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

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3 **Response to the comments on ‘Dental homologies and evolutionary transformations in**
4 **Caviomorpha (Hystricognathi, Rodentia): new data from the Paleogene of Peruvian**
5 **Amazonia’**
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41 The current note aims to respond to the comments of Verzi et al. (2018) on our published
42 works (Boivin & Marivaux 2018). Regarding the homologies of the mesial cristids in lower
43 molars in octodontoids (Boivin & Marivaux 2018: p. 8 and figures 13 and 14, p. 17–18),
44 Verzi et al. (2018) highlighted several inaccuracies and misinterpretations by us:
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- 50
51 i. the interpretation of the mesial cristids in terms of homologies in *Myocastor* by
52 Verzi et al. (2014);
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54 ii. the interpretation of the second cristid in position in *Myocastor* by Verzi et al.
55 (2016). Verzi et al. (2016) have interpreted as a mesolophid and not as a
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3 combination of a metalophulid II with a mesolophid. The term “second cristid”
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5 employed in Boivin & Marivaux (2018: p. 8) can be somewhat ambiguous and
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7 refers to the position of the cristid in this section;
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9
- 10 iii. Verzi et al. (2017) stated that the specimen MPM -PV 4193 did not correspond to
11
12 *Acarechimys*. However, this specimen is still assigned to *Acarechimys minutus* in
13
14 the review of the genus made the same year by other authors (Arnal et al., 2017);
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- 17 iv. according to Verzi et al. (2014), a combination “metalophulid II and mesolophid”
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19 is better illustrated by *Lonchotrix* (Boivin & Marivaux 2018, figure 13(C)),
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21 *Mesomys* (Boivin & Marivaux 2018, figure 13(E)) and *Trinomys* (Boivin &
22
23 Marivaux 2018, figure 13(F)) than by taxa that we have selected in Boivin &
24
25 Marivaux (2018). It is true that this combination is well illustrated by taxa cited by
26
27 Verzi et al. (2014). It is noteworthy that the term “combination” might not be
28
29 appropriate because it does not necessarily imply a connection between the
30
31 metalophulid II and the mesolophid in Boivin & Marivaux (2018);
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- 34 v. we agree that the description of the interpretations of Verzi et al. (2014, 2016,
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36 2017) in the section “Historical review and current state of caviomorph dental
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38 structures (homologies and nomenclature); lower teeth” in Boivin & Marivaux
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40 (2018: p. 8 and figure 4(F1)) was somewhat oversimplified;
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- 43 vi. the nomenclature associated with the photographs A1 and C1 of figure 13 in
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45 Boivin & Marivaux (2018) is based on interpretations of Candela & Rasia (2012)
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47 and Candela (2015), and we should have mentioned these references in the legend
48
49 of the figure.
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54 Taking into account these aforementioned points, we propose a correction of the
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56 problematic sentence p. 18 in Boivin & Marivaux (2018): “Recently, Verzi et al. (2014,
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58 2016, 2017) have considered the second cristid of lower molars in some octodontoids as a
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3 mesolophid (*Acaremys* in Verzi et al. 2014, figure 5(D), p. 763; *Myocastor* in Verzi et al.
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5 2016; gen. et sp. nov. in Verzi et al. 2017, figure 5(F), p. 418) or composed of two parts
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7 corresponding to a metalophulid II and a mesolophid. The latter case would include many
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9 configurations (not all similar), characterized by a metalophulid II and a mesolophid
10
11 linked together or not, discontinuous or not, and with a variable position (labially and/or
12
13 lingually placed) (e.g., *Proechimys*, *Lonchotrix*, *Acarechimys*, *Sallamys* in Verzi et al.
14
15 2016, figures 1–2, p. 96–97; and potentially *Acarechimys*, *Plesiacarechimys*, and
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17 *Protacaremys* in Verzi et al. 2017, figures 4(C), (F) and (G), p. 417; Figure 4 (F1)).”

