)	Jaeger et al. 1985																																																						
<i>Acrotophomys</i>	<i>A. bowri</i>	L-41 (Jebel el Qatrani Fm.), Fayum Depression, Egypt	latest Eocene		Sallam et al. 2012																																																						
<i>Birkamys</i>	<i>B. korai</i>	L-41 (lowermost Jebel Qatrani Fm.), Fayum Depression, Egypt; + Dakhla DAK-C2	latest Eocene - earliest Oligocene																																																								
<i>Phiomys</i>	<i>P. hammutai</i>	DT-Loc. 1, Bioturbated Unit, Dur Al-Talah, Libya	Late Eocene	UM (cast)	Jaeger et al. 2010																																																						
<i>Metaphomys</i>	<i>M. schaubi</i>	Quarries B, G and E (Jebel Qatrani Fm.), Fayum Depression, Egypt; + Z17, Allah Oasis, Libya	Early Oligocene	UM (cast)	Wood 1968; Coster et al. 2015																																																						
<i>Gaudemus</i>	<i>G. aegypticus</i>	Quarries A&B and E (Jebel Qatrani Fm.), Fayum Depression, Egypt	Early Oligocene		Wood 1968																																																						
	<i>G. asilus</i>	L-41 (lowermost Jebel Qatrani Fm.), Fayum Depression, Egypt; + Dakhla DAK-C2	latest Eocene - earliest Oligocene		Sallam et al. 2011																																																						
	<i>G. hylaeus</i>	L-41 (lowermost Jebel Qatrani Fm.), Fayum Depression, Egypt; + Dakhla DAK-C2	latest Eocene - earliest Oligocene		Sallam et al. 2011																																																						
<i>Paraphomys</i>	<i>P. pigotti</i>	Rusinga, Kenya	Early Miocene - late Middle Miocene	UM (original)	Lavocat 1973																																																						
<i>Thyonomys</i>	<i>T. swinderianus</i>		Recent	UM (original)																																																							
<b>CAVIOMORPHA</b>																																																											
<i>Cachiyacuy</i>	<i>C. contamanensis</i>	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Bovin et al. 2017a																																																						
	<i>C. kummeli</i>	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Bovin et al. 2017a																																																						
<i>Canaarimys</i>	<i>C. megujensis</i>	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Bovin et al. 2017a																																																						
	<i>Cansarimys</i> sp.	Contamana CTA-47 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Bovin et al. 2017a																																																						
<i>Fozomys</i>	<i>F. ucayalensis</i>	Contamana CTA-29 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Bovin et al. 2017a																																																						
<i>Eobranisamys</i>	<i>E. javierpradoi</i>	Contamana CTA-27 (Pozo Fm.), Peru	late Middle Eocene	MUSM (original)	Antoine et al. 2012; Bovin et al. 2017a																																																						
	<i>E. romeroppitmanae</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004																																																						
	<i>E. riveri</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004																																																						
<i>Eosallamys</i>	<i>E. paulacoutoi</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004																																																						
	<i>E. simpsoni</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004																																																						
<i>Eoosipina</i>	<i>E. woodi</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004																																																						
<i>Eoosachacul</i>	<i>E. lavocati</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell, 2004																																																						
<i>Tarapotomys</i>	<i>T. mayoensis</i>	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Bovin et al. 2018																																																						
	<i>T. subandinus</i>	TAR-21, TAR-22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Bovin et al. 2018																																																						
<i>cf. Tarapotomys</i>	<i>cf. Tarapotomys</i> sp.	TAR-20, TAR-21, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Bovin et al. 2018																																																						
