



# Tooth morphology of Echimyidae (Rodentia, Caviomorpha): homology assessments, fossils, and evolution

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Echimyidae constitute the most important radiation of caviomorph rodents in the Neotropical region, represented by 20 extant genera and several extinct species. Both in extant and fossil forms, this diversity is reflected by a significant morphological variation found in crown structures of the cheek teeth. Different hypotheses of primary homology have been proposed for these structures, which, in turn, support diverse dental evolutionary hypotheses. In this contribution we inspect the main structures (cusps and lophids) of the lower deciduous teeth and molars in extinct and extant Echimyidae, and establish their topological correspondences. Comparisons with cusps and lophids of Erethizontidae are emphasized. We explore the testing of alternative primary hypotheses of lophid correspondences in a cladistic context. Following a ‘dynamic’ approach, we select the hypothesis of primary homology, which produced the more parsimonious results, and evaluate the evolutionary transformations of the dental characters analysed. In this context, the phylogenetic relationships of living *Myocastor coypus* (Molina, 1782) with the extinct *Tramyocastor* and *Paramyocastor* are tested. Our results indicate that pentalophodonty is the derived condition for the lower molars in Echimyidae, that trilophodonty evolved independently at least three times during the evolutionary history of these rodents, and that tetralophodonty represents the plesiomorphic condition. This study shows that dental evolution in echimyids can be better understood when occlusal structures are expressed as reliably comparable characters, and when fossils are taken into account.

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## INTRODUCTION

The caviomorphs (or Hystricognathi of the New World) are representative of the oldest rodent radiation in South America, with a very rich fossil record, known since the ?Late Eocene–Early Oligocene (Wyss *et al.*, 1993; Frailey & Campbell, 2004; Vucetich *et al.*, 2010a). They reached an important taxonomic diversity, which is currently expressed by the existence of 12 extant families in South America (Honeycutt, Frabotta & Rowe, 2007) and several fossil taxa (e.g.

McKenna & Bell, 1997). In terms of both extant and fossil forms this diversity is reflected by an important morphological disparity found in crown structures (as loph/lophids and cusps) of the cheek teeth. Different hypotheses of primary homology (*sensu de Pinna*, 1991) were proposed for these structures, which in turn reinforce alternative hypotheses on the Holarctic or African origin of caviomorphs (e.g. Lavocat, 1971, 1976; Patterson & Wood, 1982; Jaeger, 1988; Candela, 1999, 2002; Vucetich *et al.*, 2010a). The identification of homologies in crown structures of the oldest fossil caviomorphs have become central to this debate (e.g. Wood & Patterson, 1959; Lavocat, 1976; Patterson & Wood, 1982; Candela, 1999). In spite of the important

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investigation generated, for most of the main clades of caviomorphs (i.e. Octodontoidea, Chinchilloidea, and Caviioidea), excepting the Erethizontidae (Candela, 1999, 2002), there is not a unified nomenclature for their crown structures. So, more studies on molari-form structures in caviomorphs are required to employ dental characters in phylogenetic analyses. In the case of octodontoids and erethizontids, certain fossil taxa reveal the presence of well-differentiated cusps, pointing to the essential role of fossils in the identification of homologous cheek teeth structures, as lophids/lophids. Of remarkable interest in this context are the Echimyidae, which constitute the most important radiation of caviomorphs in the Neotropical region, represented by 20 extant genera and several extinct taxa (e.g. Woods, 1993; McKenna & Bell, 1997), many of which are known nearly exclusively by dental remains (e.g. Vucetich, Kramarz & Candela, 2010b). Although profuse information on the molar morphology and systematics of the Echimyidae is available (e.g. Moojen, 1948; Patton, 1987; Emmons, 2005), the dental evolution of the family remains poorly understood because of the controversial identification of the homologies of the crown structures among different echimyid groups, and outside these rodents into a caviomorph higher-level phylogenetic framework. Recently, Carvalho & Salles (2004) made an exhaustive study of the tooth morphology in living and extinct Echimyidae, which constitutes an encouraging background to explore their phylogenetic relationships, especially of those known mainly by dental remains.

In this work we inspect crown structures of extinct and living echimyids, and evaluate alternative primary homology hypotheses for echimyid crown structures of deciduous teeth (dp4) and lower molars, comparing them particularly with those of the erethizontids (Candela, 2002). On this basis, we explore the testing of alternative primary hypotheses of lophid correspondences of Echimyidae in a phylogenetic context. Following a 'dynamic' approach, we choose the 'best' primary homology hypothesis and evaluate the evolutionary transformations of the dental characters analysed.

Among extinct taxa we especially examine *Tramycastor* and *Paramycastor*, from the Late Miocene and Pliocene of Argentina, which are mainly known by dental remains (see Candela, Noriega & Reguero, 2007). Both genera were traditionally recognized as members of Myocastorinae, within the Echimyidae (e.g. McKenna & Bell, 1997; Verzi, Deschamps & Vucetich 2002), but neither of them were included in an integrative phylogenetic analysis of the family. Following this approach, we test the monophyly of these genera and their relationships with the living *Myocastor*.

## MATERIAL AND METHODS

### HOMOLOGY HYPOTHESES

Initially, we establish the topological correspondences of lophids and cusps in the lower cheek teeth of Echimyidae and other caviomorph rodents, and compare alternative plausible proposals of homologies for these dental structures (Patterson & Wood, 1982; Candela, 2000, 2002; Carvalho & Salles, 2004). Through critical discussion of tooth morphology and following a static approach (Ramírez, 2007), we propose primary homology hypotheses (*sensu* de Pinna, 1991) for the anterior lophids of the penta- and tetralophodont patterns of the deciduous teeth (dp4) and lower molars in echimyids (see Results). In this instance, topology and connectivity were the criteria of homology employed as conceptual tools for guiding observation in the search for homologies (Rieppel, 1994; Rieppel & Kearney, 2002). We identified comparable lophids among the teeth of echimyids based on topological relations, and with potential phylogenetic information to be tested by parsimony (Rieppel, 1994).

We built two data sets (Tables 1 and 2) under two alternative hypotheses of correspondence for the crown structures of the dp4 and lower molars of echimyids, and performed two phylogenetic analyses: (1) analysis I, assuming the hypotheses of primary homologies for the lophids of the dp4 and lower molars of the Echimyidae, following Carvalho & Salles (2004); and (2) analysis II, following the hypotheses of correspondences for the lophids of the dp4 and lower molars of the echimyids proposed here. Next, through parsimony analysis (see below), we evaluated the testing of the alternative hypotheses of primary homologies that produced the most parsimonious results (Rieppel, 1996). Monophyly of Myocastorinae was found in each analysis. On the basis of the most parsimonious trees obtained, we identified the evolutionary transformations of the crown structures they imply (Ramírez, 2007). In this context, we discussed the importance of extinct taxa to understand the evolution of dental features within the Echimyidae.

### PHYLOGENETIC ANALYSIS

#### *Parsimony analyses*

The data set for analysis I (following the hypothesis of Carvalho & Salles, 2004; Table 1) consists of 51 characters scored for 36 echimyid taxa (see below) and the out-group *Coendou* (Erethizontidae). The data set for analysis II (following the hypothesis proposed here; Table 2) included 50 characters scored for the same 36 taxa of analysis I. Both data sets only differ in the scoring of the characters involved in the competing



**Table 2.** Data matrix (37 terminal taxa and 50 characters) of Analysis II; deciduous teeth (dp4) and lower molar character states involved in the homology hypotheses, as well as those that were recoded with respect to the original data set, are marked in bold. Non-informative characters are included here in order to facilitate the comparisons (see text). Non-applicable characters are coded ‘-’, cases of polymorphism are coded ‘/’, and unknown or uncertain character conditions are coded ‘?’.

	1					2					3					4					5									
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
<i>Coendou</i>	/	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hoplomys</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Mesomys</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Lonchotrrix</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Proechimys semispinosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Proechimys</i> spp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Proechimys</i> spp. 2	/	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Proechimys</i> cf. <i>brevicauda</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Proechimys riparum</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Trinomys mirapitanga</i>	0	?	?	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Trinomys dimidiatus</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Trinomys</i> spp.	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Trinomys denigratus</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Trinomys albispinus</i>	1	1	?	1	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Clyomys</i>	0	1	-	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Euryzomatomys</i>	0	1	-	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cartodon</i>	0	1	-	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thrichomys</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Theridomysops</i>	0	1	-	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Eumysops</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pampamys</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Maruchito</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Isothrix</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Echimyus chrysurus</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Echimyus semivillosus</i>	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Makalata</i> sp.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Makalata didelphoides</i>	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Makalata grandis</i>	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Phyllomys</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Diplomys</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Callistomys</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Kannabatomys</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Dactylomys</i>	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Olallamys</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Myocastor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Paramyocastor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Tramyocastor</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

hypotheses of homology (these characters are discussed in the Character analysis section). The remaining characters analysed were equally scored in both analyses, and most of them were taken from the data set of Carvalho & Salles (2004). Multistate characters were treated as described in Carvalho & Salles (2004). Characters that were recoded with respect to the original data (Carvalho & Salles, 2004) were discussed in each case (see Character Analysis section).

Both data sets were analysed by performing a heuristic search with parsimony under equal weights with TNT 1.0 (Goloboff, Farris & Nixon, 2003). The shortest trees were found by generating 200 Wagner trees, and then submitting them to tree-bisection-reconnection (TBR) branch swapping (retaining 50 trees per replicate). State transformations were considered synapomorphies for a given node only if they were unambiguous. In the two analyses, the unambiguous character state optimizations on the consensus (common optimizations over the equally parsimonious trees obtained) were edited with WIN-CLADA (Nixon, 1999).

#### Taxon sampling

Taxon sampling included 36 echimyid terminal taxa scored at the species and genus level (to genus level in the case of species that were grouped previously in a single terminal by Carvalho & Salles, 2004). All living taxa previously analysed by Carvalho & Salles (2004) were included. The extinct taxa *Maruchito*, *Theridomysops*, *Eumysops*, and *Pampamys* were selected because their inclusion within Echimyidae is strongly supported by previous studies. *Maruchito trilofodonte* Vucetich, Mazzoni & Pardiñas, 1993, from the Collon Cura Formation (Middle Miocene, Neuquén Province, Argentina; Vucetich, Mazzoni & Pardiñas, 1993), was related to the living echimyid *Callistomys* (Emmons & Vucetich, 1998). *Eumysops*, *Theridomysops*, and *Pampamys* (Late Miocene–Pliocene from Argentina) were related to the living lineage of *Thrichomys*, *Euryzygomatomys*, and *Clyomys* (see Vucetich, 1995; Verzi, Vucetich & Montalvo, 1995). *Reigechimys* (Late Miocene of Argentina; Verzi, Vucetich & Montalvo, 1994) was not included in this analysis because it is only known from scarce and poorly preserved specimens.

Some extinct taxa previously included in the study of Carvalho & Salles (2004) were excluded from this work because of the following arguments. *Paulacoutomys* is probably an erethizontid (A.M. Candela, pers. observ.). The Colhuehuapian octodontoids from Patagonian *Protadelphomys* and *Willidewu*, both probably related to the Deseadan genera *Sallamys* from Salla (Bolivia; Hoffstetter & Lavocat, 1970; Vucetich & Verzi, 1991), were considered

Octodontoidea *incertae sedis* (see Vucetich *et al.*, 2010b). Thus, their phylogenetic relationships must be analysed in a more inclusive level of generality within Octodontoidea than the one considered here, an objective that is far beyond this paper. Likewise, the affinities of the Deseadan genera *Deseadomys*, *Xylechimys*, *Platypittamys*, and *Migraveramus* (Wood & Patterson, 1959; Patterson & Wood, 1982) need to be tested, taking into account several Octodontoids and considering a higher level of generality than that of the family Echimyidae. The same situation is seen in the case of the Miocene octodontoids *Acarechimys* and *Caviocricetus*, which were considered as Octodontoidea *incertae sedis* (see Vucetich *et al.*, 2010b). On the other hand, *Sciamys* and *Acaremys* were included in the extinct family Acaremyidae (Colhuehuapian–‘Colloncuran’, Early–Middle Miocene; Vucetich & Kramarz, 2003). Finally, the Patagonian genera *Prospaniomys*, *Protacaremys*, *Stichomys*, *Adelphomys*, *Spaniomys*, and *Paradelphomys* (Ameghino, 1902; Patterson & Pascual, 1968) were traditionally considered to sit within the extinct subfamily ‘Adelphomyinae’. However, this grouping is probably a non-monophyletic group (Vucetich *et al.*, 2010b), and they need to be analysed in a broader systematic context. Certainly, a comprehensive phylogeny of octodontoids would be necessary to test the relationships of these extinct taxa, but this exceeds the scope of this study.

#### Taxonomic status of *Myocastor* and the extinct *Tramyocastor* and *Paramyocastor*

The genus *Myocastor*, at the present time including only the extant species *Myocastor coypus* (Molina, 1782), was considered as a member of Capromyidae, apart from the other echimyids (e.g. Simpson, 1945), as a member of the Myocastoridae family (e.g. Woods, 1982), or as a member of the Echimyidae family (e.g. Patterson & Pascual, 1968; Patterson & Wood, 1982). In the classification of mammals in McKenna & Bell (1997), the Myocastorinae, including *Myocastor* and several extinct taxa (see below), were considered within the family Echimyidae. The inclusion of *Myocastor* within the Echimyidae was sustained by results from molecular studies (Huchon & Douzery, 2001; Leite & Patton, 2002; Galewski *et al.*, 2005). Following McKenna & Bell (1997), the subfamily Myocastorinae contains the extinct genera *Prospaniomys*, *Spaniomys*, *Strophostephanos*, *Haplostropha*, *Proatherura*, *Tribodon*, *Isomyopotamus*, *Paramyocastor*, *Matyoscor*, and *Myocastor*. Concerning the grouping of these taxa with *Myocastor*, the next considerations are appropriate: the phylogenetic position of the Patagonian *Prospaniomys* and *Spaniomys*, traditionally considered within the extinct subfamily ‘Adelphomyinae’ (see Vucetich *et al.*, 2010b), should be

analysed in a broader systematic context, including other octodontoids besides Echimyidae. *Proatherura* is synonymous with *Eumysops*, which was recovered from the Pliocene of Argentina (Candela *et al.*, 2007 and references therein). '*Tribodon*' is actually a *nomen dubium* (see Vucetich, 1995; Vucetich & Verzi, 1995). *Isomyopotamus* is synonymous with *Paramyocastor*, with *Paramyocastor diligens* (Ameghino, 1888) being the single species of the genus (Verzi *et al.*, 2002; Candela *et al.*, 2007). *Matyoscor* is synonymous with *Myocastor*.

From these extinct taxa, in this work we incorporated the genera *Paramyocastor* and *Tramyocastor* (Late Miocene–Pliocene from Argentina; Candela *et al.*, 2007) in order to test their relationships with the living *Myocastor* and the monophyly of Myocastorinae within Echimyidae (which has not been thoroughly tested so far). *Strophostephanos* and *Haplotropha*, from the 'Mesopotamiense' (= 'Conglomerado Osifero', Ituzaingó Formation; Late Miocene; Cione *et al.*, 2000), were not included in this analysis because they are only known from scarce and poorly preserved specimens.

The specimens studied are housed in the following institutions: MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia', Mar del Plata, Argentina; MN, Museu Nacional, Rio de Janeiro, Brazil; MPS-Z, Museo de Ciencias Naturales 'P. Scasso', San Nicolás, Argentina.

