Analyzing the impact of conflictive dental characters on the phylogeny of octodontoid rodents

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Systematics of fossil octodontoids (Rodentia, Caviomorpha) is in great part based on insights into the knowledge of teeth, making the step of dental characterization certainly relevant for the evolutionary reconstruction of these rodents. Different homology hypotheses were proposed for the same tooth structures, a fact that indicates the importance of knowing on which criteria the dental characters supporting the classifications were based. In this line, I evaluate the step of characterization of certain conflictive molar characters previously used, and their impact on phylogeny of octodontoids. I explore which the criteria followed to propose the hypotheses of correspondences for these characters are in light of the anatomical evidence. Based on the outcome of phylogenetic trees obtained previously, I analyze if the evolutionary transformations are compatible with character states observed in the terminals. New cladistic analyses based on recoded molar characters indicate that, unlike results recently obtained, the unorthodox position of *Sallamys*, *Protadelphomys*, and *Willidewu* as basal ctenomyines is not recovered. The position of *Caviocricetus*, *Acarechimys–Neophanomys*as as Octodontinae is not maintained. These results indicate that reanalyses of conflictive dental characters, scrutinizing data matrices, are particularly necessary to evaluate the current controversy on the phylogeny of octodontoids. Lower molar character definition and character states delimitation in octodontoids, being relevant to phylogenetic reconstruction, should be founded on anatomical examination, following explicit criteria of homology. Alternative hypotheses of "primary homology" proposed for the same molar traits in octodontoids indicate that each main group of caviomorphs requires its own anatomical study.

Key words: Mammalia, Rodentia, Octodontidae, Echimyidae, homology, parsimony analysis, tooth morphology.

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Introduction

"It seems that we cannot carry on our business without using characters, yet there is nothing more dangerous to the proper understanding of biological processes than that first act of characterization" (Lewontin 2001: 17). Systematic studies of fossil caviomorph rodents (New World Hystricognathi), being in great part based on knowledge of tooth structures (e.g., Carvalho and Salles 2004; Vucetich et al. 2010; Antoine et al. 2012; Candela and Rasia 2012; Arnal et al. 2014; and bibliography herein), demonstrate the importance of the dental characterization in classificatory arrangements. Through the history of knowledge of caviomorphs, as in "pre-Hennigian" as well as in "Hennigian" and "Farrisian" epochs, different homology hypotheses were proposed for the same tooth structures (e.g., Wood and Patterson 1959; Lavocat 1976; Patterson and Wood 1982; Candela 1999, 2002; Candela and Rasia 2012; Verzi et al. 2014), a fact that indicates that it is problematic to transcribe certain dental structures into characters. Therefore, it turns out indispensable to know what criteria were used for the conceptualization of dental characters that support the classifications.

The interpretation of the evolutionary history of the octodontoids (the most diverse clade of caviomorphs; Woods and Kilpatrick 2005), such as that of the other mammal groups, is in great part based on insights into the evolution of teeth, making the evaluation of dental characters undoubtedly relevant for evolutionary reconstruction of these rodents. Bearing this in mind, the Verzi et al.' (2014) contribution will be used here as a basis for revisiting some conflictive dental characters originally included in their character matrix and their testability, ascribing special significance to the step of character individuation (Rieppel and Kearney 2002, 2007; Kearney and Rieppel 2006; Vogt et al. 2010), followed by a reanalysis of these characters. Thus, I stress on characterization of some of the molar characters,

coding of these characters, and their implications in the phylogenetic inferences of octodontoids.

From this approach, and taking into awareness that "the way character is defined conceptually has a profound effect on all aspects of phylogenetic inference" (Grant and Kluge 2004: 29), the focus is put on how the dental character definition impacts on the systematics of octodontoids, making of some conflictive dental characters be opened to new analyses.

In this regard, the overall goal of this paper, is not to produce the phylogeny of octodontoids using all characters available in the literature (such as those used by Verzi et al. 2014 or Arnal et al. 2014), but to provide a critical analysis of certain conflictive dental characters (an essential step in the resolution of consistent phylogenetic results), to evaluate how these characters impact on the obtained phylogenies, and to scrutinize if the evolutionary transformations that resulted from the outcome of phylogenetic trees are compatible with the character states observed in the terminals.

Accordingly, this study aims to show the importance of the first act of dental characterization in parsimony-based morphological analyses of octodontoids.

Abbreviations.—MPT, most parsimonious tree; TBR, tree bisection reconnection.

Material and methods

In line with the main objective of this work (see above), I evaluated here the impact of certain conflictive molar characters and character coding on the phylogeny of octodontoids previously proposed by Verzi et al. (2014). So, I focus only on some of the characters of the Verzi et al.' (2014) analysis which are conflictive and have a long history of alternative hypotheses of correspondences, re-evaluating specifically the dental characters 67, 68, and 69. Therefore, I do not assume all other characters of the Verzi et al. (2014) analysis as correct; I do not discuss them because this is beyond the objectives of this paper. Data were evaluated exactly as in Verzi et al. (2014) with genera as terminals. So, the dataset was analyzed using parsimony in TNT v. 1.1 (Goloboff et al. 2008a, b), based on 10000 random stepwise-addition replicates and tree bisection reconnection (TBR) branch swapping, saving 100 trees per replicate and with all characters equally weighted and all, except the ch. 49 (see Verzi et al. 2014: som 1), considered to be nonadditive. An extra round of TBR on the optimal trees was performed followed by TBR branch swapping algorithm (saving 100 trees per replicate).

In the character matrix of Verzi et al. (2014), inapplicable states and unknown conditions (e.g., character of upper molars of fossil *Xylechimys*) were not distinguished, being all scored as "?" (see Verzi et al. 2014: som 1b). As regards the latter, I discuss below on comparable character states, absences and inapplicables.

Primary homology (sensu de Pinna 1991) is used in quotation marks, because the use of primary and secondary homology and the equivalence homology with synapomorphy are questionable (see Grant and Kluge 2004; Nixon and Carpenter 2011, 2012; Brower and de Pinna 2012, 2014). Topographical correspondences are identified following the classical criteria of homology (see Rieppel 1988; and bibliography cited here).

I focus mainly on the examination of two stages of the systematic analysis of Verzi et al. (2014): the step before the creation of the character matrix, which involves character individuation and character state coding (Rieppel and Keraney 2002, 2007; Kearney and Rieppel 2006; Assis 2009; Vogt et al. 2010), and the step after the generation of character matrix, which examines the results of character optimization (characters 67, 68, and 69 of Verzi et al. 2014) on the most parsimonious trees (MPTs).

In the first stage I examine character individuation and character state coding of mesolophid and metalophulid II (corresponding to characters 67 and 68 of Verzi et al. 2014 respectively), for which alternative hypotheses of correspondences and phylogenetic information are available (Candela and Rasia 2012; Arnal 2012; Arnal et al. 2014; Verzi et al. 2014). So, I explore which the operational criteria used as guidelines to propose the hypotheses of correspondences for these structures before the generation of the character matrix are in the light of the nature of anatomical evidence. Then, I evaluate character state coding of the characters originally identified, in terms of the homologies among their states. In other words, I assess the homologies among states within the same series of transformations (Hennig 1966).

How character states were coded for each taxon in the original character matrix is also reexamined.

Character 69, which expresses occlusal patterns, is also evaluated.

In the following step, I analyze the optimization of the characters 67, 68, and 69 on the MPTs obtained from the character matrix of Verzi et al. (2014).

The common mapping of the characters on the consensus were represented as the union of the optimizations over the equally parsimonious trees ("common mapping" in TNT). Common mapping on the consensus were edited with WINCLADA (Nixon 1999). The examination of the optimization procedure is revealing because it helps to know how character states were identified, and to scrutinize if the evolutionary transformations that resulted from the outcome of phylogenetic trees are compatible with character states observed in the terminals.

On this base, new exploratory cladistic analyses were carried out on recoded characters under investigation.

Previously to these latter analyses, and in order to explore the effect of lower molar characters on the relationships of octodontoids, a first analysis was conducted making inactive characters 61–71, corresponding to lower molar characters in the original character matrix of Verzi et al. (2014: som_1b).