<i>aff. Tarapotomys</i>	<i>aff. Tarapotomys</i> sp.	TAR-21, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Bovin et al. 2018																																																						
<i>Shapajamys</i>	<i>S. labocensis</i>	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Bovin et al. 2018																																																						
<i>Mayomys</i>	<i>M. confuens</i>	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Bovin et al. 2018																																																						
<i>Caviomorpha</i> indet. 4 gen. et sp. indet.	sp. indet.	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a																																																						
	<i>Litau</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015																																																						
<i>Palaeosteiromys</i>	<i>P. amazonensis</i>	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Bovin et al. 2017b																																																						
<i>Plesiosteiromys</i>	<i>P. newelli</i>	Contamana CTA-61 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Bovin et al. 2017b																																																						
<i>Ucayalimys</i>	<i>U. crassidens</i>	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Bovin et al. 2017b																																																						
<b>Octodontidae</b>																																																											
<i>Leucocephalos</i>	<i>L. zelliae</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015																																																						
<i>Eodelphomys</i>	<i>E. almeidacompsoi</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell 2004																																																						
<i>Selvamys</i>	<i>S. paulus</i>	TAR-22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Bovin et al. 2018																																																						
<i>Dracomys</i>	<i>D. verai</i>	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a																																																						
<i>Vallehermosomys</i>	<i>V. mazzionii</i>	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a																																																						
<i>?Vallehermosomys</i>	<i>?Vallehermosomys merinae</i>	La Cantera (Sarmiento Fm.), Argentina	late Early Oligocene	UM (cast)	Vucetich et al. 2010a																																																						
<i>Migraeramus</i>	<i>M. beatus</i>	Salla (Salla Beds), Bolivia	late Early Oligocene - Late Oligocene		Patterson and Wood 1982																																																						
	<i>M. lavocati</i>	Salla (Salla Beds), Bolivia	late Early Oligocene - Late Oligocene	UM (original)	Pérez et al. 2018																																																						
	<i>M. quispea</i>	Cerro Pan de Azúcar (Moquegua Fm.), Peru	Late Oligocene	MUSM (original)	Shockey et al. 2009																																																						
<i>Sallamys</i>	<i>S. pascuali</i>	Salla (Salla Beds), Bolivia	late Early Oligocene - Late Oligocene	MNHN-Bol, MNHN & UM (original)	Hoffstetter and Lavocat 1970; Lavocat 1976; Patterson and Wood 1982																																																						
	<i>S. woodi</i>	Salla (Salla Beds), Bolivia	late Early Oligocene - Late Oligocene	UM (original)	Pérez et al. 2018																																																						
	<i>S. sp.</i>	Salla (Salla Beds), Bolivia	late Early Oligocene - Late Oligocene	UM (original)	Pérez et al. 2018																																																						
<i>?Sallamys</i>	<i>?Sallamys minutus</i>	Fazenda Santa Fé (Tremembé Fm., Brazil)	late Early Oligocene - Late Oligocene	UM (original)	Vucetich and Ribeiro 2003																																																						
<i>Lapazomys</i>	<i>L. hartenbergeri</i>	Salla (Salla Beds), Bolivia	late Early Oligocene - Late Oligocene	UM (original)	Pérez et al. 2018																																																						
<i>Paulacoutomys</i>	<i>P. paulista</i>	Fazenda Santa Fé (Tremembé Fm.), Brazil	late Early Oligocene - Late Oligocene	MLP (cast)	Pérez et al. 1993a																																																						
<i>Xylechimy</i>	<i>X. obliquus</i>	Laguna de los Machos (Sarmiento Fm.), Argentina	Late Oligocene	MLP (original)	Patterson and Pascual 1968																																																						