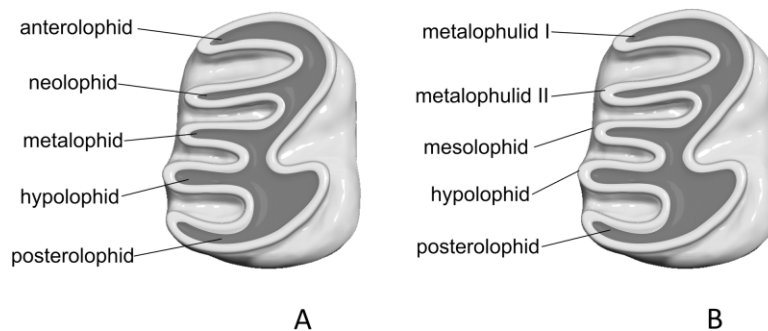
## PRIMARY HOMOLOGIES IN LOWER DECIDUOUS TEETH (= DP4) STRUCTURES

### PENTALOPHODONT DP4: PREVIOUS PROPOSALS

Patterson & Wood (1982: 501) homologized the three most anterior lophids of the pentalphodont dp4 of the caviomorphs with the anterolophid, neolophid, and metalophid, respectively (Fig. 1A). The dp4 of

the extinct octodontoid *Protacaremys* were taken to illustrate the homologies of the three most anterior lophids (Patterson & Wood, 1982: fig. 31). According to this proposal, in the pentalphodont dp4 of caviomorphs, the second lophid crossing the anterofossettid is recognized as a neomorphic structure (the neolophid), which is not homologous with the second lophid of the pentalphodont dp4 of African Hystricognathi (Phiomorpha), whereas the third lophid is the metalophid, resembling the mesolophid of phiomorphs. Consequently, this hypothesis implies that in pentalphodont dp4 of caviomorphs the second most anterior lophid is not initially connected to any recognized cusp of the tribosphenic morphology. In turn, the third lophid should be connected lingually with the metaconid and labially with the protoconid. This contrasts with what occurs in the pentalphodont dp4 of erethizontids and certain African Hystricognathi (e.g. *Phiomys andrewsi* Osborn, 1908 and *Gaudeamus aegyptius* Wood, 1968 from the Oligocene of Fayum, and *Phiomys hammudai* Jaeger *et al.*, 2010 from the Eocene of Libia), where the second lophid joins the metaconid and protoconid (Wood, 1968; Jaeger *et al.*, 2010).

Conversely, it has been proposed by Candela (2002) that the three most anterior lophids of the pentalphodont dp4 in erethizontids and probably in other caviomorphs are: the anterolophid (= metalophid I), metalophid II (= posterior arm of the protoconid), and mesolophid (Fig. 1B; see also Candela, 2002: fig. 6a), as in some phiomorphs of the Old World and extinct Asian 'Baluchimyinae' (*sensu* Flynn, Jacobs & Cheema, 1986). 'Baluchimyinae' are considered members of the Hystricognathiformes (i.e. the clade that includes, in addition to *Tsaganomys*, the 'baluchimyines' and early phiomorphs and caviomorphs; see Bryant & McKenna, 1995; Marivaux, Vianey-Liaud & Jaeger, 2004). This proposal of homologies was based on the topological correspondences of the lophids and their connecting cusps (i.e. metaconid, protoconid, mesoconid, and mesostylid), which in ere-



**Figure 1.** Primary homology hypotheses for the lophids of pentalphodont deciduous teeth (dp4) in caviomorphs. A, as proposed by Patterson & Wood (1982) and Carvalho & Salles, (2004); B, as proposed by Candela (2002).

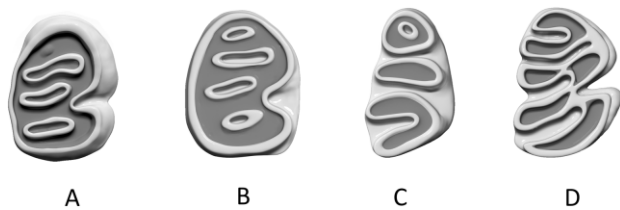
thizontids, especially in fossil species, are clearly recognized even in subadult individuals (see Candela, 2002: figs 3–4). In these rodents, the most anterior lophid is labially connected to the protoconid and lingually to the metaconid, the second lophid is labially connected to the posterior side of the protoconid and lingually to the metaconid, and the third lophid is labially connected to the mesoconid, and lingually to the mesostylid. Thus, identical topological correspondences were identified in dp4 of erethizontids, certain Phiomorpha, and ‘Baluchimyinae’ (Candela, 2002: 721).

Several erethizontids show pentalophodont dp4, such as *Coendou prehensilis* (Linnaeus, 1758) and *Eosteiomys homogenidens* Ameghino, 1902. Hexalophodont dp4 in erethizontids would result from the presence of a neomorphic structure, the neolophid, which shows variable development, such as in *Branisamyopsis australis* Candela, 2003, *Steiromys duplicatus* Ameghino, 1887, and *Steiromys detentus* Ameghino, 1887 (Candela, 2002, 2003). The neolophid of hexalophodont dp4 in erethizontids refers to a lophid that differs from the neolophid *sensu* Patterson & Wood (1982).

More recently, Carvalho & Salles (2004: fig. 4) followed the nomenclature proposed by Patterson & Wood (1982) for the three most anterior lophids of the pentalophodont dp4 of echimyids, i.e. anterolophid, neolophid, and metalophid (Fig. 1A), but without any critical position on that subject.

#### PENTALOPHODONT DP4 IN ECHIMYIDAE: ALTERNATIVE HYPOTHESIS OF PRIMARY HOMOLOGIES

Among living echimyids, several taxa exhibit pentalophodont dp4, such as *Mesomys hispidus* Desmarest, 1817 (Fig. 2A), *Lonchothrix emiliae* Thomas, 1920 (Fig. 2B), *Hoplomys gymnurus* (Thomas, 1897) (Carvalho & Salles, 2004: fig. 4), *Makalata didelphoides* (Desmarest, 1817), *Makalata grandis* (Wagner, 1845), *Makalata macrura* (Wagner, 1842), (Emmons, 2005 fig. 4c), *Echimyus chrysurus* (Zimmermann, 1780)



**Figure 2.** Pentalophodont dp4 in occlusal view of living echimyids. A, *Mesomys hispidus* (MN 27956); B, *Lonchothrix emiliae* (MN 4856, reversed); C, *Echimyus chrysurus* (MACN 31161); D, *Myocastor coypus* (MPS-Z060). Not to scale.

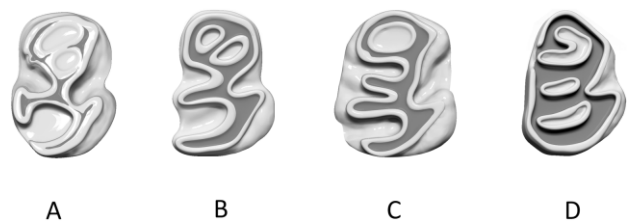
(Fig. 2C), *Phyllomys nigrispina* (Wagner, 1842) (Emmons, 2005: fig. 4h), *Diplomys labilis* (Bangs, 1901) (Emmons, 2005; fig. 4i), *Isothrix bistrata* Wagner, 1845, *Isothrix negrensis* Thomas, 1920 (Patterson & Velasco, 2006: fig. 5), at least some specimens of *Proechimys* (Patton, 1987), and *Myocastor coypus* (Fig. 2D).

One critical question in this study is to assess if the primary homologies proposed for the three most anterior lophids of the dp4 in Erethizontidae and African Hystricognathi, i.e. metalophid I, metalophid II, and mesolophid, can be applied to the pentalophodont dp4 of the echimyids.

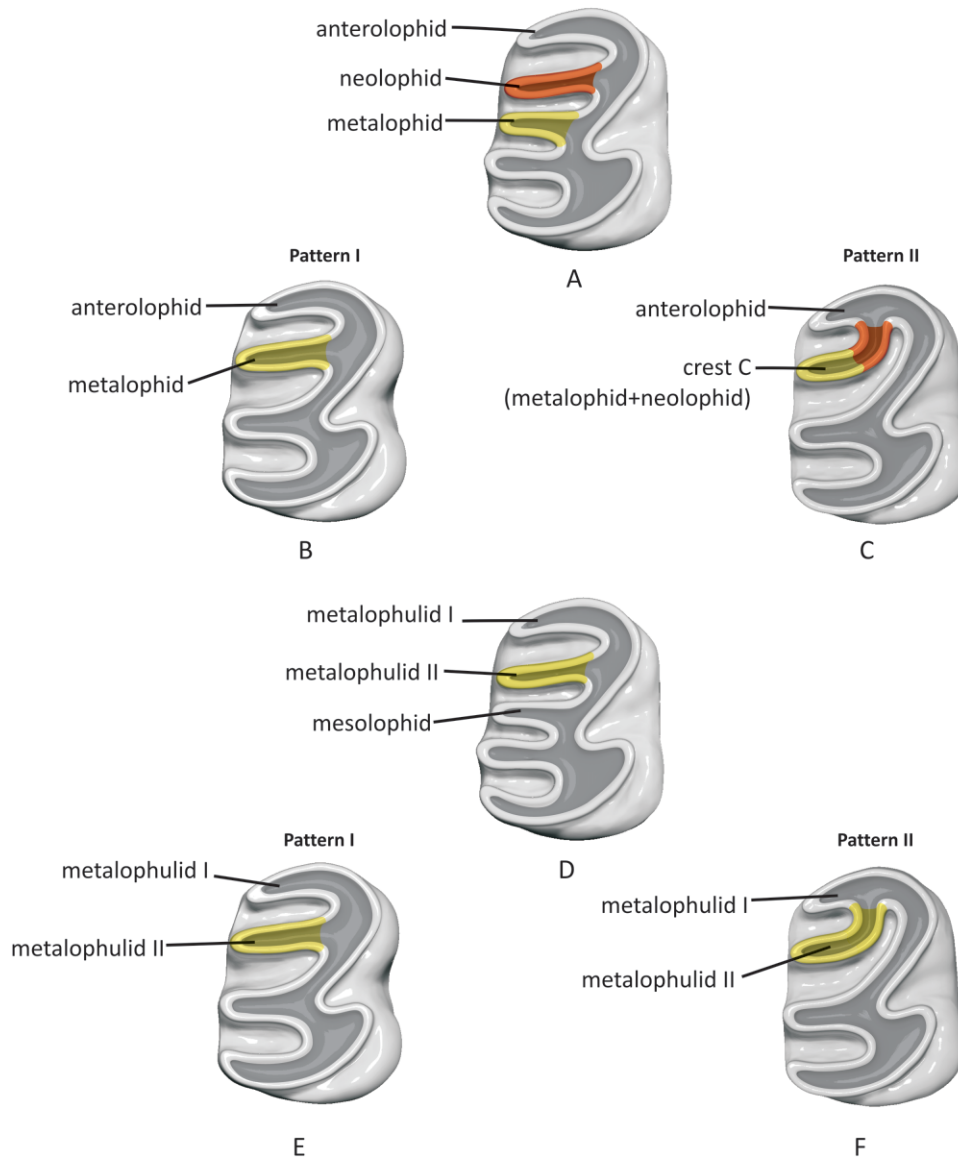
In at least some specimens of the extinct octodontoids *Plesiacaechimys*, *Acaechimys*, and *Protacaremys* (Candela, 2002; Vucetich & Vieytes, 2006; Fig. 3), the first most anterior lophid is connected to the protoconid labially, and with the metaconid lingually, both cusps, especially the metaconid, being clearly differentiated at least in the first genera. Consequently, as in porcupines, this lophid is homologized to metalophid I. The second lophid is, as the first lophid, connected labially with the protoconid and lingually with the metaconid, or with the area where this cusp occurs; therefore, it is homologized to metalophid II, making the identification of a neolophid (see above) difficult to support. The second lophid of the pentalophodont dp4 in both erethizontids and echimyids is a metalophid II, because in both cases this lophid presents the same topological relationships.

In turn, as in erethizontids, the third lophid of dp4 of echimyids can be homologized to the mesolophid, even when the mesoconid and mesostylid are not identified, at least in the available sample for this study. This lophid is recognized as the mesolophid because of its topographic location, behind metalophid II and forward of the hypolophid, originating from the middle of the ectolophid.

Lophids and cusps of the pentalophodont dp4 of erethizontids, living echimyids, and at least some



**Figure 3.** Pentalophodont dp4 in occlusal view of extinct octodontoids. A, *Plesiacaechimys koenigswaldi* (MLP 91-V-1-19); B, *Acaechimys constans* (type specimen MLP 15-391); C, *Protacaremys* sp. (MLP 85-VII-131, from Candela, 2002, fig. 7A); D, *Paramyocastor diligens* (= *Isomyopotamus albañiri*, holotype MLP 46-V-13-104). A, B, and D: reversed. Not to scale.



**Figure 4.** Homologies proposed for most anterior lophids of penta- and tetralophodont dp4. A-C, *sensu* Patterson & Wood (1982) and Carvalho & Salles (2004); A, penta-; B, tetra- (Pattern I); and C, tetralophodont (Pattern II) dp4; D-F, according to this study; D, penta-; E, tetra-(Pattern I); and F, tetralophodont (Pattern II) dp4.

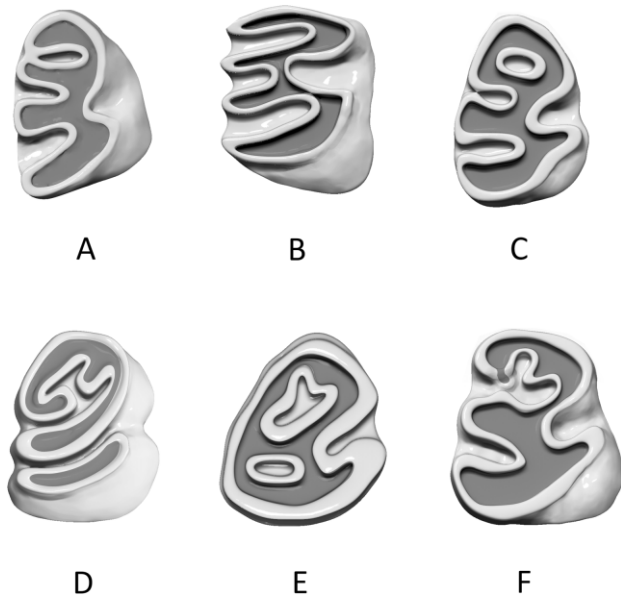
examined extinct octodontoids seem to have identical topological correspondences. Hence, for the case of echimyids, we follow the hypothesis of primary homology proposed for the pentalophodont dp4 of the erethizontids (Fig. 1B). Candela (2002) suggested these same homologies for the pentalophodont dp4 of *Mesomys* and *Lonchothrix*, and for the extinct octodontoids *Protacaremys* and *Acarechimys*.

#### TETRALOPHODONT DP4: PREVIOUS PROPOSALS

Patterson & Wood (1982) homologized the two most anterior lophids of the tetralophodont dp4 in

caviomorphs to the anterolophid (= metalophulid I) and metalophid (= metalophulid II), respectively (Fig. 4B). These homologies were proposed for the simplest patterns, such as that of the extinct octodontoid *Sciameys* and *Prospaniomys* (Patterson & Wood, 1982). This is in agreement with the homologies proposed for the tetralophodont dp4 of the Erethizontidae, as *Hypsosteiromys axiculus* (Patterson, 1958 (Candela, 2002; Candela & Vucetich, 2002: fig. 4c). The first and second lophids are both connected labially with the protoconid, and lingually with the metaconid, supporting their homologies topographically.





**Figure 5.** Tetralophodont dp4 in living and extinct Echimyidae. A, *Thrichomys apereoides*, (MACN 20.61); B, *Kannabateomys amblyonyx* (MACN 51.47); C, *Eumysops* sp. (MLP 91-IV-6-5, reversed); D, *Trinomys gratosus bonafidei* (from Carvalho & Salles, 2004: fig. 6); E, *Euryzygomatomys spinosus* (MACN 23.656); F, *Theridomysops parvulus* (type specimen MACN 8379). Not to scale.

On the other hand, following the identification of lophids proposed by Carvalho & Salles (2004: table 2; and see below), at least two different configurations for tetralophodont dp4 are identified.

