



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

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ABSTRACT

We offer brief commentaries on Boivin and Marivaux's account of caviomorph molar morphology and evolution. In accordance with Van Valen's statement 'Homology is resemblance caused by a continuity of information', we reaffirm that understanding the dental morphology of rodents should be focused on identifying, i.e. keeping in sight, a given structure undergoing multiple transformation processes in ontogeny and phylogeny. Many of these evolutionary pathways may be tracked with reasonable confidence and can provide keys to recognize widespread patterns.

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Recently, Boivin and Marivaux (2018) proposed a detailed overview of dental homologies of South American hystricognath rodents. Here we point out some misconstructions that Boivin and Marivaux have made of our published works (Verzi et al. 2014, 2016, 2017), and include additional comments regarding these authors' approach to the interpretation of morphology and evolution of molariforms in octodontoid rodents.

Boivin and Marivaux (2018) state: 'Recently, Verzi et al. (2014, 2016, 2017) have considered the second cristid of lower molars in some octodontoids as a mesolophid (*Myocastor*, *Acaremys* in Verzi et al. 2014, figure 5(D), p. 763; *Acaremys* and gen. et sp. nov. in Verzi et al. 2017, figure 5(B) and (F), p. 418) or a combination of a metalophulid II with a mesolophid (e.g. *Proechimys*, *Myocastor*, *Acarechimys* in Verzi et al. 2016, figure 1–3, p. 96–98; and potentially *Acarechimys*, *Plesiarechimys*, and *Protacaremys* in, 2017, figures 4(C), (F) and (G), p. 417; Figure 4(F1)).'

Below we present a series of clarifications regarding this very problematic paragraph.

Firstly, according to this statement, the second cristid of *Myocastor* is interpreted differently in Verzi et al. (2014) and Verzi et al. (2016). This is not the case, as this cristid of *Myocastor* is interpreted as a mesolophid in both articles. It is worth noting that in Verzi et al. (2016), schematic illustrations to identify molariform structures were only provided when they differed from the previous (adjacent) scheme. Thus, in the case of *Myocastor*, the structure is identical to that of the adjacent *Proechimys cuvieri* (which seems obvious to us when comparing Verzi et al. 2016, figures 1i and 1j), and no new schematic illustration was added (as j'). The same criterion was followed for all the figures in Verzi et al. (2016) and Verzi et al. (2017).

Secondly, the authors state that we interpret the second cristid of the lower molars as a mesolophid in *Myocastor*,

†*Acaremys* and †Gen. et sp. nov (Verzi et al. 2014, 2017). However, the condition of *Myocastor* and †*Acaremys* are not equivalent, as in †*Acaremys* there is a vestigial metalophulid II anterior to the mesolophid (Verzi et al. 2017, figure 5(A) and (B)).

Thirdly, the authors assert that we interpret this second cristid as metalophulid II + mesolophid in several genera including *Proechimys*, *Myocastor* and †*Acarechimys*. However, among these examples selected by the authors, a composite cristid, formed mainly by the mesolophid, is only present in the m2 of *Proechimys cuvieri* and *Proechimys roberti* (Verzi et al. 2016, figure 1b and d). The condition for *Myocastor* is clarified above. With respect to †*Acarechimys*, in the specimen †*Acarechimys minutus* MPM-PV 4193 of Verzi et al. (2016, figure 1k) the second cristid is not a combination of metalophulid II and mesolophid, because both structures are distinct. In addition, this specimen does not actually correspond to †*Acarechimys*, as amended by Verzi et al. (2017, p. 414, last paragraph). It seems unclear why the authors should list these examples, given that, among the genera figured by Verzi et al. (2016, figure 1) and used by Boivin and Marivaux (2018) as basis for their figure 13, this combined cristid is better illustrated by *Lonchothrix*, *Mesomys* and *Trinomys dimidiatus* (in addition to *Proechimys*).

Fourthly, contrary to the affirmation by Boivin and Marivaux (2018) that according to Verzi et al. (2017) a similar condition potentially occurs in †*Acarechimys*, †*Plesiarechimys*, and †*Protacaremys*, in these genera the second cristid is the metalophulid II, which might – eventually – include a distal fragment of the mesolophid (Verzi et al. 2017, p. 417, figure 4). Thus, this condition is clearly different from the previously described combined cristid, and the two should not be lumped together.

In addition, the schematic figure 4 of Boivin and Marivaux (2018), which purports to reflect the hypotheses of homology for penta- and tetralophodont molars, fails to reflect the hypotheses