In the second exploratory analysis a single change was made with respect to the original character matrix: in the terminal *Acaremys* group character state 1 of character 69 was replaced by the polymorphic state [01], because representative of this genus presents either transverse or slightly oblique lophids in adult stage (see below), maintaining all the remaining character states among this genus and in the remaining terminals as in the original character matrix (see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Candela_SOM.pdf).

In a third analysis the problems here identified in the character states coding and in the results of optimization of character 67 (see below) led to explore a different coding of this character for several taxa, replacing the states originally coded as "?" by state 1 (i.e., absent) in *Thrichomys*, *Carterodon*, *Theridomysops*, *Clyomys*, *Euryzygomatomys*, *Pampamys*, *Eumysops*, *Maruchito*, *Echimys*, *Phyllomys*, *Kannabateomys*, *Isothrix*, *Dactylomys*, Abromyidae, Ctenomyinae, and the most part of the "traditional" octodontines (SOM 2), because these taxa lack the structure under consideration (see below). The presence of a spur or possible mesolophid (sensu Olivares et al. 2012: fig. 6.5) in some specimens of *Eumysops* led also to consider this genus as polymorphic for this character (SOM 2).

Finally, the problem detected in character state coding of character 68 (see below) led to add a new character state for this character: state 2 (absent), which replaces the "?" in several taxa (see SOM 3). In addition, in this same analysis *Euryzygomatomys*, *Thrichomys*, *Theridomysops*, *Eumysops*, *Clyomys*, and *Carterodon* are recoded as 1. *Acaremys* is scored as "?" (as in original data set) or as polymorphic [12]. In this latter analysis character 68 is considered as additive.

Dental character conceptualization in octodontoids

Correspondences, criteria of homology and conflictive dental characters.—It has often been ascertained that congruence under parsimony does not test correspondence itself, but instead it tests if the topological correspondences relative to a hierarchy are due to common ancestry (see Rieppel 1988: 66). Thus, Rieppel and Kearney (2002: 78) remarked that "…test of congruence provides a necessary, but not a sufficient, basis for cladistics to be an empirical science" (see also Brower 2000; Kearney and Rieppel 2006: 374; Rieppel and Kearney 2007: 108; Nixon and Carpenter 2011: 166, 168).

Consequently, support of correspondences needs to be based on exhaustive anatomical comparisons of the organisms under investigation, and following explicit operational criteria of homology (Rieppel 1988; Kearney and Rieppel 2006). Even within the vision that character state individuation is becoming increasingly more severely tested through cycles of testability (Kluge 1998, 2003), empirical criteria are employed for analysis of characters (Kearney and Rieppel 2006: 375). As it was recently demonstrated, within parsimony-contingent view of cladistic character individuation (Franz 2013), anatomical examinations are relevant for character refinement during the continuous process of cladistic analysis. Intense studies of comparative anatomy are further required within the framework of dynamic homology approach as proposed by Ramirez (2007) for morphological characters, used for specific structures of debatable homology.

In any case, the importance of comparative anatomical studies as basis for character conceptualization in the step before the generation of the matrices (e.g., Kearney and Rieppel 2006; Vogt et al. 2010) is recognized. Classical criteria of homology, such as topological correspondence and connectivity, composition of structures (or structural details), and intermediate form (see Rieppel 1988), were traditionally used as a guide to propose "primary homologies" (sensu de Pinna 1991; for a discussion on the use of primary and secondary homology see Grant and Kluge 2004; Nixon and Carpenter 2011, 2012; Brower and de Pinna 2012, 2014) or topographical correspondences (Rieppel 1988) for structures which are expressed as comparable characters.

Alternative "primary homology" or hypotheses of correspondences for dental structures, particularly for conflictive dental characters, in extinct and extant octodontoids were recently proposed by Carvalho and Salles (2004) and Candela and Rasia (2012). These proposals were partially based on conflicting previous visions (e.g., Lavocat 1976; Patterson and Wood 1982). Candela and Rasia (2012) proposed a set of hypotheses of "primary homology" for lower cheek teeth structures in octodontoids (Fig. 1A, B), based on a comparative anatomical scrutiny, following mainly the topological criterion.

Dental characters of these same octodontoid taxa were recently included in the cladistic analysis of Verzi et al. (2014). However, Verzi et al. (2014) inexplicably avoided references to previous hypotheses of homology proposed for lower molar characters in octodontoid taxa, such as that of Carvalho and Salles (2004), Candela and Rasia (2012), and Arnal (2012), indicating that their dental nomenclature follows Marivaux et al. (2004: fig. 1) and Antoine et al. (2012: fig. S1) (see Verzi et al. 2014: som_1a). Both nomenclatures refer either to typical pentalophodont patterns (Marivaux et al. 2004: fig. 1), not involving tetralophodont ones as those found in several octodontoids, or to occlusal morphologies without mesolophid (Antoine et al. 2012: fig. S1), a lophid that is recognized in some tetralophodont octodontoids by Verzi et al. (2014: fig. 5D; see Fig. 1C). The mesolophid, which occupies the third position in pentalophodont forms (such as it is illustrated in Wood and Wilson 1936; Marivaux et al. 2004), was scored as absent in all caviomorphs analyzed by these latter authors (character 81 of Marivaux et al. 2004). Likewise, in the recent paper of Antoine et al. (2012) the mesolophid (their character 154) was considered absent in all caviomorphs included in their study. Therefore, by applying such nomenclatures it is unfeasible to know why

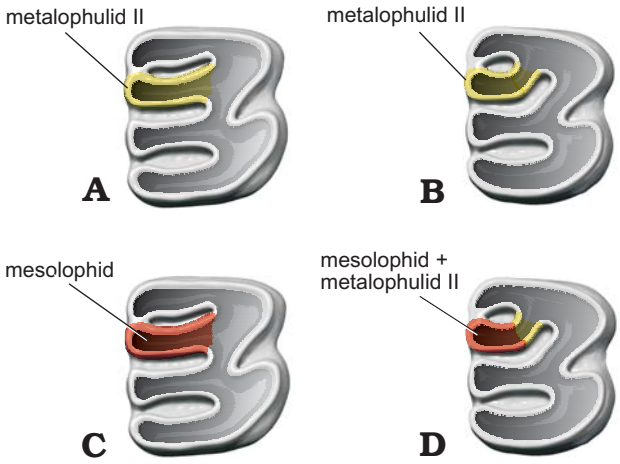

Fig. 1. Hypotheses of correspondences for most anterior lophids of tetralophodont lower molars of octodontoids, after Candela and Rasia (2012: fig. 6E, F) (**A**, **B**) and Verzi et al. (2014) (**C**, **D**). **A**. Second lophid homologued to the metalophulid II. **B**. Second lophid homologued to the metalophulid II, and connected to the metalophulid I. **C**. Second lophid homologued to the mesolophid, identified in certain octodontoid taxa (see text). **D**. Second lophid corresponding to the mesolophid + metalophulid II, forming a complex crest (see text).Yellow and red colors indicate different homologies proposed for the second lophid in Octodontoid lower molars.

certain structures are identified in tetralophodont occlusal patterns in octodontoids by Verzi et al. (2014), and so main dental structures, such as mesolophid (see below), are elusive for the case of molars of octodontoids. In other words, the study of Verzi et al. (2014) did not specify the criteria used for the identification of lophids in lower molars.

In agreement with previous proposals (Marivaux et al. 2004; Antoine et al. 2012), and specifically for the case of octodontoids, Candela and Rasia (2012) did not identify a mesolophid in these rodents. According to Candela and Rasia (2012) and Arnal (2012), for instance, the second lophid in the lower molars of typical tetralophodont *Acaremys* and *Myocastor* is homologous with the metalophulid II (Fig. 1A). These authors indicated "Therefore, topological correspondences allow us to propose that the second lophid in different tetralophodont lower molars is metalophulid II, but with different orientations and degrees of development" (Candela and Rasia 2012: 463). On the contrary, Verzi et al. homologized the second lophid in the molars of *Myocastor* and *Acaremys* with the mesolophid (see Verzi et al. 2014: fig. 5D; see Fig. 1C). It is clear that to face this problematic identification, the step of conceptualization of these characters requires particular attention. It should be necessary to know which were the criteria followed by Verzi et al. (2014) as guidelines to identify mesolophid in certain octodontoids.