1. Pattern I, in which the second lophid, homologous with the metalophid, is transversally oriented with respect to the anteroposterior axis of the teeth (Fig. 4B), such as in *Echimyus semivillosus* (I. Geoffroy, 1838) (= *Pattonomys semivillosus sensu* Emmons, 2005), *Thrichomys apereoides* (Lund, 1839), *Callistomys*, *Kannabateomys*, *Dactylomys*, *Olallamys*, and the extinct *Eumysops* (Fig. 5A–C). Then in this pattern the neolophid *sensu* Carvalho & Salles (2004), or second lophid present in the pentalophodont dp4 (Fig. 4A), is missing (Fig. 4A–B).
2. Pattern II, in which the second lophid was identified by Carvalho & Salles (2004: 454) as a combined structure, called ‘crest C’ (Fig. 4C), which results from the contact between the central portion of the neolophid and the anteriorly orientated metalophid. Unlike the first pattern, the second lophid or ‘crest C’ is obliquely oriented from the first lophid, such as in most species of *Trinomys* (Fig. 5D). Only the central portion of the second lophid would be present in *Euryzygomatomys* (Fig. 5E) and *Clyomys*. Consequently, accord-

ing to the hypothesis of Carvalho & Salles (2004), the second lophid of the different tetralophodont patterns in echimyids would be incompletely homologous (see Fig. 4B–C).

#### TETRALOPHODONT DP4 IN ECHIMYIDAE:

##### ALTERNATIVE HYPOTHESIS OF PRIMARY HOMOLOGIES

The central issue is to test if in tetralophodont dp4 of echimyids, the second lophid can be homologized with metalophulid II, beyond their diverse configurations or degree of development. So, the hypothesis proposed here is to consider that the second lophid in tetralophodont patterns corresponds to metalophulid II, but shows a different degree of development and orientation: one with a more transverse orientation with respect to the anteroposterior axis of the tooth (pattern I; Fig. 4E), and the other being obliquely oriented and curved in shape, connected to the posterior face of the metalophulid I or located between this lophid and protoconid region (pattern II; Fig. 4F).

The first of these patterns can be observed in the living *Thrichomys*, *Echimyus semivillosus*, *Callistomys*, *Kannabateomys*, and *Dactylomys*, and in the extinct *Eumysops* (Fig. 5A–C). Like tetralophodont dp4 of erethizontids, as that of *Hypsosteiromys axicululus*, the first and second lophids are both connected labially with the protoconid, and lingually with the metaconid, or to the site where these cusps occur. So, topographical correspondences support the homologies of both lophids with metalophulids I and II, respectively. In this proposal, the difference with that of Patterson & Wood (1982) is that metalophulid II in the tetralophodont dp4 corresponds to the second lophid in position of the pentalophodont dp4 (Fig. 4D; not with the third lophid of pentalophodont dp4, see Fig. 4A). According to our proposal the neolophid would be absent in the penta- as well as in the tetralophodont patterns.

With respect to the other pattern (pattern II; Fig. 4F), as it is seen in most species of *Trinomys*, it is possible to propose that the second lophid is also homologous with metalophulid II, but being obliquely oriented and sometimes curved in shape, shows a different degree of development. Note that in the extinct *Theridomysops* (Fig. 5F) the second lophid is not completely developed, as in extant *Euryzygomatomys* or *Clyomys*.

In other words, topological correspondences allow us to propose that the second lophid of a different tetralophodont dp4 is metalophulid II, but shows different orientations and degree of development. This primary homology hypothesis is here tested following a ‘dynamic’ approach (see Phylogenetic analysis).

## PRIMARY HOMOLOGIES FOR LOWER MOLAR STRUCTURES

### PENTA- AND TETRALOPHODONT LOWER MOLARS: PREVIOUS PROPOSALS

Different homology hypotheses for the lower molar structures can be identified through the systematic and anatomical studies of living and extinct caviomorphs. According to Patterson & Wood (1982) the two most anterior lophids of the tetralophodont molars are homologous with the anterolophid and metalophid, respectively (Fig. 6B). For the pentalophodont molars (Fig. 6A), as in those of certain erethizontids (e.g. *Branisamyopsis australis* Candela, 2003; *Steiromys duplicatus* Ameghino, 1887; *Neosteiromys pattoni* Candela, 2004; Candela, 2003, 2004), Patterson & Wood (1982: 496) interpreted the fifth crest, connected to the posterior face of the anterolophid, as a neomorphic structure not homologous with that of the African Hystricognathi.

Frailey & Campbell (2004) considered that the first lophid of the caviomorphs of Santa Rosa local fauna (?Late Eocene–Early Oligocene, Peru) corresponds to the anterolophid, and the second lophid, connected to the metaconid, corresponds to the metalophid.

Based on topography and connectivity, and taking into account the standard dental nomenclature of Wood & Wilson (1936), Candela (2000) proposed that the first lophid in the lower molars of erethizontids, and those of the other caviomorphs, corresponds to metalophid I, because it links the protoconid with the metaconid (Candela, 2000: 212–213). According to this proposal, metalophid I was homologized with those of African Phiomorpha and Asian ‘Baluchimyinae’ (*sensu* Flynn *et al.*, 1986). Regarding the second lophid in tetralophodont molars, it was noted in Candela (2000) that its homology (metalophid II or mesolophid) depends on the identification of their associated cusps (metaconid and protoconid or mesoconid and mesostylid), thus requiring a particular study of each case. For the pentalophodont molars present in some Erethizontidae (e.g. *Branisamyopsis australis* and *Neosteiromys pattoni*; Candela, 2003, 2004), the second small lophid in position, connected to the posterior face of metalophid I, was identified as a neomorphic structure: the neolophid, which is not homologous with any structure of the ‘Baluchimyinae’ or African Hystricognathi (Candela, 2000; see Fig. 6A and D).

In their study on the phylogenetic relationships of early Tertiary rodents, Marivaux *et al.* (2004) recognized the presence of metalophid I and metalophid II (with metalophid II showing a different degree of development) in ‘Baluchimyinae’, and in early caviomorphs such as *Platypittams* and *Branisamys*.

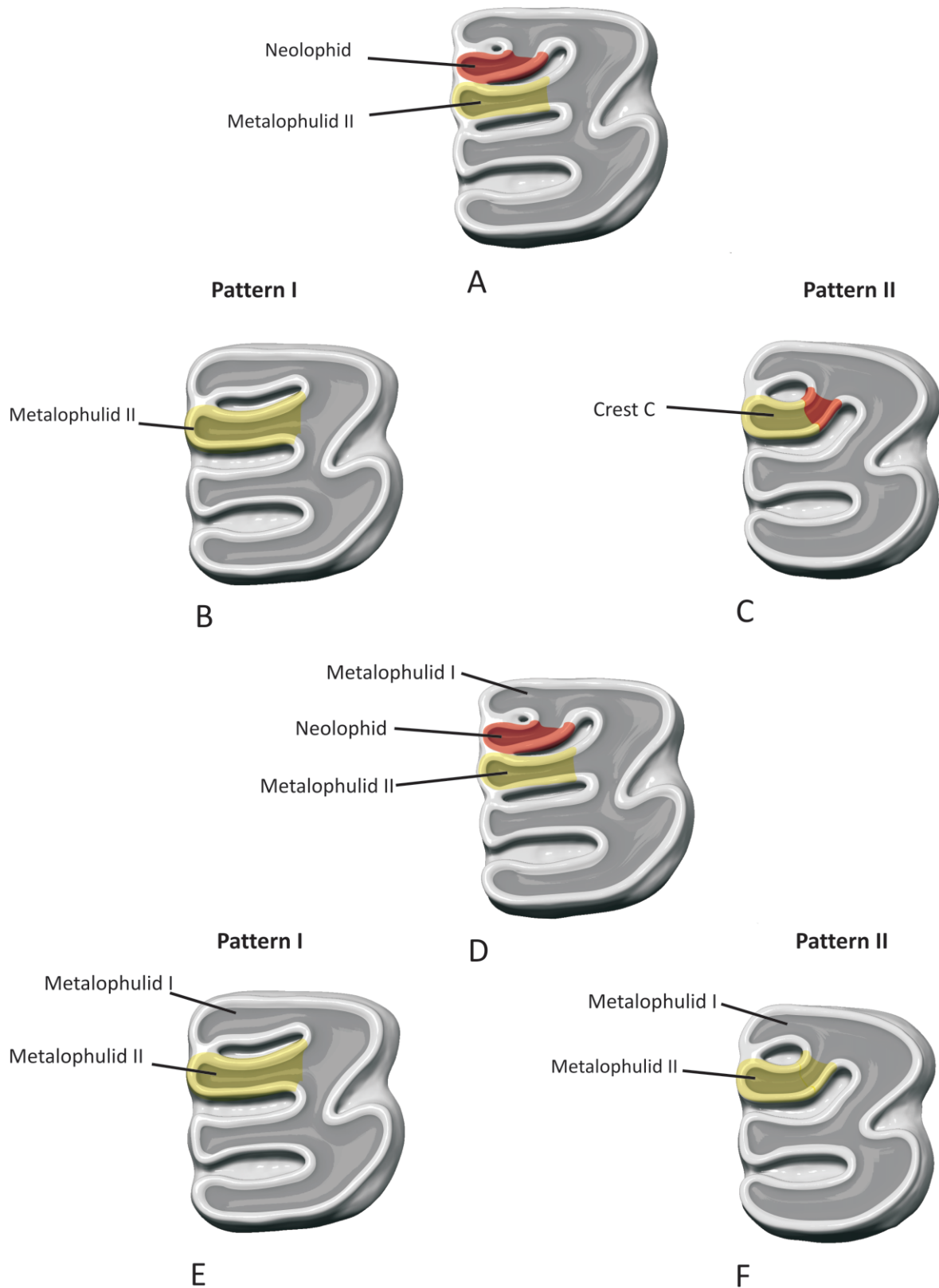
Based on the homologies proposed by Patterson & Wood (1982), Carvalho & Salles (2004) homologized the three most anterior lophids of the pentalophodont molars, as those of *Hoplomys*, with the anterolophid, neolophid, and metalophid, respectively (Fig. 6A). For the tetralophodont patterns, these authors homologized the second anteriormost lophid either with the metalophid (third lophid in the pentalophodont molars; Fig. 6A–B) or with ‘crest C’, being ‘larger and positioned more posteriorly than the typical neolophid’ (Carvalho & Salles, 2004: 454, fig 6; Fig. 6C). According to these authors, ‘crest C’ would result from contact between the central portion of the neolophid and the anteriorly orientated metalophid.

In this context, at least two tetralophodont patterns were recognized among echimyids: pattern I, with the first and second lophids homologous with the anterolophid and metalophid, respectively (Fig. 6B), and orientated approximately perpendicular to the anteroposterior axis of the tooth, often making contact with the ectolophid, as in *Paramyocastor* (Fig. 7A); and pattern II (Fig. 6C), with the two anteriormost lophids corresponding to the anterolophid and ‘crest C’, respectively, a pattern identified in living *Mesomys*, *Lonchothrix*, and *Proechimys* spp., and in most of the species of *Trinomys* (Fig. 7D–E). Therefore, the second anteriormost lophid in the tetralophodont molars corresponds either to the metalophid or to ‘crest C’ (neolophid + metalophid) (Fig. 6B–C). In both cases the second lophid would be incompletely homologous.

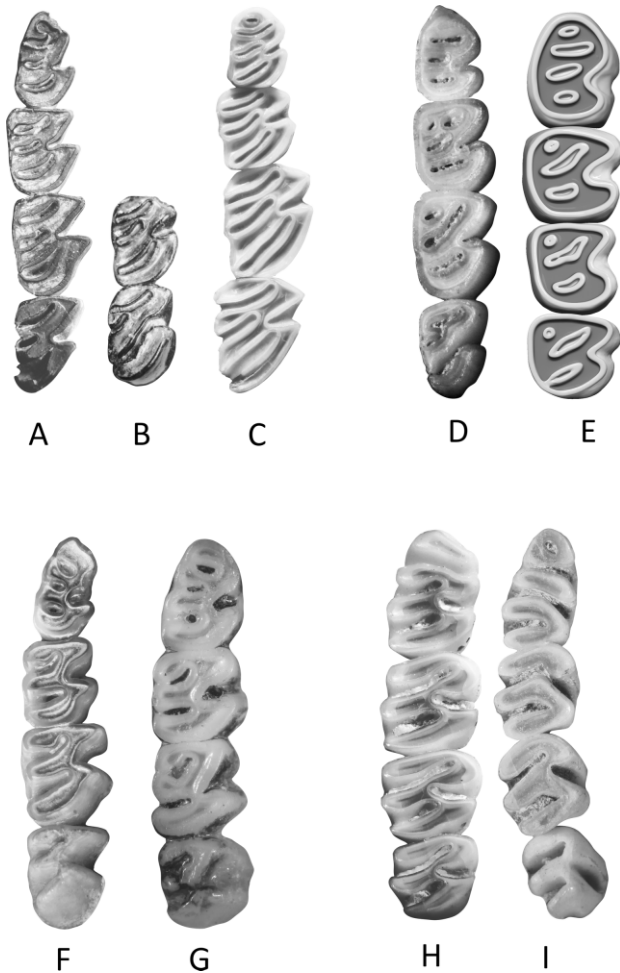
### PENTA- AND TETRALOPHODONT LOWER MOLARS IN ECHIMYIDAE: ALTERNATIVE HYPOTHESIS OF PRIMARY HOMOLOGY

Like in other members of Hystricognathiformes, such as ‘Baluchimyinae’ and Phiomoridae (Flynn *et al.*, 1986; Marivaux *et al.*, 2002, 2004; Jaeger *et al.*, 2010), and erethizontids (Candela, 2000), in several extinct octodontoids (e.g. *Sciamys*, *Acarechimys*, *Caviocrictus*, *Plesiacharechimys*, and *Galileomys*; Vucetich & Kramarz, 2003; Vucetich & Vieytes, 2006; Fig. 8), the first most anterior lophid is connected labially to the protoconid and lingually to the metaconid, with both cusps, especially the metaconid, being clearly differentiated. Consequently, the first lophid of the echimyids, as in erethizontids and other members of Hystricognathiformes (Marivaux *et al.*, 2004), is homologized as metalophid I.

The homologies of the second lophid in the tetralophodont patterns are more debatable, as this depends on the identification of associated cusps, not always identifiable, and hence different interpretations can be given on the diverse configurations that the lophids acquire. Like ‘Baluchimyinae’ and some

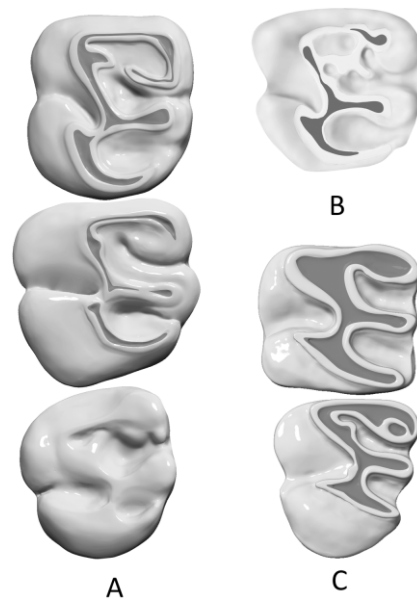


**Figure 6.** Homologies proposed for most anterior lophids of penta- and tetralophodont lower molars; A-C, sensu Patterson & Wood (1982) and Carvalho & Salles (2004); A, penta-; B, tetra- (Pattern I); and C, tetralophodont (Pattern II) lower molars; D-F, according to this study; D, penta-; E, tetra- (Pattern I); and F, tetralophodont (Pattern II) lower molars.



**Figure 7.** Lower cheek teeth of living and extinct echimyids. A, *Paramyocastor diligens* (= *Isomyopotamus albañiri*, holotype MLP 46-V-13-104, dp4-m3); B, *Tramyocastor andiai* (type specimen PVR 1134, m2-3); C, *Myocastor coypus* (MPS-Z060); D, *Proechimys* sp. (MACN 50.382); E, *Lonchothrix emiliae* (MN 4856, reversed); F, *Eumysops* sp. (MLP 91-IV-6-5, reversed); G, *Thrichomys apereoides* (MACN 20.61); H, *Kannabateomys amblyonyx* (MACN 51.47); I, *Echimyus chrysurus* (MACN 31161). Not to scale.