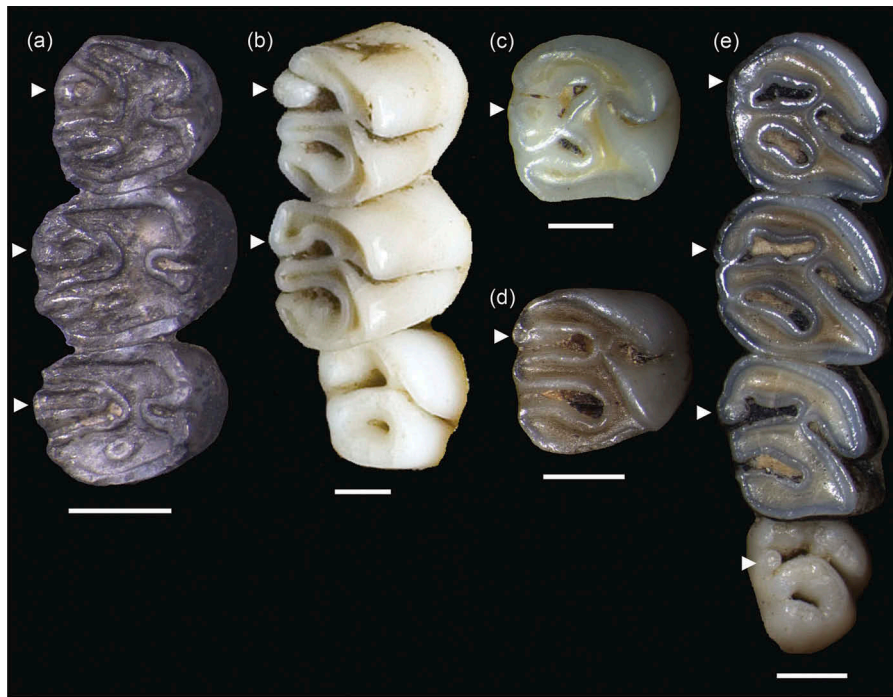


Figure 1. Occlusal morphology of right upper molariforms. (a) DP4-M2 of †*Theridomysops parvulus* GHUNLPam 9473 (late Miocene, Cerro Azul Formation, central Argentina); (b) DP4-M2 of *Clyomys laticeps* L77 (from the database for P.W. Lund collection of extant mammals, Zoological Museum, Natural History Museum of Denmark, University of Copenhagen; http://www.zmuc.dk/verweb/lund/lund_mammals.html); (c) DP4 of *Clyomys laticeps* MN 24144; (d) DP4 of *Carterodon sulcidens* MN-UFRJ 24226; (e) DP4-M3 of *Euryzygomatomys spinosus* MLP 16.VII.02.11. The white arrow indicates the protoloph or its corresponding knob. Scale = 1.0 mm. Abbreviations: GHUNLPam, Cátedra de Geología Histórica, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MN-UFRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

of homology proposed for these patterns by Verzi et al. (2014, 2016, 2017). We have not proposed any hypothesis that corresponds to the one attributed to us in Boivin & Marivaux (2018, figure 4F2), in which there is an interrupted metalophulid II. However, we have proposed a pentalophodont pattern similar to the one in Boivin and Marivaux (2018, figure 4B), which illustrates one of Candela's (2000) hypotheses for erethizontoids. Regarding the scheme in Boivin and Marivaux (2018, figure 4F1), it is an oversimplification that does not reflect our proposals for tetralophodont molars (see discussion above, and Verzi et al. 2016, 2017).

Regarding figure 13 of Boivin and Marivaux (2018), the nomenclature associated to the photographs A1 and C1 taken from figures 1a and 1c of Verzi et al. (2016), actually corresponds to the interpretations of Candela and Rasia (2012) and Candela (2015), as detailed in the legend of the original figure 1 of Verzi et al. (2016).

Having said this, we wish to make a brief commentary regarding octodontoid molars in Boivin & Marivaux's proposal. We do not agree with the underlying conceptual basis of these authors' interpretation. Their perspective requires the recognition of cusps, but the molars of most octodontoids are at an evolutionary stage in which they lack cusps (see Butler 1985; Verzi et al. 2016). An example of this is Boivin & Marivaux's (2018, figure 9) recognition of a cusp in the upper molars of *Euryzygomatomys spinosus* that would be either the paracone (assumed as resulting from the protoloph reduction) or a neoformation. Vucetich (1995) already documented the reduction of the protoloph in euryzygomatomyines; this

reduction results in a variably-sized knob, which is not a paracone but a relict of the crest (Figure 1; Vucetich 1995, figure 1).

For the lower molars, the approach adopted by Boivin and Marivaux (2018, figure 13) promotes the generation of ad-hoc hypotheses to account for similar, or even identical, morphologies between sister genera (*Hoplomys-Proechimys*; figure 13A and B, respectively; *Lonchothrix-Mesomys*, figure 13C and E, respectively), between species of a genus (*Trinomys dimidiatus* and *Trinomys elegans*, figure 13F and G, respectively), or between teeth of an individual (right and left fourth deciduous molars -dp4- of *Proechimys cuvieri* MN-UFRJ 20313, figure 13B and I; dp4 and m1 of *Hoplomys gymnurus* USP 2001, figure 13A). Van Valen (1982) stated that 'Homology is resemblance caused by a continuity of information. In biology it is a unified developmental phenomenon'. Although what we observe is similarity or identity, while homology is not observation but inference (Van Valen 1983), it seems parsimonious to assume that in the abovementioned cases, similarity is indicative of homology rather than the result of different developmental processes, i.e. 'discontinuities'.

In the search for understanding the dental morphology of rodents, efforts should be focused on using conceptual tools (Rieppel 1988) to identify, i.e. keep in sight, a given structure undergoing multiple (though not infinite) transformation processes in ontogeny and phylogeny. Many of these evolutionary pathways may be tracked with reasonable confidence, and they can provide a key to recognize widespread patterns.

The morphological variation in molars within and between species of *Proechimys* illustrated by Patton (1987) is a clear example of these pathways in octodontoids.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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