<i>Platyptamys</i>	<i>P. brachyodon</i>	Scarrit Pocket (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Wood 1949; Wood and Patterson 1959																																																						
<i>Deseadomys</i>	<i>D. arambourgi</i>	Cabeza Blanca (Sarmiento Fm.) and La Flecha, Argentina	Late Oligocene	MNHN (original)	Wood and Patterson 1959																																																						
<i>Ethelomys</i>	<i>E. loomisii</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Wood and Patterson 1959; Vucetich et al. 2015																																																						
<i>Loretomys</i>	<i>L. minutus</i>	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Bovin et al. 2017b																																																						
<i>Acarechimy</i>	<i>A. leucothea</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015; Arnal et al. 2017																																																						
	<i>A. gracilis</i>	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																																																						
<i>A. minutissimus</i>		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																																																						
<i>A. minutus</i>		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																																																						
<i>A. constans</i>		Santa Cruz Fm., Argentina	late Early Miocene	MLP (original)	Ameghino 1887; Arnal et al. 2017																																																						
<i>Galileomys</i>	<i>G. baioi</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015																																																						
	<i>G. antelucanus</i>	Bryn Gwyn, Gran Barranca (Sarmiento Fm.), Argentina	Early Miocene	MACN & MLP (original)	Vucetich and Kramarz 2003; Vucetich et al. 2010b																																																						
	<i>G. eurygnathus</i>	Pinturas Fm. (for the list of localities, see Kramarz, 2004), Argentina	late Early Miocene	MACN (original)	Kramarz 2004																																																						
<i>?Protacaremys</i>	<i>?Protacaremys adilos</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015																																																						
<i>Protacaremys</i>	<i>P. prior</i>	Gran Barranca (also collected by Ameghino; Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Ameghino 1902; Vucetich et al. 2010b																																																						
	<i>P. avunculus</i>	Gran Barranca (also collected by Ameghino; Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Ameghino 1902; Vucetich et al. 2010b																																																						
	<i>P. deniseae</i>	Localities 1 and 5 of the Catadon del Tordillo (Collón Cura Fm.), Argentina	Early Miocene	MLP (original)	Vucetich et al. 1993b																																																						
	<i>Dudumys</i>	Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Arnal et al. 2014																																																						
	<i>Cavioicetus</i>	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																																																						
<i>Acaremys</i>	<i>A. murinus</i>	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																																																						
<i>Willidewu</i>	<i>W. esteparius</i>	Paso Córdoba (Chinchinales Fm.) and Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene	MLP (original & cast)	Vucetich and Verzi 1991; Vucetich et al. 2010b																																																						
<i>Prospaniomys</i>	<i>P. priscus</i>	Gran Barranca, Bryn Gwyn?, Sacanana (also collected by Ameghino; Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Ameghino 1902; Vucetich et al. 2010b																																																						
	<i>P. cf. priscus</i>	Pampa de Gran Gan (Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Arnal and Kramarz 2011																																																						
	<i>P. sp. 1</i>	Gran Barranca (Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Vucetich et al. 2010b																																																						
<i>'Acaremys'</i>	<i>A. preminutus</i>	Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene	MACN (original)	Bordas 1939; Arnal and Vucetich 2015																																																						