Phiomysidae (Flynn *et al.*, 1986; Marivaux *et al.*, 2002, 2004; Jaeger *et al.*, 2010), in certain extinct octodontoids the second lophid can show different degrees of development (e.g. *Galileomys*, *Plesiacharechimys*, and *Acarechimys*; Fig. 8), either reaching or not the lingual end of the tooth where the metaconid occurs. In *Sciomyis* and *Protacaremys*, the lingual end connects with the metaconid or is close to this cusp, and the second lophid in these octodontoids, connected labially with the protoconid and lingually with the metaconid, can be homologized with metalophulid II, as in other Hystricognathiformes. Although in living echimyids the metaconid is not as evident as in the



**Figure 8.** Lower cheek teeth of extinct octodontoids. A, *Plesiacharechimys koenigswaldi* (MLP 91-V-1-22, left m1-3 series); B, *Galileomys antelucanus* (m1 or 2, from Vucetich & Kramarz, 2003); C, *Willidewu estepariensis* (type specimen MLP 88-V-30-1, m2-3). Not to scale.

extinct forms mentioned, when the second lophid reaches the lingual end of the teeth, it connects with the location where this cusp occurs. Therefore, as in extinct octodontoids, it is possible to claim that the second lophid of living echimyids corresponds to metalophulid II. In addition, in extinct and living echimyids there is no clear evidence of the presence of mesostylid and mesoconid, making it difficult to homologize the second lophid of these rodents with the mesolophid.

The neolophid is interpreted as a neomorphic structure only present in pentalophodont patterns (Fig. 6A), such as those present in *Hoplomys* and certain erethizontids (e.g. *Branisamyopsis australis*; Candela, 2003). Pentalophodont lower molars in caviomorphs seem to be unusual.

As mentioned above, at least two tetralophodont patterns are identified among the lower molars. One of them with the second lophid, metalophulid II (pattern I), oriented approximately perpendicular to the anteroposterior axis of the tooth (Fig. 6E), as in *Myocastor coypus* and the extinct *Tramyocastor* and *Paramyocastor* (Fig. 7A–C). Some extinct octodontoids (e.g. *Sciomyis* and *Protacaremys*) show this condition.

In the other tetralophodont pattern (pattern II), the second lophid is not transversally oriented and, being curved in shape, is more intimately connected with the posterior face of metalophulid I (Fig. 6F). For this

pattern, the second lophid was homologized with 'crest C' (central portion of the 'neolophid' plus the anteriorly oriented metalophid; Carvalho & Salles, 2004: 454). This pattern is typically represented in *Proechimys*, *Mesomys*, *Lonchothrix*, and most species of *Trinomys* (Fig. 7).

One central question is to establish if, beyond the varied configurations or degree of development seen among tetralophodont molars in echimyids, the second lophid can be homologized in all of them. If this is accepted in pattern II, the second lophid is a mixed structure (Fig. 6C), and this pattern would actually contain five lophids (i.e. anterolophid, neolophid, metalophid, hypolophid, and posterolophid). The alternative hypothesis is to consider that the second lophid is in all cases homologous with metalophid II, but showing different orientations: one with a transverse orientation with respect to the anteroposterior axis of the tooth (Fig. 6E), and the other connected to the posterior face of metalophid I or between this lophid and the protoconid region, being obliquely oriented and curved in shape (Fig. 6F). Note that in the tetralophodont molars of some extinct octodontoids, intermediate conditions in the orientation and degree of development of metalophid II can be observed (e.g. *Plesiacaechimys*, *Galileomys*, *Acaechimys*, and *Willidewu*; Fig. 8).

Therefore, topological correspondences allow us to propose that the second lophid in different tetralophodont lower molars is metalophid II, but with different orientations and degrees of development. This primary homology hypothesis is here tested following a 'dynamic' approach (see Phylogenetic analysis).

#### MOLAR MORPHOLOGY OF *TRAMYOCASTOR* AND *PARAMYOCASTOR*

Molariforms of *Paramyocastor diligens* with a biochron ranging from Montehermosan to upper Chapadmalalan (Late Miocene–Late Pliocene; see Marshall & Patterson, 1981; Verzi *et al.*, 2002; Candela *et al.*, 2007) are protohypsodont, and are about half the size of those in *Myocastor coypus*. The dp4 are pentalophodont, a condition observed mainly in scarcely worn specimens (see Candela *et al.*, 2007; Fig. 7A–C). Lower molars are tetralophodont, showing less persistent lingual flexids in relation to the hypoflexid (they transform into fossetids more quickly) than in *M. coypus*. Upper molars are pentalophodont with unilateral hypsodonty, and the flexi are less persistent labially than in *M. coypus*. M3/m3 are subequal in size to M2/m2.

*Tramyocastor* includes two species: *Tramyocastor andiai* Rusconi, 1936 and *Tramyocastor majus*

Rusconi 1945, both recovered from Late Miocene sediments of Argentina, which are known by scarce remains. *Tramyocastor* (Fig. 7B) is distinguished from *Myocastor* by having cheek teeth about half the size of those of *Myocastor*, and flexi/flexids less deep (Rusconi, 1936: 1). As in *M. coypus*, the lower molars of *Tramyocastor* are tetralophodont, with less persistent lingual flexids (they transform into fossetids much more quickly) with respect to the hypoflexid than in living species, but more persistent than in *Paramyocastor*. In the m3 of *Tramyocastor* the hypoflexid is connected with the metaflexid/metafossetid in adult specimens, whereas this connection is only present in the youngest specimens of *Myocastor*. The upper molars are pentalophodont. M3/m3 are longer than M2/m2, as in *M. coypus*.

#### PHYLOGENETIC ANALYSES

Here, following a 'dynamic' approach through parsimony analysis, we evaluate the testing of alternative hypotheses of primary homology for crown structures, according to that which produces the more congruent results (Rieppel, 1996). From this perspective, one of the principal objectives of this approach is to evaluate how characters involved in the alternative hypotheses of primary homology influence the most parsimonious trees obtained, and how these characters evolved (see Discussion).

In this context, to test alternative hypotheses of primary homology we made two phylogenetic analyses (see Material and methods): analysis I, following the hypothesis of homologies of Carvalho & Salles (2004), and analysis II, applying the hypothesis of homologies proposed herein. In successive sections we first analyse the characters used in these two analyses (see Character analysis), and then comparatively evaluate the alternative primary statements in the light of the resultant phylogenetic trees (see Results and Discussion).

#### CHARACTER ANALYSIS

The characters of dp4 involved in the alternative homology hypotheses, being scored differently in both analyses, are characters 1–5 in analysis I (Table 1), lifted exactly from the original formulation in Carvalho & Salles (2004), and scored as in the original data set (Carvalho & Salles, 2004: table 2), and characters 1–5 in analysis II (Table 2), redefined according to the homology hypothesis proposed herein.

The lower molar characters involved in the alternative homology hypotheses, being scored differently in both analyses, are characters 13–15 in analysis I, exactly as originally formulated by Carvalho & Salles

(2004), and characters 13 and 14 in analysis II, redefined in terms of our homology hypotheses.

The remaining characters were taken from the Carvalho & Salles' (2004) study (see the Appendix), and are identically scored in both data sets (Tables 1 and 2). Characters that were recoded with respect to the original data (Carvalho & Salles, 2004) were discussed in each case. One character not previously considered was added in both analyses (i.e. character 51 in analysis I = character 50 in analysis II; see Appendix). Character states scored in the fossil taxa *Tramyocastor* and *Paramyocastor* are discussed in detail.

#### DP4 CHARACTERS – ANALYSIS I (TABLE 1)

1. dp4; central (= labial) portion of neolophid (*sensu* Carvalho & Salles, 2004): (0) present; (1) absent.

Following the hypothesis of homologies of Carvalho & Salles (2004), the second anteriormost lophid in pentalophodont dp4 corresponds to the neolophid (Fig. 4A), which is represented by two portions: the central portion, extended posterolingually from the most anterior lophid, and the lingual portion. As they proposed, the central portion is considered to be present when it is directly observed as a distinct structure, or when it is interpreted to be part of a continuous neolophid or part of 'crest C' (*sensu* Carvalho & Salles, 2004; i.e. central portion of neolophid + metalophid or third lophid; Fig. 4C). Thus, as in Carvalho & Salles (2004: table 2), *Hoplomys*, *Mesomys*, *Lonchothrix*, most species of *Proechimys*, *Isothrix*, *Echimys chrysurus*, *Phyllomys*, *Diplomys*, *Makalata didelphoides*, *Makalata grandis*, *Myocastor coypus*, and the extinct *Maruchito trilofodonte*, all displaying pentalophodont dp4, are scored as 0 (see Table 1). *Paramyocastor* is also scored as 0, in spite of the central portion, at least in some specimens, being not completely connected to the first lophid in at least some juvenile specimens (see Candela *et al.*, 2007; Fig. 3D). Taxa with 'crest C', as in most species of *Trinomys*, are also scored as 0. As in Carvalho & Salles (2004), *Proechimys cf. brevicauda* (Gunther, 1877), *Proechimys riparum* Moojen, 1948, *Thrichomys*, *'Echimys' semivillosus*, *Callistomys*, *Kannabateomys*, *Dactylomys*, *Olallamys*, and the extinct *Eumysops*, all with tetralophodont dp4, without 'crest C' (Fig. 4B), are scored as 1.

2. dp4, lingual portion of neolophid: (0) present; (1) absent.

All analysed taxa are scored as in Carvalho & Salles (2004: table 2) (see Table 1). The lingual portion of the neolophid (state 0) is found in taxa with pentalophodont dp4. Thus *Hoplomys*, *Mesomys*, *Lonchothrix*, most of the species of *Proechimys*, *Isothrix*, *Phyllomys*, *Diplomys*, *Makalata didelphoides*, *Makalata grandis*, *Myocastor coypus*, and the extinct *Maruchito*

*trilofodonte* are scored as 0. *Paramyocastor* is also scored as 0. Taxa with tetralophodont dp4, without the lingual portion of the neolophid, such as *Eumysops*, *Thrichomys*, *Kannabateomys*, *Euryzygomatomys*, *Clyomys*, and most of the species of *Trinomys*, are scored as 1.

3. dp4, medial contact between the central portion of neolophid and other crown structures: (0) already in contact with the lingual portion of neolophid (forming a continuous neolophid) in little or non-worn teeth; (1) contact with the lingual portion of neolophid only present after considerable wear; (2) already in contact with the metalophid (forming crest C) in little or non-worn teeth; (3) contact with the metalophid only present after considerable wear; (4) no contact observed.

All taxa analysed are scored as in Carvalho & Salles (2004: table 2). Taxa with pentalophodont dp4, such as *Hoplomys*, *Mesomys*, and *Lonchothrix* are scored as 0. *Paramyocastor* is also scored as 0. Following this hypothesis, in pentalophodont dp4, the third lophid corresponds to the metalophid, often making contact with the ectolophid (Fig. 4A). Taxa with tetralophodont dp4 show two possible states for this character. If the central portion of the neolophid is absent (character 1, state 1), this character is scored as non-applicable (–), as in *Thrichomys*, *Eumysops*, *Callistomys*, *Kannabateomys*, *Dactylomys*, *Olallamys*, and *'Echimys' semivillosus*. In this pattern, the second lophid corresponds to the metalophid (Fig. 4B). On the other hand, when the central portion of neolophid is part of the 'crest C' (Fig. 4C), i.e. connected with the anteriorly oriented metalophid, taxa with this pattern, as with most species of *Trinomys*, are scored as 2 (Table 1). *Euryzygomatomys* and *Clyomys* are scored as 3. *Carterodon* is the only taxon in which no contact is observed (state 4). In taxa with 'crest C', the lingual portion of the neolophid is absent (character 2, state 1). Therefore, it is possible to suppose the logical dependency of character 3 with character 1. In addition, their logical dependency with character 5 is also suspected (see below). So, we exclude this character in the final analysis and evaluate the sensitivity of the results to their inclusion/exclusion (see results).

4. dp4, metalophid: (0) present; (1) absent.

According to the hypotheses of homology of Carvalho & Salles (2004), the third lophid in pentalophodont dp4 is the metalophid. Their presence (state 0) may be either directly observed or assumed in specimens that have 'crest C'. In the available sample this character is non-informative.

5. dp4, medial contact between metalophid and ectolophid/protoconid region: (0) in contact in little or non-worn teeth; (1) contact only present after considerable wear; (2) no contact observed.

The metalophid (*sensu* Carvalho & Salles, 2004) is either connected to the ectolophid or connected with the central portion of the neolophid, forming 'crest C'. As Carvalho & Salles (2004: 455) supposed, 'the presence of one of these contacts almost excludes the presence of the other. However, as both contacts were observed for some taxa (e.g. *Clyomys*), they are at least partially independent, and were considered as separate characters. Thus, following these authors, this character is considered independent from character 3. As in the original data set *Pampamys*, *Maruchito* and *Eumysops* are scored as 0. *Paramyocastor* is also scored as 0. Taxa with 'crest C' are scored as 2, *Clyomys* are scored as 1, and *Theridomysops* is scored as unknown.

#### PENTA- AND TETRALOPHODONTY OF THE DP4 EXPRESSED AS CHARACTER STATES

From an atomistic viewpoint, and following the hypothesis of correspondences proposed by Carvalho & Salles (2004), the penta- and tetralophodonty can be expressed as sets of character states, corresponding to characters 1–5 (Table 1). Echimyids with pentalophodont dp4, such as *Hoplomys*, *Mesomys*, *Lonchothrix*, most of the species of *Proechimys*, *Isothrix*, *Echimys chrysurus*, *Phyllomys*, *Diplomys*, *Myocastor coypus*, and the extinct *Maruchito trilofodonte* and *Paramyocastor* are scored as 00000 (see Table 1), exactly as in Carvalho & Salles (2004: table 2). *Makalata didelphoides* and *Makalata grandis* were scored as 00100.

Following the identifications of Carvalho & Salles (2004), two tetralophodont patterns are recognized.

1. Pattern I, with the second lophid, i.e. metalophid *sensu* Carvalho & Salles (2004), transversally oriented with respect to the anteroposterior axis of the tooth (Fig. 4B), and the neolophid absent, such as in '*Echimys*' *semivillosus*, *Thrichomys*, *Callistomys*, *Kannabateomys*, *Dactylomys*, *Olallamys*, and the extinct *Eumysops*. Consequently in analysis-I echimyids with this pattern are scored as 11–00 for characters 1–5 listed above, respectively (Table 1), exactly as in Carvalho & Salles (2004: Table 2).
2. Pattern II (Fig. 4C) shows the second lophid obliquely oriented, forming 'crest C', such as in most species of *Trinomys*. Accordingly, taxa with this pattern are scored as 01202 (as in species of *Trinomys*). *Euryzygomatomys* is scored as 01302 and *Clyomys* is scored as 01301.

#### DP4 CHARACTERS – ANALYSIS II (TABLE 2)

Characters 1–5 of dp4 listed above are redefined to be included in the second analysis, following the hypothesis of primary homologies proposed herein.

1. dp4, labial (= central) portion of metalophid II: (0) present; (1) absent.

According to the hypothesis of homology proposed herein, the neolophid in caviomorphs is only present in hexalophodont dp4 (see above), such as certain erethizontids (Candela, 2003). We consider that the second lophid in position in pentalophodont dp4 does not correspond to the neolophid (see character 1 of analysis I), but instead corresponds to the metalophid II, which is frequently represented by labial and lingual portions, more evident during early stages of wear. The lingual portion is present in penta- as well as in tetralophodont patterns. Thus, the pentalophodont echimyids, such as *Hoplomys*, *Mesomys*, *Lonchothrix*, extinct *Maruchito trilofodonte* and *Paramyocastor* are scored as 0, like taxa with tetralophodont dp4, such as *Thrichomys*, '*Echimys*' *semivillosus*, *Callistomys*, *Kannabateomys*, *Dactylomys*, *Olallamys*, several species of *Trinomys*, and the extinct *Eumysops*. In the case of *Tramyocastor* this character is not available (?). Only *Trinomys albispinus* (I. Geoffroy, 1838) is scored as 1, making this character non-informative in the context of echimyids analysed. Anyway, we prefer to retain this character to facilitate the comparison between analyses I and II and that of Carvalho & Salles (2004).