Testing alternative hypotheses of correspondences.—In view of that the way character is conceptualized has a significant impact on phylogenetic analyses, it is key to bear in mind that the individuation of certain dental features in octodontoids, such as the mesolophid, neolophid, and metalophulid II, has been object of debate (see Candela and Rasia 2012 for review), and hence requires particular investigation. As mentioned above, alternative schemes of correspondences that differ in anatomical terms were proposed for these structures (e.g., Wood and Patterson 1959; Patterson and Wood 1982; Carvalho and Salles 2004; Candela and Rasia 2012; Arnal 2012; Verzi et al. 2014).

For some of these cases, the application of classical homology criteria may be not completely definitive to select one hypothesis over another. In this framework, Candela and Rasia (2012) tested alternative homology correspondences for certain specific structures of debatable homology according to the evolutionary transformations that they imply, and selected the one that produces the more congruent results. Their "dynamic approach" required a detailed comparative anatomical study of octodontoid taxa under investigation.

Assuming that specific homology criteria were followed by Verzi et al. (2014) to justify their hypotheses of correspondences (as the presence of mesolophid in *Acaremys* and *Myocastor*), alternative hypotheses of correspondences (involving previous hypotheses) may well have been examined under parsimony analysis. So, although congruence does not test correspondence, the test of congruence can lead to a rigorous defensible selection among competing hypotheses and provide objective criterion to choose among them (Rieppel 1996; see Ramirez 2007 and bibliography cited considering examples involving homology as a parsimony problem).

Hypotheses of correspondences for certain dental features as proposed by Verzi et al. (2014) remain to be tested from this perspective.

On the other hand, we can assume that prior published character hypotheses proposed by Carvalho and Salles (2004) and Candela and Rasia (2012) for example, were refuted in an initial round of testing by Verzi et al. (2014), and hence these character hypotheses were never submitted to the test of congruence, but if that was the case it should have been specified.

In summary, it is important not to overlook which are the dental characters of debatable homology in octodontoid taxa under investigation and, on this basis, to test the alternative homology hypotheses of correspondences.

The lower molar character effect on the relationships of octodontoids.—In the context the characters included in the analysis of Verzi et al. (2014), I here explore if the lower dental characters have a significant effect on the relationships of octodontoids, making inactive characters 61–71 corresponding to lower molar characters in the original character matrix (first exploratory cladistic analysis; see materials and methods). The result of the phylogenetic analysis changes strongly, obtaining 3800 MPT of 117 steps, with a great polytomy in the topology of consensus. Therefore, lower dental characters seem to be relevant to the knowledge of the relationships in the context of all characters used by Verzi et al. (2014). If only specific characters, those discussed here (characters 67 and 68, see below), are eliminated from the analysis, this has no effect in the resultant relationships from Verzi et al.

(2014). However, the knowledge of the distribution of these characters obtained on MPTs become significant in the context of the evolutionary history of octodontoids (see Candela and Rasia 2012). Evolution of particular dental characters, as those associated to simplification of molar patterns, for example, was considered potentially related to environmental change during Late Cenozoic interval (Candela and Rasia 2012). Inclusion of these characters in the analysis of Verzi et al. (2014) turns out to be also key for defining groups (characters 67-1 and 68-1 are recovered as synapomorphies of different clades; see Verzi et al. 2014). So, the knowledge of the evolution of the cheekteeth in octodontoids seems to be pivotal for understanding the evolution of octodontoids, and in particular those known only by dental characters.

Character state coding and optimization

Assuming that before generating the character matrix, operational criteria had been followed by Verzi et al. (2014) as guidelines to propose hypotheses of correspondences, particularly for the mesolophid and metalophulid II of m1–2 (see below), I evaluate here character states coding of the characters associated to these structures, and the optimization of the character states on the MPTs obtained from the data matrix. So, dental character states proposed by Verzi et al. (2014) are open to refutation through a reanalysis of these characters.

The "mesolophid": comparable character states, absences and inapplicables.—Character 67 of Verzi et al. (2014) correspond to "Mesolophid of m1–2 (or the corresponding spur) ", for which these authors identified three character states: present at least during early ontogenetic stages (0); absent (1); fused to metalophulid II forming a complex crest (2).

This character was scored as 0 in *Myocastor* and *Acaremys* "group" (including *Sciamys*), which have tetralophodont m1–2 (Fig. 2A, B), in opposition to Candela and Rasia (2012) and Arnal (2012) who, for these same taxa, homologued the second lophid with the metalophulid II (Fig. 1A). Anyway, accepting the hypothesis proposed by Verzi et al. (2014), the important point here is to evaluate the way character states of this character were delimited and how these states were scored for each taxa analyzed. According to Verzi et al. (2014), state 0 of this character corresponds to the presence of mesolophid at least during early ontogenetic stages, but it is not possible to accurate the morphological variation into the state "presence" because the variable for this was not identified (see Sereno 2007 about the need to define the variable of the character statements). In fact, the simple presence of mesolophid can involve different degrees of development or/and topological positions and connections of this lophid with others structures. On the

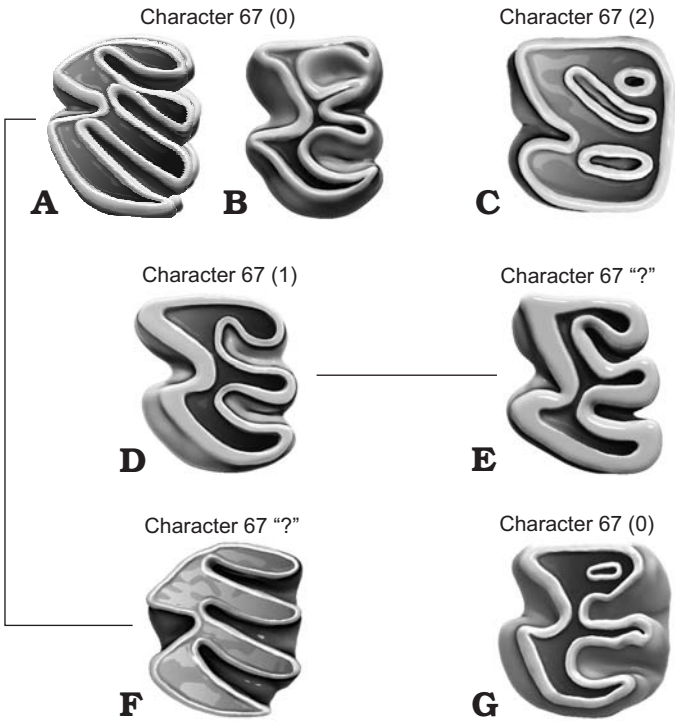

Fig. 2. Character state coding of character 67 of Verzi et al. (2014), "Mesolophid of m1–2 or the corresponding spur" as scored by these authors for several octodontoid taxa. **A**. *Myocastor*, scored as 67-0 (i.e., present, at least during early ontogenetic stages). **B**. *Acaremys* (including *Sciamys*), scored as 67-0 (i.e., present, at least during early ontogenetic stages). **C**. *Proechimys*, scored as 67 [02], showing a specimen corresponding to character state 67-2 (i.e., fused to metalophulid II forming a complex crest). **D**. *Neophanomys*, scored as 67-1 (i.e., absent). **E**. *Thrichomys*, scored as "?". **F**. The tetralophodont *Spaniomys*, scored as "?". **G**. *Sciamys*, showing persistence of transverse lophids in an adult specimen (MLP 15-218). Vertical and horizontal lines indicate essentially the same occlusal patterns that were differently scored.

other hand, character state 67-2 (identified according to Verzi et al. (2014) in *Proechimys*, *Trinomys*, and *Mesomys*; see Fig. 2C), corresponding according to these authors to the fusion the mesolophid with the metalophulid II forming a complex crest, refers to the position or topological condition of the mesolophid and their connections. Therefore, both character-states 67-0 and 67-2 are not clearly delimited one from another and they imply ambiguity in the understanding of homology among states. Indeed, state 0 (defined merely as presence) may include the condition expressed by character-state 67-2, and the latter state inevitably involves character-state 67-0, and thus a problem arises with respect to the demarcation of both character-states, which are not noticeably defined as to be understood without uncertainty. Bearing in mind character-states as transformation stages of the same character ("transformation series" sensu Hennig 1966) that result from heritable transformation events (see also Grant and Kluge 2004), each character-state of the same series of transformation is conjectured to have undergone a transformation event from an existing condition. However, such as was conceptualized, character-states 67-0 and 67-2 of Verzi et al. (2014) do not necessarily indicate that some

transformation event or modification took place from one character-state to another. In this context, the original individuation of these character-states was not totally adequate.