<i>Pseudoacaremys</i>	<i>P. kramarzi</i>	Santa Cruz, River Cliffs, La Cueva, Kilik Ak (Santa Cruz Fm.), Argentina	Early Miocene	MACN (original)	Arnal and Vucetich 2015																																																						
<i>Prostichomys</i>	<i>P. bowri</i>	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																																																						
<i>Adelphomys</i>	<i>A. candidus</i>	Lago Cardiel and Gobernador Gregores (Pinturas Fm.) and Santa Cruz Fm., Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1887; Kramarz 2004																																																						
<i>Paradelphomys</i>	<i>P. fissus</i>	Gran Barranca (Sarmiento Fm.), Argentina	Early Miocene	MLP (original)	Patterson and Pascual 1968; Vucetich et al. 2010b																																																						
<i>Protadelphomys</i>	<i>P. latus</i>	Gran Barranca, 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																																																						
<i>Plesiacarechimy</i>	<i>P. koenigswaldi</i>	Estancia Cerro San Antonio (Collón Cura Fm.), Argentina	Middle Miocene	MLP (original)	Vucetich and Vieytes 2006																																																						
<i>Spaniomys</i>	<i>S. modestus</i>	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																																																						
	<i>S. riparius</i>	Santa Cruz Fm., Argentina; Pampa Castillo (unnamed Fm.), Chile	late Early Miocene	MACN & MLP (original)	Ameghino 1887, 1894; Flynn et al. 2002																																																						
	<i>S. regularis</i>	Santa Cruz Fm., Argentina	late Early Miocene	MACN (original)	Ameghino 1887																																																						
<i>Sciomy</i>	<i>S. principalis</i>	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; Pérez et al. 2002																																																						
	<i>S. petisensis</i>	El Petiso, Argentina	Middle Miocene		Arnal and Pérez 2013																																																						
<i>Ricardomys</i>	<i>R. longidens</i>	La Venta (Villavieja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997																																																						
<i>Quebradachondomys</i>	<i>O. potosiensis</i>	Quebrada Honda (unnamed Fm.), Bolivia	late Middle Miocene		Croft et al. 2011																																																						
<i>Pithanotomys</i>	<i>P. colummaris</i>	Monte Hermoso Fm., Argentina	Early ?Pliocene	MACN (original)																																																							
	<i>Abrocoma</i>		Recent	MNHN (original)																																																							
	<i>S. bernettii</i>		Recent	MNHN (original)																																																							
	<i>S. cyanus</i>		Recent	UM (original)																																																							
	<i>O. dugesi</i>		Recent	MLP & UM (original)																																																							
	<i>Ctenomys</i>		Recent	UM (original)																																																							
<i>Mesocapromys/Mysasteles</i>	<i>Mesocapromys/Mysasteles</i> sp.		Recent	MLP & MNHN (original)																																																							
<i>Euryzygomatops</i>	<i>E. spinosus</i>		Recent	UM (original)																																																							
<i>Makalata</i>	<i>M. didelphoides</i>		Recent	UM (original)																																																							

Genre	Species	Locality and/or Formation (Fm.)	Age	Observed material (original or cast)	Primary references
<i>Echimy</i>	<i>E. chrysurus</i>		Recent	UM (original)	
<i>Trichomys</i>	<i>T. apereoides</i>		Recent	MNHN (original)	
<i>Proechimys</i>	<i>P. cuvieri</i>		Recent	UM (original)	
<i>Myocastor</i>	<i>M. copys</i>		Recent	UM (original)	
<b>Erethizontoidea</b>					
	<i>E. wignoni</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell 2004
<i>Kiichastoromys</i>	<i>K. raimondii</i>	TAR-21, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
<i>Protosteoromys</i>	<i>P. medianus</i>	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene	MACN & MNHN (original)	Ameghino 1903; Wood and Patterson 1959
	<i>P. osmodeophilus</i>	La Flecha (Sarmiento Fm.), Argentina	Late Oligocene	MNHN (original)	Wood and Patterson 1959
	<i>P. pattersoni</i>	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Candela 2000; Pérez et al. 2018