2. dp4, lingual portion of metalophid II: (0) present; (1) reduced or absent.

Among the taxa analysed, only *Euryzygomatomys*, *Clyomys*, *Carterodon*, and the extinct *Theridomysops* are scored as 1.

3. dp4, medial contact between the central and lingual portions of metalophid II: (0) already in contact with the lingual portion of metalophid II (forming a continuous metalophid II) in little or non-worn teeth; (1) contact with the lingual portion of metalophid II only present after considerable wear.

Character 3 is here redefined considering that the second lophid, in penta- as well as in tetralophodont dp4, is metalophid II. Thus, the presence of a mixed structure, i.e. 'crest C', is not recognized here. According to this hypothesis, states 2–4 that were considered for character 3 in analysis I are not pertinent in this analysis. Even considering only two states for this character (see above), this continues to be a problematic character. In fact, contact between portions of metalophid II depend not only on tooth wear, but also on the degree of the development of these portions. In addition when the lingual portion of metalophid II is very reduced or absent, as in *Euryzygomatomys* (see character 2, state 1), character 3 is non-applicable (Table 2). As in analysis I, we exclude this character in the posterior analysis (but it is included in the data matrix to facilitate comparisons; Table 2).

4. dp4, mesolophid: (0) present; (1) absent.

According to the hypothesis proposed herein, the third lophid in position in pentalophodont dp4 is the mesolophid (not the metalophid, see character 4 analysis I), which is absent (state 1) in tetralophodont forms.

5. dp4, metalophulid II: (0) transversally oriented; (1) obliquely oriented from the protoconid region or metalophulid I.

This character is redefined following the alternative hypothesis of homology, so that it now presents two conditions, which undoubtedly are logically independent of character 3, as was suspected in the first analysis. Taxa with penta- (e.g. *Myocastor coypus*, *Paramyocastor*, *Mesomys*, *Lonchothrix*, and *Hoplomys*) and tetralophodont patterns (e.g. *Thrichomys*, *Eumysops*, and *Callistomys*), with metalophulid II transversally orientated, are scored as 0 (Table 2). Taxa with a tetralophodont pattern, with metalophulid II associated with the posterior face of metalophulid I or the protoconid region, obliquely oriented, and more or less curved in shape, like most species of *Trinomys*, are scored as 1. *Euryzygomatomys* and *Theridomysops* are also scored as 1, considering the orientation of the central portion. Here, the second lophid is considered to be metalophulid II in all tetralophodont patterns.

#### PENTA- AND TETRALOPHODONTY OF DP4 EXPRESSED AS CHARACTER STATES

Following the hypothesis of correspondences proposed here, penta- and tetralophodonty can be expressed as sets of character states corresponding to characters 1–5 listed above (Table 2). In agreement with these character states the pentalophodont pattern, such as that of *Myocastor coypus*, *Hoplomys*, *Mesomys*, *Lonchothrix*, *Maruchito*, *Proechimys semipinosus*, and the extinct *Paramyocastor*, is expressed by character states 00000 for characters 1–5, respectively (Table 2). Note that in both analyses, I and II, the pentalophodonty is represented by the same five character states, although reflecting different hypotheses of primary homologies. Pentalophodont dp4 of *Makalata didelphoides* and *Makalata grandis* (*sensu* Emmons, 2005; but see Iack-Ximenes, de Vivo & Percequillo, 2005) were scored as 00100.

Taxa with tetralophodont dp4, with metalophulid II transversally oriented with respect to the transverse axis of the teeth (pattern I; Fig. 4E), such as *Thrichomys*, '*Echimys*' *semivillosus*, *Callistomys*, *Kannabateomys*, *Dactylomys*, and *Eumysops* are scored as 00010 for characters 1–5 listed above (Table 2).

The tetralophodont pattern with metalophulid II associated with the posterior face of metalophulid I

or protoconid, and obliquely oriented (pattern II; Fig. 4F), as most species of *Trinomys*, is expressed by character states 00011 for characters 1–5 as described above (Table 2). Taxa with the lingual portion of metalophulid II reduced or absent and the labial portion obliquely oriented, as in *Euryzygomatomys*, *Clyomys*, and *Carterodon*, and in the extinct *Theridomysops*, are scored as 01–11. Under this hypothesis the second lophid in all tetralophodont dp4 is metalophulid II.

#### LOWER MOLAR CHARACTERS – ANALYSIS I (TABLE 1)

13. m1–m3, central portion of neolophid: (0) present; (1) absent.

Following the hypothesis of homology of Carvalho & Salles (2004), the central portion of neolophid would be present in the pentalophodont *Hoplomys*, and in tetralophodont patterns with 'crest C'. *Hoplomys*, *Mesomys*, *Proechimys* spp., and most of the species of *Trinomys* are scored as 0. *Lonchothrix* is scored as polymorphic, as in original data from Carvalho & Salles (2004). The remaining taxa, including the extinct *Pampamys*, *Eumysops*, *Theridomysops*, *Maruchito*, *Tramyocastor*, and *Paramyocastor*, are scored as 1 (Table 1).

14. m1–m3, medial contact between the central portion of neolophid and other crown structures: (0) contact with the lingual portion of neolophid (forming a continuous *neolophid*); (1) contact with the metalophid (forming crest C).

In the original analysis another state for character 14 is defined: (2) no contact observed. This is a condition that is only present in the extinct octodontoid *Migraveramus*; consequently, this latter state is not considered in analysis I. *Myocastor coypus*, *Tramyocastor*, and *Paramyocastor*, with tetralophodont lower molars and the metalophid oriented approximately perpendicular to the anteroposterior axis of the tooth, are scored as non-applicable (–). As in Carvalho & Salles (2004), taxa with 'crest C', such as *Lonchothrix*, *Proechimys*, and *Trinomys*, are scored as 1 (Table 1; Fig. 7). Dactylomyines, 'echimyines', living eumysopines, and the extinct *Pampamys*, *Eumysops*, *Theridomysops*, and *Maruchito*, with trilophodont lower molars (see Fig. 7), are scored as non-applicable (–). In the available sample it is a non-informative character (but is included in Table 1 to facilitate comparisons).

15. m1–m3, metalophid: (0) present; (1) absent.

According to Carvalho & Salles (2004), the metalophid is present in the tetralophodont molars, as in *Myocastor coypus*, with the metalophid oriented approximately perpendicular to the anteroposterior axis of the tooth, as well as in the tetralophodont patterns with 'crest C', such as those of *Mesomys*, *Proechimys*, and most species of *Trinomys*. *Paramyo-*



*castor* and *Tramyocastor* are scored as 0 because they have the same condition as *Myocastor coypus*. All taxa with trilophodont molars, such as those of the living Eumysopinae, 'Echimyinae', and Dactylomyinae, and the extinct *Pampamys*, *Eumysops*, *Theridomysops*, and *Maruchito*, are scored as 1, as in the analysis of Carvalho & Salles (2004).

#### PENTA-, TETRA-, AND TRILOPHODONTY OF LOWER MOLARS EXPRESSED AS CHARACTER STATES

Penta-, tetra-, and trilophodonty can be identified in the particular combination of the three character states corresponding to Carvalho & Salles' (2004) 'molar characters 13, 14, and 15', respectively. Pentalophodont pattern is expressed by character states 000. The tetralophodont pattern, such as that of *Myocastor coypus* (pattern I; Figs 6B and 7), is expressed by character states 1–0 ('-', non-applicable character) for characters 13, 14, and 15, respectively (Table 1). A tetralophodont pattern with 'crest C' (pattern II; Figs 6C and 7), such as those of *Mesomys*, *Proechimys*, and most species of *Trinomys*, is expressed by character states 010 for characters 13, 14, and 15 mentioned above (Table 1). Taxa with three lophids, such as *Clyomys*, *Euryzygomatomys*, *Carterodon*, and *Thrichomys*, and living Echimyinae and Dactylomyinae *Isothrix*, *Callistomys*, *Makalata*, '*Echimys*' *semivillosus*, *Santamartamys* (Emmons, 2005), *Makalata grandis*, *Phyllomys*, *Diplomys* (Emmons, 2005), *Kannabateomys*, *Dactylomys*, and *Olallamys*, are scored as 1–1 (Fig. 7; Table 1).

#### LOWER MOLAR CHARACTERS – ANALYSIS II (TABLE 2)

According to this new hypothesis of primary homologies, characters 13, 14, and 15 are redefined.

13. m1–m3, neolophid: (0) absent; (1) present.

This character now involves the complete neolophid (not just the central portion). According to our hypothesis, the neolophid is only present in pentalophodont lower molars, such as in *Hoplomys* and certain erethizontids. Among the echimyids only *Hoplomys* is scored as 1. Thus, it is a non-informative character. We prefer to retain this character to facilitate the comparison concerning homology hypotheses between analyses I and II and that of Carvalho & Salles (2004).

14. m1–m3, metalophulid II: (0) transversally oriented; (1) obliquely oriented and associated with the posterior face of metalophulid I or with the protoconid region, and obliquely oriented and curved in shape (taking the orientation and position of 'crest C'); (2) reduced or absent. (Ordered.)

This character involves characters 14 and 15 of Carvalho & Salles (2004), which are redefined as a single multistate character. Taxa with tetralophodont patterns, with metalophulid II transversally oriented (pattern I; Fig. 6E), such as that of *Myocastor coypus*, *Paramyocastor*, and *Tramyocastor*, are scored as 0 (Table 2; Fig. 7). Taxa with a tetralophodont pattern, with metalophulid II associated with the posterior face of metalophulid I or protoconid (pattern II; Fig. 6F), as in *Mesomys*, *Lonchothrix*, *Proechimys* spp., and most species of *Trinomys*, are scored as 1 (Fig. 7). Taxa with trilophodont lower molars, such as living Eumysopinae, 'Echimyinae', and Dactylomyinae, and extinct *Pampamys*, *Eumysops*, *Theridomysops*, and *Maruchito*, are scored as 2.

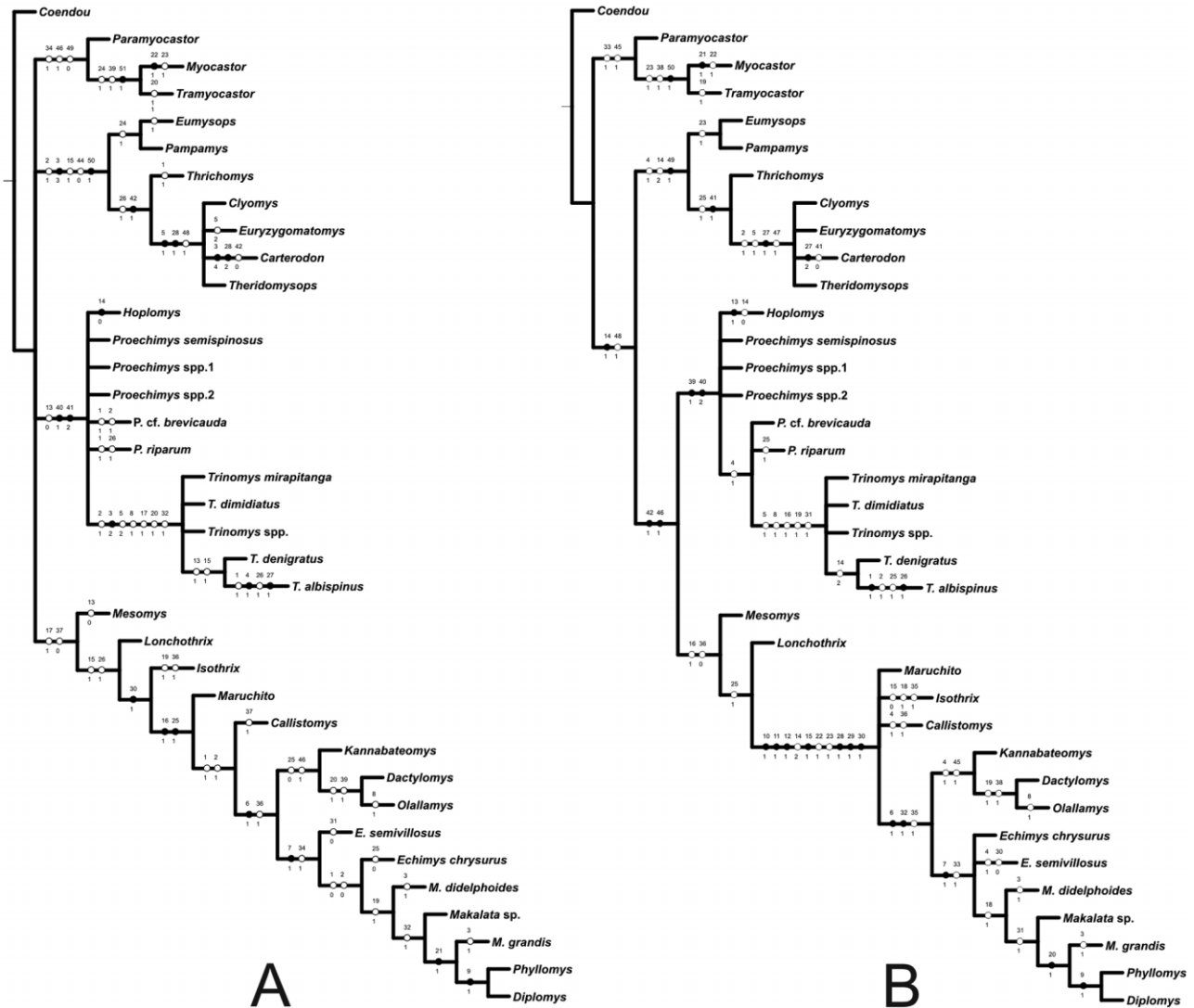
The extinct Miocene octodontoid *Willidewu* shows what was described as a 'capture' process of the second lophid by the first one (Vucetich & Verzi, 1991; Fig. 8C). In m3, metalophulid II is closely connected to the first lophid, and in others metalophulid II is not distinguishable. Conditions observed in *Willidewu*, besides those observed in certain specimens of *Proechimys*, justify the consideration of this character as an ordered multistate character. Polarity of this character and the inferred evolution of metalophulid II is discussed below (Tooth evolution).

#### PENTA-, TETRA-, AND TRILOPHODONTY OF LOWER MOLARS EXPRESSED AS CHARACTER STATES

Only *Hoplomys*, with pentalophodont lower molars is scored as 10 (Fig. 6D). Taxa with tetralophodont lower molars, with metalophulid II transversally oriented (pattern I; Fig. 6E), such as that of *Myocastor coypus*, *Paramyocastor*, and *Tramyocastor*, are scored as 00 for characters 13 and 14, respectively (Table 2). Taxa with tetralophodont patterns, with metalophulid II associated with the posterior face of metalophulid I (pattern II, Fig. 6F), such as those of *Mesomys*, *Lonchothrix*, *Proechimys* spp. and most species of *Trinomys*, are scored as 01. Taxa with trilophodont patterns, such as those of the living Eumysopinae *Clyomys*, *Euryzygomatomys*, *Carterodon*, and *Thrichomys*, and the living 'Echimyinae' and Dactylomyinae *Isothrix*, *Callistomys*, *Makalata*, *Pattonomys*, *Echimys*, *Santamartamys*, *Toromys* (*sensu* Iack-Ximenes, de Vivo & Percequillo, 2005; = *Makalata sensu* Emmons, 2005), *Phyllomys*, *Diplomys*, *Kannabateomys*, *Dactylomys*, and *Olallamys*, are scored as 02.

#### RESULTS FROM PHYLOGENETIC ANALYSES

Analysis I, including 37 terminal taxa and 51 characters (Table 1), resulted in 50 most parsimonious trees



**Figure 9.** A, strict consensus from 50 MPTs obtained from Analysis I; B, strict consensus from 9 MPTs obtained from Analysis II. Only unambiguous synapomorphies are shown.