With respect to character state 67-1 of Verzi et al. (2014) (absence of mesolophid), it is implicitly accepted that the absence is an alternated or transformed condition, being part of the same transformational character. Concerning the absent state, one question arises with respect to why the absence of mesolophid was identified by Verzi et al. (2014) in some taxa (scored as 1) but not in others, which were scored as "?", when in all cases, these taxa, showing essentially the same occlusal pattern, the mesolophid seem to be absent (Fig. 2D–E). Thus, for instance, *Chasichimys* and *Neophanomys* (both with m1–2 basically trilophodont, without "mesolophid" at least in *N. biplicatus* for this latter genus) were scored by Verzi et al. (2014) as 1 (i.e., absent; Fig. 2D; but see *N. recens* specimen GHUNLPam 19604 in Verzi et al. 2011: fig. 3i), whereas, for example, *Thrichomys*, *Carterodon*, *Euryzygomatomys*, and *Pampamys*, all having m1–2 also trilophodont, character 67 was scored as "?" (Fig. 2E). *Chasicomys* having lophids in juvenile forms was scored as "?".

In this context, it is difficult to understand why some taxa analyzed by Verzi et al. (2014) with m1–2 that lack the structure under consideration were scored as 1, while other taxa that also lack the same structure under consideration were scored as "?", if there is any reason, it has not been specified (see below and SOM 2 for recoding of this character).

A similar question is detected for the case of tetralophodont forms such as *Acaremys* (including *Sciamys*) and *Myocastor* for which this character was scored as 0 (i.e., mesolophid present), assuming in both cases that the second lophid in position corresponds to this structure (Fig. 2A, B), whereas for the case of the *Spaniomys* (Fig. 2F), also tetralophodont, this character was coded as "?". Why the second lophid is homologued to the mesolophid in *Myocastor* but not in *Spaniomys*?

In addition, it is important to remark that the second lophid or mesolophid (sensu Verzi et al. 2014) in the tetralophodont *Acaremys* (including *Sciamys*) persists until adult stages (Fig. 2B, G). The presence of transverse lophids in adult specimens of *Acaremys* (including *Sciamys*) indicates that this genus should be scored as polymorphic [01] for the character state 69 (see below). Moreover, only a few specimens of *Acaremys* acquire an eight occlusal pattern, unlike specimens of *Sciamys* (being the crown height one of the characters that distinguish both genera; see Arnal 2012).

Finally, it is difficult to understand character state 67-2 (Fig. 2C), i.e., "mesolophid fused to metalophulid II forming a complex crest", without considering the context of variation of this lophid among the taxa analyzed. With respect to this character state Verzi et al. (2014: som1: 6) remarked that "A complete sequence showing the formation of the latter complex crest is presented in Patton (1987: figs. 24–30)". These latter figures illustrate the patterns of different species of *Proechimys*, having penta-, tetra- and trilophodont lower molars. This variation indicates that at least certain specimens referred to this genus have mesolophid (character state 67-0), whereas in other specimens no evidence of mesolophid is identified, which seem to have the state 1 (absent). Character 67 in *Proechimys* was scored as [02], without involving the state 1. In turn, regarding to this character state it is noted that the hypothesis of "primary homology" implied in character state 67-2 is in conflict with that of Candela and Rasia (2012: fig. 6F: pattern II), because according to these authors the second lophid in *Trinomys*, *Mesomys*, and *Lonchotrix* represents the metalophulid II (Fig. 1B), not a complex crest (Fig. 1D).

Optimization of mesolophid (character 67) and occlusal patterns of terminals.—Accepting the character state coding of Verzi et al. (2014) such as it was originally proposed for character 67, and going now to analyze the results of their cladistic analysis, I examine if this can be interpreted as biologically consistent with respect to the occlusal patterns, as represented by their character states, observed in the terminals.

Inapplicable coding of character 67 produced problematic optimizations (Maddison 1993) in the phylogenetic analysis of Verzi et al. (2014), because it assumes the existence of mesolophid (character state 67-0) in the clade comprising traditional octodontines (node Q in the strict consensus obtained by Verzi et al. 2014: fig. 1; see Fig. 3). This clade includes *Octodontomys* + *Pseudoplataeomys innominatus*, *Octomys*, *Abalosia*, *Tympanoctomys*, *Octodon*, *Spalacopus*, *Pithanotomys*, and *Aconaemys*, in which, with the exception of juveniles of *Octodontomys gliroides* (with flexids and fossettids; see Verzi 1994), the lophids are not differentiated (and therefore the mesolophid is not recognized, it is absent). No character state transformation of this original character is detected within this clade, whereas that some transformation event must have occurred to explain the absence of mesolophid in at least the most part of the terminals of traditional octodontines.

Optimization also assumed the presence of a mesolophid in the clade that includes trilophodont forms without mesolophid differentiated (such as *Carterodon*, *Theridomysops*, *Clyomys*, and *Euryzygomatomys*; Fig. 3).

Therefore, common transformation events involving evolution of mesolophid explicate neither observed trilophodont nor figure eight-shaped occlusal morphologies found in several terminals. These occlusal patterns should be as plausible as expressed by the optimization of the character-states of character 67 on the outcome phylogeny.

The absence of the mesolophid in m1–2 (character-state 67-1) resulted in one of the two synapomorphies (Verzi et al. 2014: som_1d) that support the grouping of *Protadelphomys–Willidewu–Sallamys*, *Chasicomys*, *Chasichimys* and traditional ctenomyines (node K in the consensus obtained by Verzi et al. 2014: fig. 1; see Fig. 3). In view of the controversy here identified in the character-state coding of character 67 (see above), phylogenetic results of Verzi et al. (2014) should thus be revised.