<i>Cholamys</i>	<i>C. tetralophodonta</i>	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	UM (original)	Pérez et al. 2018
<i>Hyposteoromys</i>	<i>H. axiculus</i>	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
	<i>H. nectus</i>	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
<i>Steoromys</i>	<i>S. detentus</i>	Santa Cruz Fm., Argentina	Early Miocene	MACN & MLP (original)	Ameghino 1887; Candela 2000; Candela et al. 2012; Kay et al. 2012
	<i>S. duplicatus</i>	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
<i>Parasteoromys</i>	<i>P. uniformis</i>	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
	<i>P. friantae</i>	Southern Cliff of Lake Colhué Huapi (Gran Barranca; Sarmiento Fm.), Argentina	Early Miocene	MLP (original)	Candela 1999, 2000; Vucetich et al. 2010b
<i>Eosteoromys</i>	<i>E. homogidens</i>	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
<i>?Eosteoromys</i>	<i>?Eosteoromys</i> sp. nov.		Early Miocene		Candela 2002
<i>Branisamys</i>	<i>B. australis</i>	Southern Cliff of Lake Colhué Huapi (Gran Barranca; Sarmiento Fm.), Argentina	Early Miocene	MLP & MNHN (original)	Candela 2000, 2003; Vucetich et al. 2010b
	<i>B. praegraciloides</i>	Pinturas Fm. (for the list of localities, see Kramarz, 2004), Argentina	Early Miocene	MACN (original)	Kramarz 2004
<i>?Neosteoromys</i>	<i>?Neosteoromys</i> <i>tortillense</i>	Cañadón de Tortillo (Colón Cura Fm.), Argentina	Middle Miocene		Vucetich et al. 1993b
<i>Microsteoromys</i>	<i>M. jacobsi</i>	La Venta (Villaveja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997
	<i>cf. Microsteoromys</i> sp.	Madre de Dios MD-67 (unnamed Fm.), Peru	Middle Miocene	MUSM (original)	Antoine et al. 2013
<i>Neosteoromys</i>	<i>N. pattoni</i>	Catamarca Province (Andahuala Fm.), Argentina	late Miocene		Candela 2000, 2004
	<i>N. bombifrons</i>	Andahuala Fm., Argentina	late Miocene	MACN (original)	Candela 2000, 2004
<i>Coendou</i>	<i>C. prehensilis</i>		Recent	MLP & MNHN (original)	Candela 1999
	<i>C. insidiosus</i>		Recent	MLP & MNHN (original)	
<i>Erethizon</i>	<i>E. dorsatum</i>		Recent	MNHN (original)	
<i>Chaetomys</i>	<i>C. subspinatus</i>		Recent	MHNG (pictures)	Martin 1994
<b>Chinchilloidea</b>					
<i>Eoicamys</i>	<i>E. ameghinoi</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell 2004
	<i>E. pascuali</i>	Santa Rosa (Yahuarango Fm.), Peru	?Late Eocene / Early Oligocene	INGEMMET (holotype)	Frailey and Campbell 2004
	<i>E. cf. pascuali</i>	TAR-01, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
	<i>E. valverdei</i>	TAR-13, TAR-20–22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
	<i>E. parvus</i>	TAR-20–22, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
<i>?Eoicamys</i>	<i>?Eoicamys</i> sp.	TAR-13, Shapaja (Pozo Fm.), Peru	Early Oligocene	MUSM (original)	Boivin et al. 2018
<i>Loncolicu</i>	<i>L. treses</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
<i>Scotomys</i>	<i>S. antiquus</i>	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene		Loomis 1914; Wood and Patterson 1959
<i>Incasmys</i>	<i>I. merrinerum</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
	<i>I. bolivianus</i>	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Hoffstetter and Lavocat 1970; Lavocat 1976; Patterson and Wood 1982
<i>Chambiramy</i>	<i>C. shipboron</i>	Contamana CTA-32 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
	<i>C. sylvaticus</i>	Contamana CTA-61 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
<i>Maquiamys</i>	<i>M. praecursor</i>	Contamana CTA-61 (Chambira Fm.), Peru	Late Oligocene	MUSM (original)	Boivin et al. 2017b
<i>Eoivascacia</i>	<i>E. frassinetti</i>	Tinguiririca Termas del Flaco (Abanico Fm.), Chile	Early Oligocene		Wyss et al. 1993; Bertrand et al. 2012
	<i>E. boliviana</i>	Lacayani (unnamed Fm.), Bolivia	Oligocene - Miocene boundary	MNHN (original)	Vucetich 1989
	<i>E. australis</i>	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
<i>Garrimomys</i>	<i>G. cumunuguem</i>	near Barda Negra (Cerro Bandera Formation), Argentina	Early Miocene		Kramarz et al. 2013
<i>Soleromys</i>	<i>S. quadrangulatus</i>	Pinturas Fm. (for the list of localities, see Kramarz, 2006), Argentina	late Early Miocene	MACN & MLP (original)	Kramarz 2006
	<i>S. angustus</i>	Santa Cruz Fm., Argentina	late Early Miocene	MACN (original)	Ameghino 1887