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22 Vucetich (1995) noted the reduction of the second transverse crest on upper molars in
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24 Euryzygomatomyinae and we should have cited this work. Vucetich (1995), followed by
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26 Verzi et al. (2018), interpreted this second crest as a protoloph, the paracone being
27
28 lacking. However, the lack of well-defined cusps in caviomorphs does not necessarily
29
30 mean the loss of cusps. Indeed, cusp(-id)s and loph(-id)s can also be merged together,
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32 thereby generating crestiform structures (see Boivin & Marivaux 2018; Rasia & Candela
33
34 2018). In Euryzygomatomyinae, the reduction of this crest seems to occur lingually: this
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36 crest is long but does not link the mure-posterior arm of the protocone in the extinct
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38 *Theridomysops* (Late Miocene), and it is reduced to a labial small knob in extant species
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40 (*Clyomys*, *Euryzygomatomys*) (Verzi et al. 2018, figure 1). Therefore, the second
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42 transverse crest on upper molars in Euryzygomatomyinae could be the result of the fusion
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44 between the paracone and the protoloph. Accordingly, the small knob in
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46 *Euryzygomatomys* would be a relic of the crestiform structure “paracone + protoloph”

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52 In our approach for recognition of dental homologies, there are ambiguities regarding
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54 the identification of some structures (e.g., in *Hoplomys*, *Lonchotrix*...; Boivin & Marivaux
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56 2018, figures 13 and 14). These ambiguities derive from the fact that teeth are worn and/or
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58 that cusps (-ids) cannot be recognized. It is true that the comparison between different
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3 specimens/loci of the same taxon or close taxa would allow identification of their possible
4 homologous status. However, our observations made over a large taxonomic sample have
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6 proven that the intraspecific variation is far from being negligible in caviomorphs.
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10 Between individuals of a same species, it can be expressed by morphological
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12 modifications of pre-existing structures (in terms of connections, shape...) and the
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14 appearance of several neostructures (i.e., supernumerary cusp(-id)s and loph(-id)s). They
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16 can involve different structures on a same locus or across different loci (e.g., *Cachiyacuy*
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18 *contamanensis*, *Incamys bolivianus*), in occupying analogous (similar) positions and
19
20 configurations, and with a same final functional action during chewing movements. Many
21
22 of these dental structures exist and are functional, but remain constrained by the need of
23
24 preserving an occlusal integrity and the associated functional aspects. For these
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26 ambiguous cases in the structural determination/recognition linked to variation, two
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28 cladistic methods could be used in order to select one homology hypothesis over another:
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30 i. to assess alternative homology correspondences for the ambiguous structure (production
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32 of several matrices), and proceed to a selection of the one that produces the most
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34 consistent results (Candela 2015); ii. not to score ambiguities (“?” in the matrix), and
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36 consider *a posteriori* the most parsimonious state (i.e., optimization = hypothesis on what
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38 could be a non-scored character state, deduced from the phylogenetic inferences
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40 reconstructed by the whole characters assembled in the matrix). We have carried out the
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42 latter approach in our large-scale cladistic analyses (Boivin 2017; Boivin et al. in press),
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44 which was performed on one hundred terminal taxa. The matrix assembled includes both
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46 fossil and modern caviomorphs, but certain taxa could not be considered, such as
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48 *Hoplomys*, *Lonchotrix*, *Mesomys* and *Trinomys*. The inclusion of all extant representatives
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50 of caviomorphs would be prohibitively time consuming and was beyond the scope of the
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52 analyses (Boivin 2017; Boivin et al. in press).
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3 Finally, based on comparisons among caviomorph taxa, but also with taxa outside this
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5 clade, notably with phiomorphs and other taxa of the Ctenohystrica clade (or even with
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7 members of the mouse-related clade or of the squirrel related clade), and using a cladistic
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9 assessment of the dental evidence (i.e., providing a phylogenetic context; Boivin 2017;
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11 Boivin et al. in press), it is clear for us that structural similarities in dental patterns are
12
13 often not necessarily synonym of homologies. Phylogenies highlight the existence of
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15 homoplasies on structures, which were considered *a priori* as primary homologies due to
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17 their topographical and configuration similarities (Boivin 2017; Boivin et al. in press).
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19 These phylogenetic results indicate that some final dental patterns, although similar, can
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21 be convergent and may have resulted from very different evolutionary transformations.
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23 Fossils, notably ancient species, in providing unusual dental patterns often characterized
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25 by intermediary dental morphologies, are particularly useful for deciphering such
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27 morphological evolutionary aspects.
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