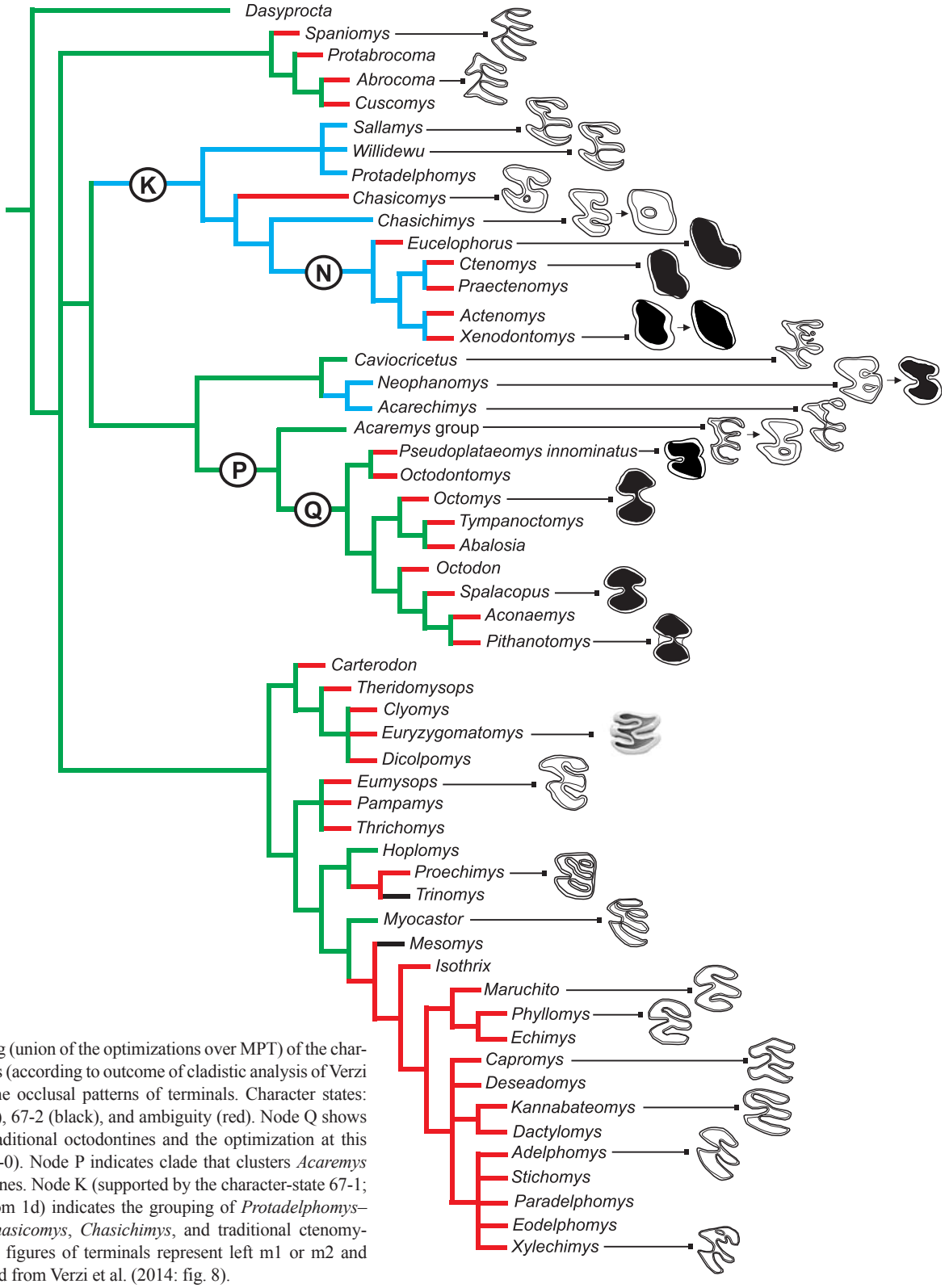

Fig. 3. Common mapping (union of the optimizations over MPT) of the character 67 on the consensus (according to outcome of cladistic analysis of Verzi et al. 2014), showing the occlusal patterns of terminals. Character states: 67-0 (green), 67-1 (blue), 67-2 (black), and ambiguity (red). Node Q shows the clade comprising traditional octodontines and the optimization at this node (character state 67-0). Node P indicates clade that clusters *Acaremys* and traditional octodontines. Node K (supported by the character-state 67-1; see Verzi et al. 2014: som 1d) indicates the grouping of *Protadelphomys–Willidewu–Sallamys*, *Chasicomys*, *Chasichimys*, and traditional ctenomyines (node N). Occlusal figures of terminals represent left m1 or m2 and were essentially modified from Verzi et al. (2014: fig. 8).

Metalophulid II: comparable character states, absences and inapplicables.—Character 68 of Verzi et al. (2014) corresponds to "Metalophulid II in non-laminar m1–2" for which two states were identified: forming a complete crest (0); reduced, proximal portion forming a spur or absent, distal portion fused to metalophulid I so that the lingual end of the latter is usually expanded (1). A first question arises concerning the condition of "non-laminar" m1–2 for the evaluation of metalophulid II, whereas that for the evaluation of mesolophid (character 67) this condition was not considered. Why does the laminar/non-laminar condition become important or not in one or the other case?

As in character 67, I analyzed here the way in which the character states of this character were delimited and how these states were scored for each taxa analyzed.

Hoplomys was scored as 0, i.e., with metalophulid II forming a complete crest, like, sensu these authors, *Proechimys* (scored also only as 0). With reference to this, it is notable that considerable variability in the occlusal pattern of lower molars exists within this genus (see above; which is illustrated by Patton 1987: figs. 24–30; see also Fig. 2C). Thus, *Proechimys* would show a polymorphic condition for this character, not considered for this taxon, which was scored as 0. *Trinomys*, with a pattern essentially similar to some specimens of *Proechimys* (see Carvalho and Salles 2004: figs. 6, 8A), was scored as "?".

With respect to character state 68-1, it is not understandable why some taxa (such as *Sallamys*, *Willidewu*, *Chasicomys*, *Chasichimys*, *Neophanomys*, *Acarechimys*; Fig. 4A) were scored as 1 (i.e., with metalophulid II "reduced, proximal portion forming a spur or absent, distal portion fused to metalophulid I so that the lingual end of the latter is usually expanded"), while others that also have the morphology under consideration were scored as "?" (e.g., *Euryzygomatomys*, *Thrichomys*, *Theridomysops*, *Eumysops*, *Clyomys*, and *Carterodon*; Fig. 4B, C); if there is any reason, it has not been specified. Thus for instance, the extinct *Acarechimys minutissimus* shows the second lophid proximally reduced or absent and the end lingual portion of metalophulid I expanded, a similar morphology to that of *Euryzygomatomys* or *Theridomysops*. At least certain specimens of *Neophanomys* (scored as 1) show the proximal portion of metalophulid II absent, and the end lingual portion of metalophulid I expanded, a similar condition to that of *Thrichomys* (scored as "?") (Fig. 2D, E, see SOM 3). In any case, if no remain of metalophulid II (proximal or distal rest) is identified for the case of *Euryzygomatomys*, *Thrichomys*, or *Eumysops*, these taxa should be scored as absent, a state not considered in Verzi et al. (2014) analysis (see below).

Acaremys, with at least a specimen having metalophulid II reduced, such as was illustrated by Verzi et al. (2014: fig. 5c), was scored as "?" not as 1.

The genus *Mesomys* was scored as having mesolophid fused to metalophulid II forming a complete crest (character 67-2). In turn, this taxon was scored as "?" for the character 68, assuming that it is not possible to identify if this genus have complete or reduced Metalophulid II. Thus, the character coding of character 68 is not expressing the presence of metalophulid II in this genus.

As a final point concerning this character, it is relevant to remark that several taxa were scored by Verzi et al. (2014) as "?". Actually, the metalophulid II is not present in several terminals, consequently it is not represented by any of the two defined character-states (67-0 and 67-1). In these cases, and considering the context of morphologic variation of metalophulid II, it could be accepted that the absence of metalophulid II is an "observable" state of this character (Brower and de Pinna 2014). The supposedly "?" states scored by Verzi et al. (2014) for many octodontoid taxa (e.g., traditional octodontinaes and ctenomyines), seem to be in reality indicating the absence of metalophulid II. If complete and reduced metalophulid II are identified states of metalophulid II among compared taxa, the absence of this structure could be considered corresponding and homologous state within a same series of transformation (Hennig 1966). As noted by Nixon and Carpenter (2013: 2) "Hennig accepted absence of a feature as a homology in the context of comparison with taxa possessing the feature". So ''absence'' (such as it was considered by Verzi et al. 2014 for the case of mesolophid in character 67, see above) could be recognized as a character-state comparable or homologous to or that actually exists in some altered condition of the series of transformations. In other words, absence of metalophulid II in the context of variation of character 68 would be a reasonable hypothesis of homology. Inclusion of absence as a state of this character that is expressing that an event takes place in the context of development of metalophulid II, instead of "?" condition, should be evaluated among octodontoid taxa analyzed (see below and SOM 3).

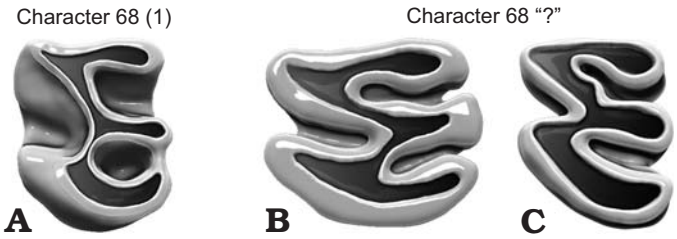

Fig. 4. Character state coding of character 68 of Verzi et al. (2014). "Metalophulid II in non-laminar m1–2", as scored by these authors for several octodontoid taxa. **A**. *Acarechimys minutissimus*, scored as 68-1 (i.e., metalophulid II, "reduced, proximal portion forming a spur or absent, distal portion fused to metalophulid I so that the lingual end of the latter is usually expanded"). **B**. *Euryzygomatomys*, scored as "?". **C**. *Eumysops*, scored as "?", see also *Thrichomys* among others taxa scored as "?".