(MPTs) of 98 steps. The strict consensus (Fig. 9A) shows four clades emerging from the basal polytomy. One of these clades includes *Paramyocastor* as sister taxon of the *Myocastor*–*Tramyocastor* clade. Another clade groups the extinct *Pampamys*–*Eumysops* clade as sister taxon of *Thrichomys* (*Clyomys* and *Euryzgomatomys*–*Carterodon*–*Theridomysops*) clade. A third clade includes the species of *Proechimys*, *Hoplomys*, and *Trinomys*. In the fourth clade, *Mesomys*, *Lonchothrix*, *Isothrix*, and *Maruchito* emerge as successive sister taxa of the extant dactylomyines and ‘echimyines’. Within this clade, *Callistomys* appears as the most basal taxon, and dactylomyines and the remaining echimyines appear as sister taxa to each other.

When character 3 was excluded (see Character analysis) analysis I also resulted in 50 MPTs, each of

93 steps. The strict consensus of these trees is the same that that obtained including character 3 (Fig. 9A).

Analysis II, following the homologies proposed here, including character 3 (37 terminal taxa and 50 characters), resulted in the recovery of nine MPTs, each of 89 steps. The strict consensus of these trees is shown in Figure 9B. Because of problems of logical dependence, this analysis was additionally performed without character 3 (37 terminal taxa and 49 characters), resulting in the recovery of nine MPTs, each of 87 steps. The strict consensus of the nine MPTs and unambiguous common character state optimizations are depicted in Figure 9B. Note that the nine MPTs obtained from analysis II have less steps than those obtained from analysis I. This indicates that the MPTs obtained from analysis II, which represent the trees

that minimize the global sum of transformations over all characters, should be selected instead of those obtained from analysis I. Therefore, phylogenies obtained from analysis II can be regarded as representing those best supported by observations. The strict consensus tree (Fig. 9B) indicates a *Paramyocastor* (*Tramyocastor*–*Myocastor*) clade supported by two unambiguous synapomorphies (see Fig. 9B), thereby justifying their taxonomic assignment to Myocastorinae, which appears as the sister taxon of the remaining echimyids analysed. Among these, three main clades are recovered, as in analysis I. One of them groups the *Pampamys*–*Eumysops* clade as the sister taxon of the clade depicting *Thrichomys* as sister of the *Theridomysops*–*Clyomys*–*Euryzygomatomys*–*Carterodon* clade, which appears as unresolved in the consensus tree. Thus, the most parsimonious hypothesis of this analysis depicts the Eumysopinae as a monophyletic group (supported by two unambiguous synapomorphies; see Fig. 9B), including the extinct *Eumysops*, *Theridomysops*, and *Pampamys*. This result is congruent with previous proposals that place *Eumysops*, *Pampamys*, and *Theridomysops* as closely related to living Eumysopinae (see Discussion). The other main clade includes *Hoplomys*, the species of *Proechimys*, and a clade with the species of *Trinomys*. Another clade groups *Mesomys* and *Lonchothrix* as successive sister taxa of the clade including *Isothrix*, *Maruchito*, and *Callistomys*, plus the clade that groups dactylomyine and the remaining ‘Echimyines’. Note that the four main groups depicted in the consensus of the optimal trees in analysis II are the same as the four main groups obtained in the consensus found in analysis I. Topologies of Myocastorinae and Eumysopinae obtained from analysis II are identical with that recovered in analysis I.

## DISCUSSION

Hypotheses of primary homologies used in analysis II may be considered as those that produce most parsimonious results (see above). The common mapping of dental characters on the consensus of analysis II allows us to identify the ancestral dp4 and lower molar conditions of the Echimyidae, and to evaluate the evolutionary transformations of the crown structures they imply (Ramírez, 2007). Although the results from Analysis II are those that best explain the observations, alternative schemes of correspondences are evaluated in order to compare the level of change that each one requires.

### EVOLUTION OF DP4: PENTA- AND TETRALOPHODONTY

#### *Analysis I*

The optimization of character 1 (presence/absence of central portion of ‘neolophid’) produces seven steps

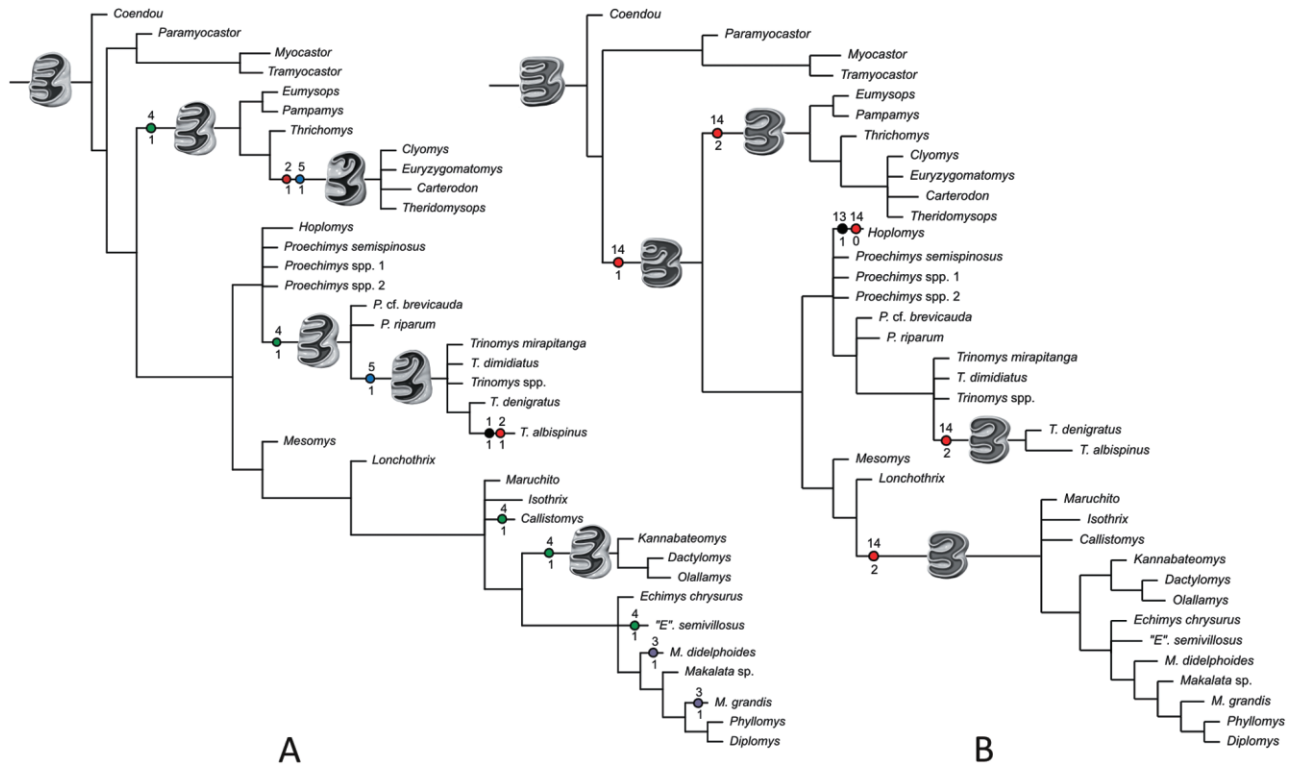
(Fig. 9A). It indicates that it is lost independently in *Eumysops*, *Thrichomys*, *Proechimys riparum*, *P. cf. brevicauda*, and *Trinomys albispinus*. The central portion is also lost in the clade that includes Dactylomyinae and ‘Echimyinae’, and within this clade it is successively acquired (state 0) in the clade that includes *Echimys chrysurus*, *Phyllomys*, *Diplomys*, and *Makalata* spp. It is possible that this newly acquired structure is not homologous with the central portion of the neolophid. Optimization of character 2 (presence/absence of lingual portion of neolophid) indicates that it is lost independently in several taxa (five steps). As with character 1, successive losses and acquisitions of this character expresses implausible transformation events for this structure. The optimization of character 3 (contact between central portion of neolophid and other crown structures, which is eliminated from the final results) produces five steps. It is a problematic character with cases of non-applicable states. When the central portion of the neolophid is absent, all its subsidiary characters are non-applicable. Thus, illogical optimization results for this character (Maddison, 1993), assuming the connection of neolophid with other structures in *Eumysops*, *Thrichomys*, *Theridomysops*, *Callistomys*, dactylomyinae, and ‘*Echimys*’ *semivillosus*, when in fact the neolophid is absent in these taxa. Optimization of character 4 is noninformative, but we maintain it in order to evaluate the evolution of the penta- and tetralophodont dp4 patterns following the hypotheses of correspondence used in analysis I. The optimization of character 5 produces three steps, indicating that contact between the metalophid and the ectolophid/protoconid region is the plesiomorphic condition.

In sum, optimizations of the five first dp4 characters involved in the primary homology hypotheses used in analysis I results in 21 steps. Illogical optimization (character 3) and successive loss and acquisition of the same structure yield not completely adequate transformation costs.

#### *Analysis II*

Optimizations of the five first dp4 characters involved in the homology hypotheses used in analysis II (Fig. 10A) result in lesser events of evolutionary transformations (12 steps) than in analysis I. Cases of inapplicability are less than in analysis I, and successive losses and acquisitions of the same character state are not detected. Therefore, the hypotheses of correspondences involved in analysis II minimize the events of evolutionary transformations and result in more reasonable evolutionary changes than in the first analysis.

Character 1 (presence/absence of central portion of metalophid II) is a non-informative character, but we



**Figure 10.** Common mapping of characters 1-5 (A) and 13-14 (B) on the strict consensus obtained from Analysis II, showing evolution of dp4 (A), and lower molar (B) patterns.

maintain this character to show that the central portion of metalophulid II is a conservative structure, only lost in *Trinomys albispinus*. Optimization of character 2 (presence/absence of the lingual portion of metalophulid II) produces two steps. This portion is lost independently in the *Theridomysops*–*Clyomys*–*Euryzygomatomys*–*Carterodon* clade and in *Trinomys albispinus*. Optimization of this character indicates plausible transformation events involved in the simplification of dp4. Optimization of character 3 (contact between the central and lingual portions of metalophulid II, which is eliminated from the final results) produces two steps. It is a problematic character with cases of non-applicable states (Maddison, 1993). When the lingual portion of metalophulid II is absent, all its subsidiary characters are non-applicable. Illogical optimization of this character assumes the connection of central and labial portions of metalophulid II in the clade that includes *Euryzygomatomys*, *Theridomysops*, *Carterodon*, and *Clyomys*, when in fact the lingual portion of this lophid is absent in these taxa. Optimization of character 4 (presence/absence of mesolophid) produces five steps. It indicates that the mesolophid is independently lost in the clade that includes *Eumysops*, *Pampamys*, *Thrichomys*, *Euryzygomatomys*, *Clyomys*, *Theridomysops*, and *Carterodon*, in the clade that comprises two species of *Proechimys* and

*Trinomys* spp., in the *Dactylominyae* clade, in *Callistomys*, and in '*Echimyus*' *semivillosus*. Optimization of this character indicates that the simplification by loss of mesolophid occurred several times in the echimyids. Optimization of character 5, concerning the orientation of metalophulid II, produces two steps. It indicates that a metalophulid II obliquely oriented is a synapomorphy of the *Theridomysops*–*Euryzygomatomys*–*Clyomys*–*Carterodon* clade and of the clade that groups species of *Trinomys*.

The common optimization of these characters on MPTs (Fig. 10A) indicates that pentalophodonty would be the ancestral condition for echimid dp4, and that tetralophodonty was independently acquired in different clades. Pentolophodonty was also recognized as the ancestral condition of erethizontids (Candela, 2002). In turn, according to this analysis, the tetralophodont pattern with transverse metalophulid II (character 5, state 0) would have evolved towards one pattern, with metalophulid II obliquely united to metalophulid I (character 5, state 1), which is present in most of species of *Trinomys*. The tetralophodont pattern with transverse metalophulid II also appears as the condition antecedent to the acquisition of the pattern of the *Clyomys*–*Euryzygomatomys*–*Carterodon*–*Theridomysops* clade, which has the central portion of metalophulid II obliquely oriented.

## EVOLUTION OF THE LOWER MOLARS: PENTA-, TETRA-, AND TRILOPHODONTY

*Analysis I*

The optimization of character 13 (presence/absence of central portion of neolophid) produces three steps. It appears independently in *Hoplomys* and, forming 'crest C', in the clade that groups *Proechimys* and *Trinomys* species, and in *Mesomys* (Fig. 9A). Character 14 (contact between the central portion of neolophid and other crown structures) is a non-informative character, and is a problematic character with the cases of non-applicable states (Maddison, 1993), assuming the connection of the neolophid with other structures, when in fact the neolophid is absent (trilophodont taxa). Character 15 produces three steps, and indicates that trilophodonty (character 15, state 1) appeared independently in the *Trinomys denigratus*–*Trinomys albispinus* clade, in the ((*Pampamys*–*Eumysops*) *Thrichomys* (*Clyomys*–*Euryzygomatomys*–*Carterodon*–*Theridomysops*)) clade, and in dactylomyines and 'echimyines'. Tetralophodonty would be the primitive condition of Echimyidae. From the tetralophodont pattern, trilophodonty evolved independently several times within Echimyidae. Tetralophodonty evolved for the acquisition of the neolophid towards one pattern with crest C, and towards the pentalophodonty of *Hoplomys*.

*Analysis II*

The common optimization of lower dental characters 13 (absence/presence of neolophid) and 14 (concerning the development and orientation of metalophulid II) on the MPTs (see Fig. 10B) indicates that the tetralophodont pattern with metalophulid II transversally oriented (pattern I) would be the ancestral condition for the Echimyidae. It is in agreement with the ancestral pattern present in basal Hystricognathiformes (such as 'Baluchimyinae' and extinct African Hystricognathi; see Marivaux *et al.*, 2004). Tetralophodonty was also recognized as the ancestral condition to the erethizontids (Candela, 2000). Among the Echimyidae analysed, this condition (character 13, state 0; character 14, state 0) is present in *Paramyocastor*, *Myocastor*, and *Tramyocastor*. In some extinct octodontoids (e.g. *Acarechimys*, *Galileomys*, and *Plesiacaechimys*; Fig. 8) metalophulid II shows diverse degrees of development, as it occurs in some basal Hystricognathiformes (Marivaux *et al.*, 2004). The optimization of character 14 (Fig. 10B) indicates that the tetralophodont pattern with transverse metalophulid II (character 14, state 0) evolved towards one occlusal morphology, with metalophulid II united to metalophulid I, and obliquely oriented (character 14, state 1), which is present in *Proechimys*, *Mesomys*, and *Lonchothrix*, and in most

species of *Trinomys*. From this tetralophodont pattern, trilophodonty (character 14, state 2) evolved independently in the *Trinomys denigratus*–*Trinomys albispinus* clade, in the ((*Pampamys*–*Eumysops*) (*Thrichomys*(*Clyomys*–*Euryzygomatomys*–*Carterodon*–*Theridomysops*)) clade, in the clade that includes *Isothrix*, *Maruchito*, *Callistomys*, and Dactylomyinae, and in the clade that groups *Echimys*, *Makalata*, *Diplomys*, and *Phyllomys*. Therefore, the tetralophodont pattern with metalophulid II obliquely oriented (pattern II) is revealed as the condition prior to the acquisition of trilophodonty (Fig. 10B). So, metalophulid II would have evolved from transverse towards oblique orientation, and towards absence. The molar pattern of certain fossil octodontoids illustrates this evolutionary transformation, expressing even intermediate conditions (not contemplated in the cladistic analysis). In the Oligocene *Sallamys* (Lavocat, 1976), for instance, a 'capture' process of metalophulid II by metalophulid I before loss can be observed.

As mentioned above, in *Willidewu* (Fig. 8) metalophulid II in the m3 is very close to metalophulid I, being almost fused, such as in m1–m2, in which metalophulid II is a non-distinguishable structure. The case of *Willidewu* illustrates how a trilophodont pattern in lower molars could be acquired, showing a rearrangement of the connections of metalophulid II (Vucetich & Verzi, 1991). In some forms of the Late Miocene this process of evolutionary transformation would have been completed with the acquisition of trilophodonty, as in *Pampamys* or *Theridomysops*. This series of transformation is logical and consistent with the phylogeny. Intermediate morphology resulted as a plausible evolutionary intermediate condition in the phylogeny, providing adequate transformations for tooth characters.