	<i>S. osbornianus</i>	Santa Cruz Fm. and Pinturas Fm., Argentina	late Early Miocene	MACN (original)	Ameghino 1894; Kramarz 2006
<i>Perimys</i>	<i>P. intermedius</i>	Pinturas Fm. (for the list of localities, see Kramarz, 2002), Argentina	late Early Miocene		
<i>Drytomomys</i>	<i>D. aequatorialis</i>	near the hacienda de Señor Carrasco (near Nabon), Equador; La Venta (Villaveja Fm.), Colombia	late Middle Miocene		Anthony 1922; Fields 1957; Walton 1997; Candela and Nasif 2009
	<i>D. typicus</i>	Ituzaingo Fm., Argentina	Late Miocene		Ameghino 1889; Candela and Nasif 2006
<i>Microscleromys</i>	<i>M. paradoxalis</i>	La Venta (Villaveja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997
	<i>M. cribrifolius</i>	La Venta (Villaveja Fm.), Colombia	late Middle Miocene		Walton 1990, 1997
<i>Potamarchus</i>	<i>P. murinus</i>	Solimoes Fm. (for the list of localities, see Kerber et al., 2016), Brazil	Late Miocene		Kerber et al. 2016
<i>Neopseblema</i>	<i>N. ambrosasabianus</i>	Niterói locality (Solimoes Fm.), Brazil	Late Miocene	UFAC (original)	Kerber et al. 2017
	<i>N. horridula</i>	Talismã and Cachoera do Bandeiro localities (Solimoes Fm.), Brazil	Late Miocene	UFAC (original)	Kerber et al. 2017
<i>Chinchilla</i>	<i>C. langenia</i>		Recent	MLP (original)	
<i>Lagidium</i>	<i>L. viscacia</i>		Recent	MLP & MNHN (original)	
<i>Lagostomus</i>	<i>L. maximus</i>		Recent	MLP & MNHN (original)	
<i>Dinomys</i>	<i>D. branickii</i>		Recent	MNHN (original)	
<b>Caviioidea</b>					
<i>Andemys</i>	<i>A. temasi</i>	Tinguiririca Termas del Flaco (Abanico Fm.), Chile	Early Oligocene		Bertrand et al. 2012
<i>Chubutomys</i>	<i>C. simpsoni</i>	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
	<i>C. navaensis</i>	Punta Nava (Sarmiento Fm.), Argentina	Late Oligocene		Pérez et al. 2012
<i>Branisamys</i>	<i>B. lurbayensis</i>	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Hoffstetter and Lavocat 1970; Lavocat 1976; Patterson and Wood 1982
<i>Australoprocta</i>	<i>A. fleagei</i>	Bryn Gwyn, Sacanana (Sarmiento Fm.) and Paso Córdoba (Chichinales Fm.), Argentina	Early Miocene		Kramarz 1998; Vucetich et al. 2010b
<i>Neoreomys</i>	<i>N. pinturenensis</i>	Gran Barranca (Sarmiento Fm.) and Carmen Lower and Potezuelo Sumich Norte (Pinturas Fm.), Argentina	Early Miocene		Kramarz 2006; Kramarz et al. 2010
	<i>N. australis</i>	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
	<i>Luanus</i>	Pinturas Fm. (for the list of localities, see Kramarz, 2006), Argentina	late Early Miocene		Kramarz 2006
<i>Dasyprocta</i>	<i>D. sp.</i>		Recent	MLP & UM (original)	
<i>Cuniculus</i>	<i>C. paca</i>		Recent	UM (original)	
	<i>C. taczanowski</i>		Recent	UM (original)	
	<i>Cavia</i>		Recent	MLP (original)	
<i>Galea</i>	<i>G. spixii</i>		Recent	MNHN (original)	
<i>Dolichotis</i>	<i>D. patagonum</i>		Recent	UM (original)	
<i>Hydrochoerus</i>	<i>H. hydrochaeris</i>		Recent	MLP & MNHN (original)	
<b>Incertae sedis extinct superfamily</b>					
<i>Litodontomys</i>	<i>L. chubutomys</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene		Loomis 1914; Wood and Patterson 1959
<i>Cephalomys</i>	<i>C. arciferus</i>	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene	MNHN (original)	Ameghino 1897; Wood and Patterson 1959
	<i>C. plexus</i>	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	Late Oligocene		Ameghino 1897; Wood and Patterson 1959
	<i>C. caelae</i>	Cabeza Blanca (Sarmiento Fm.), Argentina	Late Oligocene	UM (cast)	Vucetich et al. 2015
<i>Asteromys</i>	<i>A. punctus</i>	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
<i>*Asteromys*</i>	<i>*A. bolivianus</i>	Salla (Salla Beds), Bolivia	late Early Oligocene – Late Oligocene	MNHN-Bol, MNHN & UM (original)	Lavocat 1976; Patterson and Wood 1982; Pérez et al. 2018
<i>Banderomys</i>	<i>B. leanzai</i>	Cerro Bandera Fm. and La Estrella (Sarmiento Fm.), Argentina	Early Miocene		Kramarz 2005; Busker et al. 2017
<i>Soriomys</i>	<i>S. gaimanensis</i>	Bryn Gwyn (Sarmiento Fm.), Argentina	Early Miocene		Kramarz 2001c; Vucetich et al. 2010b
	<i>S. ganganensis</i>	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 Paleontológica, 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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