Note that the addition of state "absence" of metalophulid II in a "multistate" coding, i.e., as a character state alongside transformational character states that record variation in the development of this lophid, does not pose problems regarding character independence (Maddison 1993) or redundancy of the "absent" state, because there is not another character in the original analysis that involve "absence" as a state of metalophulid II, so the state absent appears only one time. In the case of including absence, problems related to coding of inapplicable features would not be generated either (see below for the results of considering absence as a possible character state of this character).

Finally, it would be also valuable to explore the obtained results by using an alternative coding method for the characters 67 and 68 by splitting them into separate characters "absence/presence" from the character states concerning its variation, using inapplicable for those taxa lacking the structure considered. In any case, the use of the absent state for the character 68, as is here examined, is a proposal to be considered.

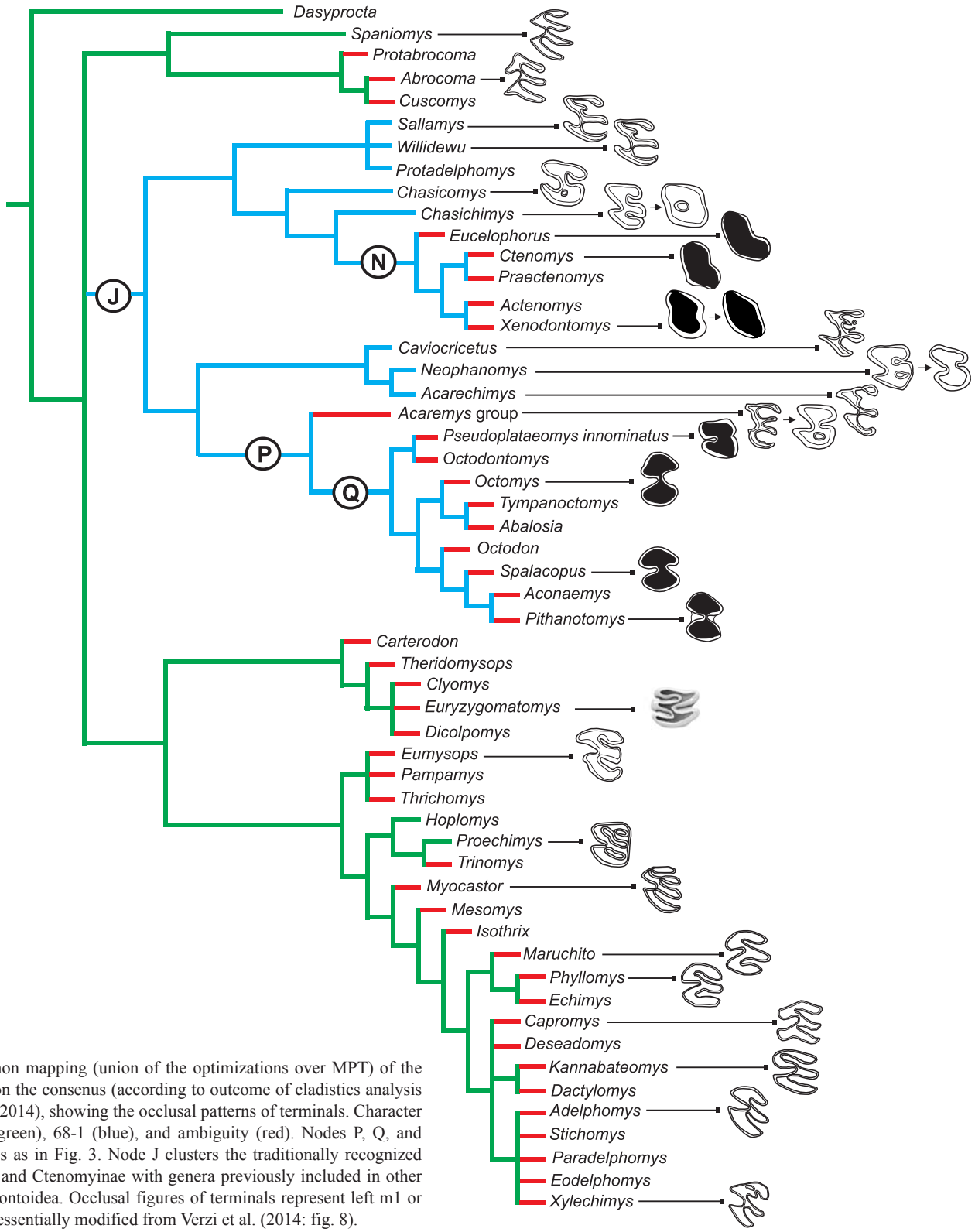

Fig. 5. Common mapping (union of the optimizations over MPT) of the character 68 on the consenus (according to outcome of cladistics analysis of Verzi et al. 2014), showing the occlusal patterns of terminals. Character states: 68-0 (green), 68-1 (blue), and ambiguity (red). Nodes P, Q, and N show clades as in Fig. 3. Node J clusters the traditionally recognized Octodontinae and Ctenomyinae with genera previously included in other taxa of Octodontoidea. Occlusal figures of terminals represent left m1 or m2 and were essentially modified from Verzi et al. (2014: fig. 8).

Optimization of metalophulid II (character 68) and occlusal patterns of terminals.—Inapplicable coding of character 68 produced problematic optimizations (Maddison 1993) in the phylogenetic analysis of Verzi et al. (2014)since it assumed the existence of reduced metalophulid II (character state 68-1) in the clade comprising traditional ctenomines (node N of Verzi et al. 2014, with simplified occlusal morphologies), and in several traditional octodontines (Fig. 5), such as *Abalosia*, *Tympanoctomys*, *Octodon*, *Spalacopus*, *Aconaemys*, *Pithanotomys*, and *Aconaemys*, which have figure eight-shaped occlusal morphologies, lacking of metalophulid II.