On the other hand, the pentalophodonty in lower molars of Echimyidae is the least usual condition, which results from the acquisition of the neolophid (character 13, state 1), in this sample present only in *Hoplomys*. Among extinct octodontoids, *Migraveramus* presents a small neolophid.

In sum, the hypotheses of correspondences used in analysis II result in plausible transformations of lower molar characters that are consistent with the information provided by fossil forms. Unlike analysis I, cases of inapplicability are not identified.

## PHYLOGENETIC RELATIONSHIPS

The main aim in this work was not to determine the relationships of Echimyidae, but to evaluate how assuming a specific primary homology a priori may modify the obtainment of more parsimonious recon-

structions. Nonetheless, it is important to discuss some of the results obtained in relation to previous phylogenetic hypotheses.

Our results (Fig. 9B) support the association of *Myocastor* with *Tramyocastor* and *Paramyocastor*, as previously considered (e.g. Candela *et al.*, 2007). This clade (Myocastorinae s.s., according to this study) is supported by two unambiguous synapomorphies (character 33, state 1; character 54, state 1). *Paramyocastor* appears as the sister taxon to the *Tramyocastor*–*Myocastor* clade, which is supported by three unambiguous synapomorphies (character 23, state 1; character 38, state 1; character 50, state 1). In this analysis Myocastorinae emerged as sister taxon of the remaining analysed. The inclusion of *Myocastor*, and associated fossil taxa, within the Echimyidae is not tested in this study, but is assumed following previous proposals (e.g. McKenna & Bell, 1997; Huchon & Douzery, 2001; Galewski *et al.*, 2005). Traditionally, three subfamilies were recognized within extant Echimyidae: Dactylomyiinae, Echimyinae, and Eumysopinae (=Heteropsomyinae according to some authors, e.g. Patterson & Pascual, 1968; McKenna & Bell, 1997; Emmons, 2005; see Carvalho & Salles, 2004 for a comprehensive historical background). Eumysopinae currently groups the extant *Euryzygomatomys*, *Clyomys*, *Carterodon*, *Thrichomys*, *Proechimys*, *Mesomys*, and *Lonchothrix*, and diverse fossil taxa, like *Eumysops*. However, the composition and monophyly of Eumysopinae have been questioned by several proposals (e.g. Vucetich & Verzi, 1991; Lara, Patton & da Silva, 1996; Leite & Patton, 2002; Carvalho & Salles, 2004). Contributions from Vucetich and co-workers have substantially increased the knowledge of the systematic and evolutionary history of fossil echimyids, in particular of the Eumysopinae from Argentina (e.g. Verzi *et al.*, 1994, 1995; Vucetich, 1995). Most of their proposals of phylogenetic relationships on fossil taxa are supported in this analysis. The extant *Clyomys*, *Euryzygomatomys*, *Carterodon*, and *Thrichomys*, and the fossil *Theridomysops*, emerge as a clade that is sister to the *Eumysops*–*Pampamys* clade. Thus, as proposed by Vucetich (1995), the extinct *Theridomysops* is recovered as a member of the clade that includes the living *Clyomys* and *Euryzygomatomys*. The extinct *Pampamys*, from the late Miocene of Argentina, and *Eumysops* would also be closer to eumysopines than the remaining echimyids (Verzi *et al.*, 1995). In sum, this study corroborates the close association of the extinct *Eumysops*, *Theridomysops* and *Pampamys* to the extant eumysopinae, regardless of the precise relationships among them. Although the phylogenetic analysis resulted in a resolved placement of *Pampamys* as sister taxon of *Eumysops*, these

results should be interpreted with caution. Relationships among extinct and extant eumysopines should be seen as tentative, subject to further revision for most of the character and taxon sampling of these forms. More complete remains of *Pampamys* and *Theridomysops*, for instance, would greatly improve our knowledge of phylogenetic affinities.

The extant *Hoplomys*, *Proechimys*, and *Trinomys* form a single group in this analysis (e.g. Patton & Reig, 1989; Carvalho & Salles, 2004), but it is located out of the Eumysopinae.

The association of *Mesomys* and *Lonchothrix* with echimyines and dactylomyines also supports previous proposals (Lara *et al.*, 1996; Leite & Patton, 2002; Carvalho & Salles, 2004). The supposedly resolved position of *Mesomys* and *Lonchothrix* as successive sister taxon to the remaining taxa needs to be revised. The extant genera *Callistomys* and *Isothrix* appear in a basal polytomy that also includes the fossil *Maruchito* and the ‘Echimyinae’–Dactylomyiinae clade. In most MPTs, the association of *Callistomys* and *Maruchito* is recovered, in agreement with Emmons & Vucetich (1998), who proposed that the two genera are closely related. Note that the genus *Isothrix* was considered of uncertain affinity, but provisionally retained within the Echimyinae by Emmons (2005).

In a recent molecular study, Galewski *et al.* (2005) pointed out that most of the extant echimyid genera appear to have diverged during the Middle Miocene. The relations of sister taxa of *Thrichomys* and the *Theridomysops*–*Clyomys*–*Euryzygomatomys*–*Carterodon* clade indicates that the lineage of *Thrichomys* would have been differentiated at least during the Late Miocene. In addition, the presence of *Myocastor* and *Tramyocastor* in the Late Miocene of Argentina (Candela & Noriega, 2004; Candela *et al.*, 2007) also indicates that the Late Miocene could be a strict minimum age for the origin of these genera. *Paramyocastor* and the *Myocastor*–*Tramyocastor* clade would have diverged very early, at least during the Late Miocene.

The phylogenetic position of *Maruchito*, recovered from the Middle Miocene, indicates an early differentiation, of at least Middle Miocene for the more basal nested extant *Mesomys*, *Lonchothrix*, and ancestor of the Dactylomyiinae–Echimyinae clade. This is in agreement with molecular data that suggest a Middle Miocene origin for most modern genera of echimyids (Galewski *et al.*, 2005). In sum, the phylogenetic analysis of extinct and extant echimyids produced results that were concordant with several traditional proposals and early times of divergence of extant genera proposed by molecular data.

## REMARKS AND CONCLUSIONS

A central debatable topic with respect to the use of dental characters in phylogenetic analyses concerns their independence, as these characters are connected both developmentally and functionally (e.g. Jernvall & Jung, 2000; Jernvall, Keränen & Thesleff, 2000; Kangas *et al.*, 2004; Kavanagh, Evans & Jernvall, 2007), and each tooth must be considered as an integrated whole. Paradoxically, the study of dental characters involves the deconstruction of teeth into fundamental elements, following an atomistic vision that entails an element of arbitrariness (see Rieppel, 1988 for a discussion on this matter). In caviomorphs in particular, their molar morphology, altered with respect to the typical tribosphenic morphology, is sometimes difficult to interpret. In fact, homologies of structures (cusps and loph/lophids) were largely debatable (e.g. Lavocat, 1976; Patterson & Wood, 1982; Candela, 2002; Frailey & Campbell, 2004). In addition, occlusal morphology may transform during tooth wear. This contributes to the absence of a comprehensive phylogeny of caviomorphs based on an integral set of dental characters, including fossil and extant taxa. In spite of this difficult scenario, we consider that dental characters (even those suspected of a lack of independence) can be included in phylogenetic analyses, and their supposed dependence evaluated a posteriori on the trees obtained (see Pol & Gasparini, 2009; Prevosti, 2010). At least in the context of our analysis, for instance, character states involved in trilophodonty can be interpreted as independent units of phylogenetic evidence, with trilophodonty showing different evolutionary histories. Several extinct octodontoids, reported from the ?Late Eocene–Early Oligocene (Frailey & Campbell, 2004; Vucetich *et al.*, 2010a), are mostly or only known by their teeth, with dental characters thus acquiring a noticeable value for reconstructing their evolutionary history. Among these rodents, certain taxa reveal the presence of well-differentiated cusps, even more than in living species, and exclusive connections between crown structures, pointing to the role of fossils in the identification of homologies. Morphological data and fossil records of this group should be taken into account to understand the evolutionary history of extant forms. Extinct *Tramyocastor* and *Paramyocastor* provide insight into the evolutionary sequence of dental characters of living *Myocastor*. Note that the molar evolutionary transformations that emerge from the phylogeny obtained in this study are logical and consistent with the information provided by fossils. Pentalophodont dp4 represents the plesiomorphic condition for echimyids. Tetralophodont dp4 would have been acquired at least during Late Miocene–Early Pliocene, when *Theridomysops* and *Eumysops*

are recovered. Trilophodont lower molars would have evolved independently at least three times during the evolutionary history of the Echimyidae. In the case of Eumysopine (*sensu* this study), trilophodonty would have been acquired at least as early as the Late Miocene, when *Theridomysops* and *Pampamys* first occur. In Eumysopinae, trilophodonty may be correlated with the climatic and environmental changes that occurred during the Late Miocene (Pascual, Ortiz Jaureguizar & Prado, 1996), but more studies are necessary to test this hypothesis.

We think that the identification of the crown structures (cusps and loph/lophids), based on a deep knowledge of dental occlusal morphology, continues to be a central recourse if we wish to understand the evolutionary history of the echimyids over more than 20 Myr in South America. A ‘dynamic’ approach is followed to select the ‘better primary homology hypothesis’ as that resulting in a more parsimonious evolution of characters (Rieppel, 1996). In this sense, results based on the hypotheses of correspondences followed in analysis II indicate a different view of certain dental characters used in analysis I.

We expect that this study will be useful for future phylogenetic analyses that integrate molecular data from extant echimyids with morphological data from fossil and extant taxa, and that a process of reciprocal illumination may test primary homology hypotheses. Yet, potential correlations between the evolution of dental features in octodontoids and the extrinsic selective forces that occurred during the Cenozoic are still to be analysed.

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## REFERENCES

- Ameghino F. 1902.** Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. *Boletín de la Academia Nacional de Ciencias en Córdoba* **17**: 71–138.
- Bryant JD, McKenna MC. 1995.** Cranial anatomy and phylogenetic position of *Tsaganomys altaicus* (Mammalia:

- Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. *American Museum Novitates* **3156**: 1–42.
- Candela AM. 1999.** The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity of *Parasteiromys* Ameghino 1904. *Palaeovertebrata* **28**: 53–73.
- Candela AM. 2000.** Los Erethizontidae (Rodentia, Hystricognathi) fósiles de Argentina, Sistemática e historia evolutiva y biogeográfica. Unpublished Ph. D. Thesis, Facultad de Ciencias Naturales y Museo.
- Candela AM. 2002.** Lower deciduous tooth homologies in Erethizontidae (Rodentia, Hystricognathi): evolutionary significance. *Acta Paleontologica Polonica* **47**: 717–723.
- Candela AM. 2003.** A new porcupine (Rodentia, Erethizontidae) from the early-middle Miocene of Patagonia. *Ameghiniana* **40**: 483–494.
- Candela AM. 2004.** A new giant porcupine (rodentia, erehizontidae) from the late Miocene of Argentina. *Journal of Vertebrate Paleontology* **24**: 732–741.
- Candela AM, Noriega JI. 2004.** Los coipos (Rodentia, Caviomorpha, Myocastoridae) del ‘Mesopotamiense’ (Mioceno tardío; Formación Ituzaingó) de la provincia de Entre Ríos, Argentina. In: Aceñolaza FG, eds. Temas de la Biodiversidad del Litoral fluvial argentino. *INSUGEO Miscelánea* **12**: 77–82.
- Candela AM, Noriega JI, Reguero MA. 2007.** The first Pliocene mammals from the northeast (mesopotamia) of Argentina: biostratigraphic and paleoenvironmental significance. *Journal of Vertebrate Paleontology* **27**: 476–483.
- Candela AM, Vucetich MG. 2002.** *Hypsosteiromys* (Rodentia, Hystricognathi) from the early Miocene of Patagonia (Argentina), the only Erethizontidae with a tendency to hypsodonty. *Geobios* **35**: 153–161.
- Carvalho GAS, Salles LO. 2004.** Relationships among extant and fossil echimyids (Rodentia: Hystricognathi). *Zoological Journal of the Linnean Society* **142**: 445–477.
- Cione AL, Azpelicueta MM, Bond M, Carlini AA, Casciotta JR, Cozzuol MA, de la Fuente MS, Gasparini Z, Goin FJ, Noriega JI, Scillato-Yané GJ, Soilbelzon L, Tonni EP, Verzi D, Vucetich MG. 2000.** Miocene vertebrates from Entre Ríos province, eastern Argentina. In: Aceñolaza FG, Herbst R, eds. El Mio-neógeno Argentino. *INSUGEO Serie Correlación Geológica* **14**: 191–237.
- Emmons LH. 2005.** A revision of the genera of arboreal Echimyidae (Rodentia: Echimyidae, Echimyinae), with descriptions of two new genera. In: Lacey EA, Myers P, eds. *Mammalian Diversification: From chromosomes to phylogeography*. Berkeley: University of California Press, 247–309.
- Emmons LH, Vucetich MG. 1998.** The identity of Winge’s *Lasiuromys villosus* and the description of a new genus of Echimyid Rodent (Rodentia: Echimyidae). *American Museum Novitates* **3223**: 1–12.
- Flynn LJ, Jacobs L, Cheema IU. 1986.** Baluchimyinae, a new Ctenodactyloid rodent subfamily from the Miocene of Baluchistan. *American Museum Novitates* **2841**: 1–58.
- Frailey C, Campbell K. 2004.** Paleogene rodents from Amazonian Peru: the Santa Rosa Local Fauna. In: Campbell KE, ed. *The paleogene mammalian fauna of Santa Rosa, Amazonian Peru*. Science Series 40. Los Angeles, CA: Natural history Museum of Los Angeles County, 71–130.
- Galewski T, Mauffrey J-F, Leite YLR, Patton JL, Douzery EJP. 2005.** Ecomorphological diversification among South American spiny rats (Rodentia; Echimyidae): a phylogenetic and chronological approach. *Molecular Phylogenetics and Evolution* **34**: 601–615.
- Goloboff PA, Farris JS, Nixon K. 2003.** T.N.T. Tree Analysis Using New Technology. Program & documentation available from the authors and Available at: <http://www.zmuc.dk/public/phylogeny/tnt>
- Hoffstetter R, Lavocat R. 1970.** Découverte dans le Déséadien de Bolivie des genres pentalophodontes appuyant les affinités africaines des Rongeurs Caviomorphes. *Comptes rendus des séances de l’Académie de Sciences, Paris* **271**: (Série D):172–175.
- Honeycutt RL, Frabotta LJ, Rowe DL. 2007.** Rodent evolution, phylogenetics, and biogeography. In: Wolff JO, Sherman P, eds. *Rodent societies: an ecological and evolutionary perspective*. Chicago, IL: University of Chicago Press, 8–13.
- Huchon D, Douzery EJP. 2001.** From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. *Molecular Phylogenetics and Evolution* **18**: 127–135.
- Iack-Ximenes GE, de Vivo M, Percequillo AR. 2005.** A new genus for *Loncheres grandis* Wagner, 1845, with taxonomic comments on other arboreal echimyids (Rodentia, Echimyidae). *Arquivos do Museu Nacional* **63**: 89–112.
- Jaeger JJ. 1988.** Rodent phylogeny: new data and old problems. In: Benton MJ, ed. *The phylogeny and classification of the tetrapods*. Vol. 2. The Systematics Association, Special Volume No.35 B. Oxford: Clarendon Press, 177–199.
- Jaeger JJ, Marivaux L, Salem M, Bilal AA, Benammi M, Chaimanee Y, Düringer P, Marandat B, Métais E, Schuster M, Valentin X, Brunet M. 2010.** New rodent assemblages from the Eocene Dur At-Talah escarpment (Sahara of central Libya): systematic, biochronological, and palaeobiogeographical implications. *Zoological Journal of the Linnean Society* **160**: 195–213.
- Jernvall J, Jung HS. 2000.** Genotype, phenotype and developmental biology of molar tooth characters. *Yearbook of Physical Anthropology* **43**: 171–190.
- Jernvall J, Keränen SVE, Thesleff I. 2000.** Evolutionary modification of development in mammalian teeth: quantifying gene expression patterns and topography. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 14444–14448.
- Kangas AP, Evans AR, Thesleff I, Jernvall J. 2004.** Non-independence of mammalian dental characters. *Nature* **432**: 211–214.
- Kavanagh KD, Evans AR, Jernvall J. 2007.** Predicting evolutionary patterns of mammalian teeth from development. *Nature* **449**: 427–432.
- Lara MC, Patton JL, da Silva MNF. 1996.** The simultaneous diversification of South American Echimyid rodents