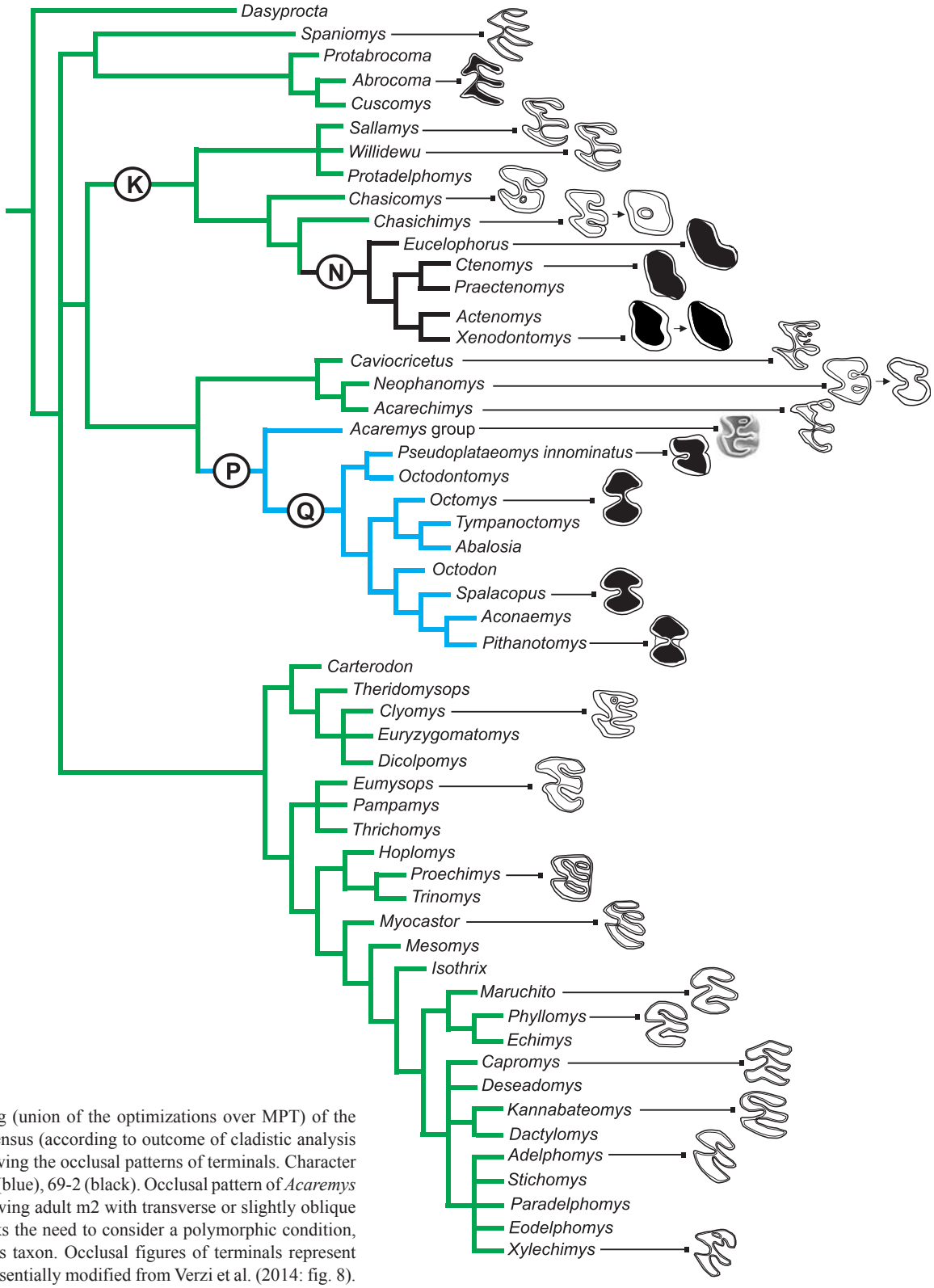

Fig. 6. Common mapping (union of the optimizations over MPT) of the character 69 on the consensus (according to outcome of cladistic analysis of Verzi et al. 2014), showing the occlusal patterns of terminals. Character states: 69-0 (green), 69-1 (blue), 69-2 (black). Occlusal pattern of *Acaremys* (including *Sciamys*), showing adult m2 with transverse or slightly oblique lophids (see text), remarks the need to consider a polymorphic condition, character 69 [01], for this taxon. Occlusal figures of terminals represent left m1 or m2 and were essentially modified from Verzi et al. (2014: fig. 8).

Likewise character 67, any transformation event of the character 68 is detected within this clade, neither at internal nodes nor at terminal taxa, this in spite of that some transformation must have occurred to be compatible with the absence of the metalophulid II in adult patterns of the traditional octodontinaes (Fig. 5).

Optimization of this character also assumed the presence of a complete metalophulid II in the clades represented by trilophodont taxa (Fig. 5). In short, optimization of character states of this character on the outcome phylogeny is not totally compatible with the morphologies found in the terminals.

The presence of a reduced metalophulid II on m1–2 (character state 68-1) was recovered by Verzi et al. (2014: som 1d) as one of four synapomorphies that supported the clade that clusters the traditionally recognized Octodontinae and Ctenomyinae with genera previously included in other taxa of Octodontoidea (node J; Fig. 5), a result that should be revised.

Character 69 and occlusal patterns of terminals.—Character 69 of Verzi et al. (2014) corresponds to occlusal morphology of adult m1–m2, for which these authors identified three character states: with transverse or slightly oblique lophids and flexids/fossettids (0); figure eight-shaped (1); subrhombic to crescent-shaped (2). So, such as these character states were defined, the figure eight-shaped (69-1) is a mutually exclusive condition with respect to the presence of transverse or slightly oblique lophids.

With respect to this character, it should be noted that species of *Acaremys* show a transverse or slightly oblique lophids well differentiated even with high degree of wear (Fig. 2B). *Sciamys* having higher crown than *Acaremys* (Arnal 2012), acquires figure eight-shaped occlusal pattern in a previous phase during ontogeny, although it also retains well differentiated lophids in adult stages (Fig. 2G). So, if *Acaremys* and *Sciamys* are considered as a one terminal taxon (but see Arnal 2012), a polymorphic condition [01] for character 69 should be scored for this taxon. In other words, *Acaremys* should be scored as polymorphic (see below and SOM 1). Note that a particular terminal taxon, as *Acaremys*, may express the coexistence of character states that were once interpreted as mutually exclusive.

In this context, the only synapomorphy of node P (Fig. 6), which supported the clade that clusters *Acaremys* and the traditional Octodontinae, would need be reexamined.

Results from cladistic analyses using recoded characters

Problems detected in the way the character states were identified, and in the results from optimization conduct to new exploratory cladistic analyses based on specific recoded character states (see discussion above and SOM 1–3).

The analysis in which only in *Acaremys* character state 1 of character 69 was replaced by the polymorphic state [01] (see justification above), maintaining all remaining character states in this genus and in remaining terminals as in original character matrix (see data matrix in SOM 1), resulted in 27 MPTs of 139 steps. The strict consensus of these trees shows different topology from those obtained by Verzi et al. (2014; see Fig. 7A, B). Unlike the phylogeny of Verzi et al. (2014), the grouping of *Protadelphomys*, *Willidewu*, *Sallamys*, *Chasicomys*, and *Chasichimys* with traditional ctenomyines (node K of Verzi et al. 2014; see Fig. 3) is not completely recovered. Thus, the unorthodox position of *Sallamys*, *Protadelphomys*, and *Willidewu* as basal ctenomyines is not totally supported. The *Acaremys* group is not recovered as the sister group of the traditional octodontines (Fig. 7B). The position of *Caviocricetus*, *Acarechimys*–*Neophanomys* as Octodontinae is no completely maintained (Fig. 7B). These extinct genera are here recovered as octodontoids incertae sedis (see Arnal et al. 2014 for an alternative proposal on phylogenetic relationships of extinct octodontoids).

Results from rescoring of character 69 for *Acaremys* (see above), and character 67, replacing the "?" by character state 67-1 (absent) for *Thrichomys*, *Carterodon*, *Theridomysops*, *Clyomys*, *Euryzygomatomys*, *Pampamys*, *Eumysops*, *Maruchito*, *Echimys*, *Phyllomys*, *Kannabateomys*, *Isothrix*, *Dactylomys*, abrocomyids, ctenomyines, and the most part of the traditional octodontines (SOM 2), resulted in 45 MPTs, each of 142 steps. The strict consensus of these trees (Fig. 7C) also shows different topology from those obtained by Verzi et al. (2014), containing several extinct taxa (e.g., *Sallamys*, *Acaremys*, *Caviocricetus*, *Acarechimys*) with uncertain relationships (the same results were obtained when *Eumysops* was scored as polymorphic for character 67).

Finally, results obtained from adding to the previous modified matrix, the new character state "absent" (character state 2) for character 68, which replaces the originally scored as "?" for several taxa (such as ctenomyines, octodontines, abrocomyids), and recoding the originally scored "?" as 1 in *Euryzygomatomys*, *Thrichomys*, *Theridomysops*, *Carterodon*, *Clyomys*, and *Eumysops* (SOM 3), resulted in the recovery of 42 MPTs, each of 146 steps. The strict consensus, different from Verzi et al. (2014), is showed in Fig. 7D.

So, these exploratory cladistic analyses produced more ad hoc hypotheses of homoplasy, and then more character state transformations that require explanation. However, based on recoded characters, from the new analyses, I intended to yield more accurate homology assessments and not particularly "successful" results in terms of resolved phylogenies. In addition, the new analyses are based on reviewing characters and states, so that it reflects morphological variation observed in virtually all terminals for each character. In any case, the new character coding is another possible proposal to be considered in future phylogenetic studies of these rodents.

In the new analyses, and in agreement with previous studies, the traditional octodontines and ctenomyines are also recovered. Like in the analysis from Verzi et al. (2014), *Spaniomys* is clustered with *Protabrocoma* and living abrocomyids. However, the unorthodox position of certain extinct taxa (see Fig. 7A) as sister taxa of octodontine and ctenomines is not supported anymore (see Fig. 7B–D).

These results indicate that reanalyses of conflictive dental characters, scrutinizing data matrices, are particularly necessary to evaluate the current controversy on the phylogeny of octodontoids (e.g., Candela and Rasia 2012; Arnal et al. 2014; Verzi et al. 2014).

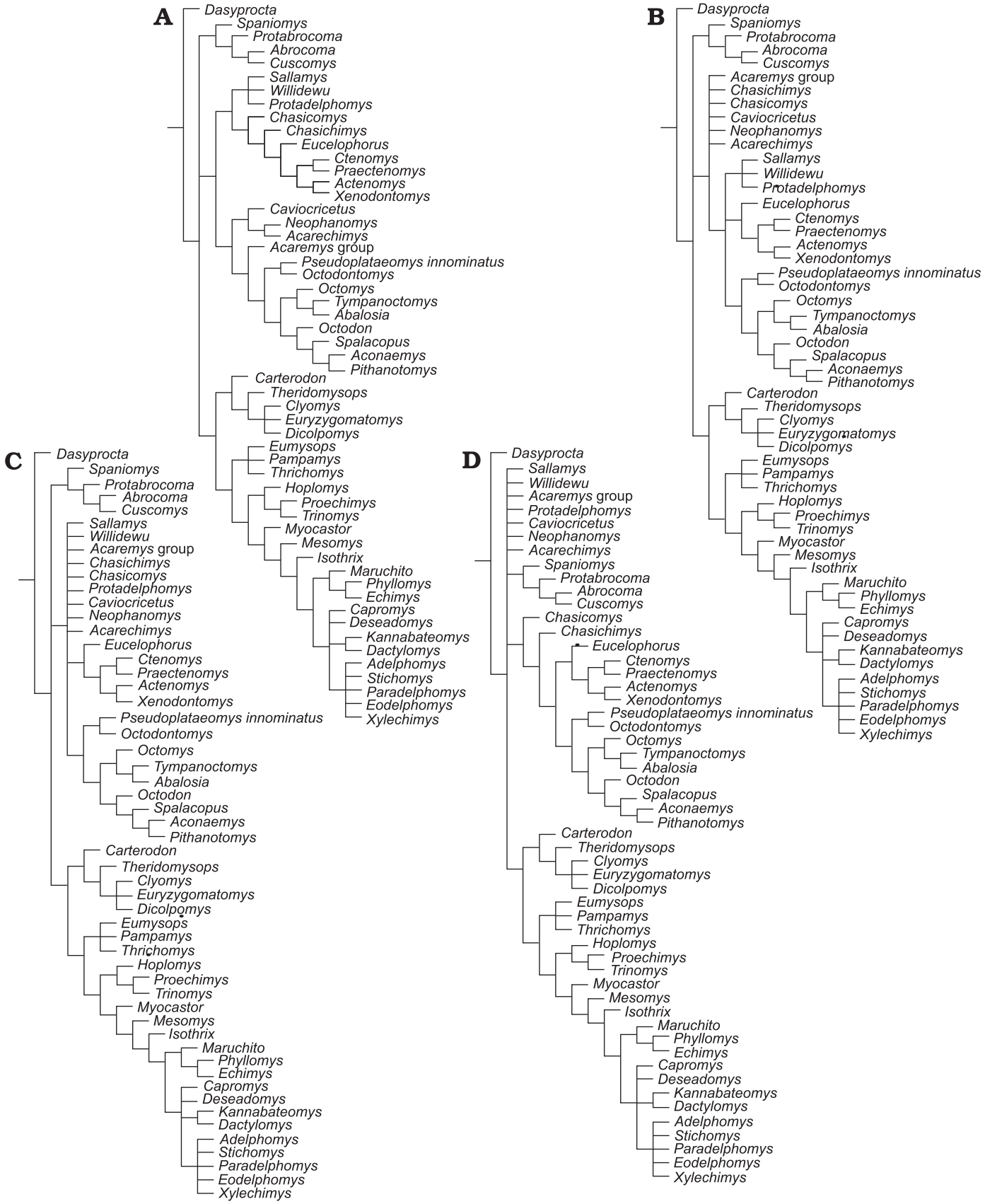

Fig. 7. **A**. Strict consensus trees from analysis of Verzi et al. (2014). **B**. Strict consensus of 27 MPTs of 139 steps resulting from the cladistic analysis of data matrix given in SOM 1. **C**. Strict consensus of 45 MPTs of 142 steps that resulted from cladistic analysis of data matrix given in SOM 2. **D**. Strict consensus of 42 MPTs of 146 steps that resulted from cladistic analysis of data matrix given in SOM 3.

Remarks and conclusions

The history of classification of caviomorphs expresses an active debate concerning the identification of homologies of molar traits. Such as noted in other groups of organisms (Hermsen and Hendricks 2008), in "pre-Hennigian" times extinct taxa were central to explore the origin and evolution of these rodents. So, the reconstruction of early evolution of caviomorphs was made according to the conception that the oldest fossils represent the ancestral forms, and the paleontology took a position at the top of a hierarchy of knowledge of caviomorph origin (Wood and Patterson 1959; Hoffstetter and Lavocat 1970; Hoffstetter 1976; Lavocat 1976). Moreover, following a relatively extreme reductionist vision, homologies of dental traits turned crucial to elucidate phylogenetic and biogeographic origin of the group (e.g., Wood and Patterson 1959). Posteriorly, fossils become less important for phylogenetic reconstruction (being as important as living taxa, or only considered to calibrate nodes in molecular systematics). More recently, important findings of fossil caviomorphs, including the oldest caviomorphs, stimulated the renaissance of the consideration of fossils in the studies on the origin, early diversification, and evolution of the group (Vucetich et al. 2010; Antoine et al. 2012; Arnal et al. 2014). Tooth characters, the single or main evidence of the earliest caviomorphs, become central to explicate the origin and the earliest evolutionary history of the group. Consequently, dental character conceptualization continues to priority topic in these studies, evoking "pre-Hennigian" times, but with new methods of analyses.

Previous proposals of homologies for dental structures in octodontoids (such as those of Carvalho and Salles 2004; Candela and Rasia 2012; see also Arnal 2012) should not be omitted when dental characters are contemplated in phylogenetic analysis. Lower molar character definition and character states delimitation in octodontoids, being relevant to evolutionary reconstruction, should be founded on anatomical examination, a priori following explicit criteria of "primary homology". Alternative hypotheses of "primary homology" proposed for the same molar traits in caviomorphs, and particularly in octodontoids, indicate that each main group requires its own thorough anatomical study. The use of nomenclatures of dental features proposed outside specific taxa of octodontoids, obviating without justification those based on octodontoids (Carvalho and Salles 2004; Arnal 2012; Candela and Rasia 2012) is not a logical posture from a systematic perspective.

Problems detected here in the study of Verzi et al. (see above) concerning the characterization of certain dental characters, the coding of character states and the results from the optimization of these characters indicate that phylogenetic analysis of Verzi et al. (2014) as basis for identifying an historical explanation of dental characters is not entirely supported. Homologies that resulted from cladistic analysis of Verzi et al. (2014) (including both synapomorphies and symplesiomorphies; for a discussion of this topic see for example Nixon and Carpenter 2011; Brower and de Pinna 2012; Farris 2013) should be tested through new cycles of testability (Kluge 1998, 2003). Their novel proposals with respect to the traditional visions, such as the phylogenetic position of *Willidewu*, *Acaremys*, or *Spaniomys* within octodontoids, are very interesting. However, if the first act of characterization and coding of character state is not sufficiently supported, the "innovative" clades into the cladograms will not be maintained. Considering that for certain dental features in octodontoids there are alternative correspondence hypotheses (see discussion above), a future dynamic approach would be necessary as a discovery procedure for inferring historical homology of conflictive dental characters.

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