- (Hystricognathi) based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution* **5**: 403–413.
- Lavocat R. 1971.** Affinités systématiques des caviomorphes et des phiomorphes et origine africaine des caviomorphes. *I Simpósio Brasileiro de Paleontologia, Anais da Academia Brasileira de Ciências* **43** (Suppl): 515–522.
- Lavocat R. 1976.** Rongeurs caviomorphes de l'Oligocène de Bolivie. II. Rongeurs du Bassin Déséadien de Salla-Luribay. *Paleovertebrata* **7**: 15–90.
- Leite YLR, Patton JL. 2002.** Evolution of South American spiny rats (Rodentia, Echimyidae): the star-phylogeny hypothesis revisited. *Molecular Phylogenetics and Evolution* **24**: 455–464.
- Maddison WP. 1993.** Missing data versus missing characters in phylogenetic analysis. *Systematic Biology* **42**: 576–581.
- Marivaux L, Vianey-Liaud M, Jaeger J-J. 2004.** High-level phylogeny of early Tertiary rodents: dental evidence. *Zoological Journal of the Linnean Society* **142**: 105–134.
- Marivaux L, Welcomme JL, Vianey-Liaud M, Jaeger J-J. 2002.** The role of Asia in the origin and diversification of hystricognathous rodents. *Zoologica Scripta* **31**: 225–239.
- Marshall LG, Patterson B. 1981.** Geology and geochronology of the mammal-bearing Tertiary of the Valle de Santa María and Río Corral Quemado, Catamarca province, Argentina. *Fieldiana Geology (New Series)* **9**: 1–80.
- McKenna MC, Bell SK. 1997.** *Classification of mammals above the species level*. New York: Columbia University Press.
- Moojen J. 1948.** Speciation in the Brazilian spiny rats (genus *Proechimys*, family Echimyidae). *University of Kansas Publications, Museum of Natural History* **1**: 301–406.
- Nixon KC. 1999.** *Winclada, Version 0.9.99m24 (BETA)*. Ithaca, NY: Nixon KC.
- Pascual R, Ortiz Jaureguizar E, Prado JL. 1996.** Land mammals: paradigm for Cenozoic South American geobiotic evolution. In: Arratia G, ed. *Contribution of Southern South America to vertebrate paleontology*. Munich: Munchner Geowissenschaftliche Abhandlungen, **30**, 265–319.
- Patterson B, Pascual R. 1968.** New Echimyid rodents from the Oligocene of Patagonia, and a synopsis of the family. *Breviora* **301**: 1–14.
- Patterson B, Wood AE. 1982.** Rodents from the Deseadien Oligocene of Bolivia and the relationships. *of the Caviomorpha. Bulletin of the Museum of Comparative Zoology* **149**: 371–543.
- Patterson BD, Velazco PM. 2006.** A distinctive new cloud-forest rodent (Hystricognathi: Echimyidae) from the Manu Biosphere Reserve. *Peru. Mastozoología Neotropical* **13**: 175–191.
- Patton JL. 1987.** Species group of spiny rats, genus *Proechimys* (Rodentia: Echimyidae). *Fieldiana: Zoology New Series* **39**: 305–346.
- Patton JL, Reig OA. 1989.** Genetic differentiation among echimyid rodents with emphasis on spiny rats, genus *Proechimys*. In: Eisenberg JF, Redford KH, eds. *Neotropical mammalogy*. Gainesville, FL: Sandhill Crane Press Inc, 75–96.
- de Pinna MCC. 1991.** Concepts and tests of homology in the cladistic paradigm. *Cladistics: The International Journal of the Willi Hennig Society* **7**: 367–394.
- Pol D, Gasparini Z. 2009.** Skull Anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Palaeontology* **7**: 163–197.
- Prevosti FJ. 2010.** Phylogeny of the large extinct South American Canids (Mammalia, Carnivora, Canidae) using a 'totalevidence' approach. *Cladistics: The International Journal of the Willi Hennig Society* **26**: 456–481.
- Ramírez MJ. 2007.** Homology as a parsimony problem: a dynamic homology approach for morphological data. *Cladistics: The International Journal of the Willi Hennig Society* **23**: 588–612.
- Rieppel O. 1988.** *Fundamentals of comparative biology*. Basel: Birkhäuser Verlag.
- Rieppel O. 1994.** Homology, topology, and typology: the history of modern debates. In: Hall BK, ed. *Homology: the hierarchical basis of comparative biology*. New York: Academic Press, 63–100.
- Rieppel O. 1996.** Testing homology by congruence: the pectoral girdle of turtles. *Proceedings of the Royal Society of London B* **263**: 1395–1398.
- Rieppel O, Kearney M. 2002.** Similarity. *Biological Journal of the Linnean Society* **75**: 59–82.
- Rusconi C. 1936.** Nuevo género de roedores del Puelchense de Villa Ballester. *Boletín Paleontológico de Buenos Aires* **7**: 1–4.
- Rusconi C. 1945.** Varias especies de roedores del Puelchense de Buenos Aires. *Anales de la Sociedad Científica Argentina* **140**: 369–376.
- Simpson GG. 1945.** The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* **85**: 1–350.
- Verzi DH, Deschamps CM, Vucetich MG. 2002.** Sistemática y antigüedad de *Paramyocastor diligens* (Ameghino, 1888) (Rodentia, Caviomorpha, Myocastoridae). *Ameghiniana* **39**: 193–200.
- Verzi DH, Vucetich MG, Montalvo CI. 1994.** Octodontid-like Echimyidae (Rodentia): an Upper Miocene episode in the radiation of the family. *Paleovertebrata* **23**: 199–210.
- Verzi DH, Vucetich MG, Montalvo CI. 1995.** Un nuevo Eumysopinae (Rodentia, Echimyidae) del Mioceno tardío de la Provincia de La Pampa y consideraciones sobre la historia de la subfamilia. *Ameghiniana* **32**: 191–195.
- Vucetich MG. 1995.** *Theridomysops parvulus* (Rovereto, 1914), un primitivo Eumysopinae (Rodentia, Echimyidae) del Mioceno tardío de Argentina. *Mastozoología Neotropical* **2**: 167–172.
- Vucetich MG, Kramarz AG. 2003.** New Miocene rodents from Patagonia (Argentina) and their bearing on the early radiation of the octodontoids (Hystricognathi). *Journal of Vertebrate Paleontology* **23**: 435–444.
- Vucetich MG, Kramarz AG, Candela AM. 2010b.** Colhuahuapian rodents from Gran Barranca and other Patagonian localities: the state of the art. In: Madden R, Carlini AA, Vucetich MG, Kay R, eds. *The paleontology of gran*

- barranca*. Cambridge: Cambridge University Press, 206–219.
- Vucetich MG, Mazzoni MM, Pardiñas UFJ. 1993.** Los roedores de la Formación Collón Cura (Mioceno medio), y la Ignimbrita Pilcaniyeu. Cañadon del Tordillo, Neuquén. *Ameghiniana* **30**: 361–381.
- Vucetich MG, Verzi DH. 1991.** Un nuevo Echimyidae (Rodentia, Hystricognathi) de la Edad Colhuehuapense de Patagonia y consideraciones sobre la sistemática de la familia. *Ameghiniana* **28**: 67–74.
- Vucetich MG, Verzi DH. 1995.** Los roedores caviomorfos. In: Alberdi MT, Leone G, Tonni EP, eds. Evolución Biológica y Climática de la Región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental. *Monografías Museo Nacional de Ciencias Naturales de Madrid* **12**: 213–225.
- Vucetich MG, Vieytes EC. 2006.** A middle Miocene primitive octodontoid rodent and its bearing on the early evolutionary history of the Octodontoidea. *Palaeontographica Abteilung A* **277**: 81–91.
- Vucetich MG, Vieytes EC, Pérez ME, Carlini AA. 2010a.** The rodents from La Cantera and the early evolution of caviomorphs in South America. In: Madden R, Carlini AA, Vucetich MG, Kay R, eds. *The paleontology of gran barranca*. Cambridge: Cambridge University Press, 193–205.
- Wood AE. 1968.** Early Cenozoic mammalian faunas, Fayum province, Egypt. Part II. The African Oligocene Rodentia. *Peabody Museum of Natural History Bulletin* **28**: 29–105.
- Wood AE, Patterson B. 1959.** The rodents of Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin of the Museum of Comparative Zoology* **120**: 280–428.
- Wood AE, Wilson RW. 1936.** A suggested nomenclature for the cusps of the cheek teeth of rodents. *Journal of Paleontology* **10**: 388–391.
- Woods CA. 1982.** The history and classification of South American hystricognath rodents: reflections on the far away and long ago. In: Mares MA, Genoways HH, eds. *Mammalian biology in South America*. Special Publications Series, Pennsylvania: Pymatuning Laboratory of Ecology, University of Pittsburgh, 377–392.
- Woods CA. 1993.** Suborder hystricognathi. In: Wilson DE, Reeder DM, eds. *Mammal species of the world: a taxonomic and geographic reference*. Washington, DC: Smithsonian Institution Press, 771–806.
- Wyss AR, Flynn JJ, Norell MA, Swisher CCIII, Charrier R, Novacek MJ, McKenna MC. 1993.** South America's earliest rodent and recognition of a new interval of mammalian evolution. *Nature* **365**: 434–437.
- ever some of these characters are redefined or whenever taxa are re-scored, we discuss each case (see below). The character states of *Tramyocastor* and *Paramyocastor* are noted.
- In analysis II the numbering of characters (Table 2) from character 15 onwards, is one less than in analysis I. This is because characters 14 and 15 were combined as a single character (see below) in analysis I.
- The number of each character for each analysis is specified, indicating in the first place the number corresponding to analysis II. In both analyses one character more than in the analysis of Carvalho & Salles (2004) was added: character 51 in analysis I (= 50 in analysis II).
6. dp4, sulcus (= flexid) between the protoconid region and the anterolophid (= metalophid I) in little-worn teeth: (0) absent (or quite shallow); (1) deep. *Paramyocastor* is scored as 0, *Tramyocastor* as unknown. The remaining taxa are scored exactly as described in Carvalho & Salles (2004).
  7. dp4, sulcus between hypolophid and ectolophid/protoconid region in little-worn teeth: (0) absent (or quite shallow); (1) deep. *Paramyocastor* is scored as 0, *Tramyocastor* as unknown. The remaining taxa are scored exactly as described in Carvalho & Salles (2004).
  8. dp4, sulcus (= flexid) between hypolophid and hypoconid region in little-worn teeth: (0) absent (or quite shallow); (1) deep. This sulcus corresponds to the labial opening of the metaflexid (with the hypoflexid continuous to the metaflexid). *Paramyocastor* is scored as 0, *Tramyocastor* is scored as unknown. The remaining taxa are scored exactly as described in Carvalho & Salles (2004).
  9. dp4, sulcus between the hypoconid region and posterolophid in little-worn teeth: (0) absent (or quite shallow); (1) deep. This sulcus corresponds to a posterolabial opening of the metaflexid. *Paramyocastor* is scored as 0; *Tramyocastor* is scored as unknown. The remaining taxa are scored exactly as described in Carvalho & Salles (2004).
  10. dp4, lingual opening of the anteroflexid in little-worn teeth: (0) absent (or quite shallow); (1) deep. *Paramyocastor* is scored as 0; *Tramyocastor* is scored as unknown. The remaining taxa are scored exactly as described in Carvalho & Salles (2004).
  11. dp4, lingual opening of the mesoflexid in little-worn teeth: (0) absent (or quite shallow); (1) deep. This opening corresponds to a lingual flexid between the hypolophid and the lophid anterior to it. *Paramyocastor* is scored as 0; *Tramyocastor* is scored as unknown. *Coendou* is re-scored as 0 (uncertain in original data). The remaining taxa are scored exactly as described in Carvalho & Salles (2004).

## APPENDIX

Here, we provide a brief discussion on the characters that are not directly involved in the alternative hypotheses of primary homology inspected above, i.e. characters that are identically coded in analyses I and II. Most of these characters are not modified with respect to Carvalho & Salles (2004: table 2). When-

12. dp4, lingual opening of the metaflexid in little-worn teeth: (0) absent (or quite shallow); (1) deep. *Paramyocastor* is scored as 0, *Tramyocastor* as uncertain. The remaining taxa are scored exactly as described in Carvalho & Salles (2004).

15. m1–m3, ectolophid (= Character 16 in analysis I and Carvalho & Salles, 2004): (0) posteriorly orientated; (1) poorly developed and not posteriorly orientated.

*Tramyocastor* and *Paramyocastor* are scored as 0. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2), with the exception of *Coendou*, which is re-scored as 0 because its ectolophid is posteriorly orientated. The results are the same when *Coendou* is scored as unknown, as originally.

16. m1–m3, medial contact between metalophid (= metalophid II) and ectolophid/protoconid (character 17 in analysis I and Carvalho & Salles, 2004): (0) present; (1) absent.

*Paramyocastor* and *Tramyocastor* are scored as 0. The remaining taxa are scored exactly as described in Carvalho & Salles (2004). Taxa with trilophodont molars, without metalophid II, as *Clyomys*, *Euryzygomatomys*, *Thrichomys*, *Eumysops*, *Pampamys*, *Theridomyops*, Dactylomyinae and 'Echimyinae', are scored as non-applicable.

17. m1–m3, sulcus between the protoconid region and the anterolophid (= metalophid I) in little-worn teeth (= character 18 in analysis I and Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

In the sample it is a non-informative character (Table 2), but it is maintained in this analysis to facilitate comparison with Carvalho & Salles (2004; table 2). *Tramyocastor* and *Paramyocastor* are scored as 0.

18. m1–m3, sulcus between hypolophid and the ectolophid in little-worn teeth (= character 19 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

*Tramyocastor* and *Paramyocastor* are scored as 0, with the remaining taxa scored as described in Carvalho & Salles (2004).

19. m1–m3, sulcus between hypolophid and the hypoconid region in little-worn teeth: (0) absent (or quite shallow); (1) deep.

*Paramyocastor* is scored as 0. *Tramyocastor* is scored as 1. A sulcus between the hypolophid and the hypoconid is evident in the m3 (a worn tooth) of *Tramyocastor andiaei* (Fig. 7B). The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

20. m1–m3, sulcus between the hypoconid region and the posterolophid in little-worn teeth (= character 21 in Analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

*Tramyocastor* and *Paramyocastor* are scored as 0. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

21. m1–m3, lingual opening of the anteroflexid in little-worn teeth: (0) absent (or quite shallow); (1) deep.

*Myocastor* is re-scored as 1 (uncertain in original data). *Paramyocastor* and *Tramyocastor* are scored as 0. The remaining taxa are scored as described in Carvalho & Salles (2004).

This character is non-applicable in the trilophodont taxa.

22. m1–m3, lingual opening of mesoflexid in little-worn teeth (= character 23 in analysis I and Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

This flexid is anterior to the hypolophid. *Coendou* is re-scored as 0 (coded as 1 in the original data) because this flexid is shallower than in echimyids such as *Phyllomys*, *Diplomys*, or *Callistomys*, all of which are scored as 1. *Myocastor* is re-scored as 1 (uncertain in original data). *Tramyocastor* and *Paramyocastor* are scored as 0.

*Euryzygomatomys*, *Thrichomys*, *Pampamys* are re-scored as 0 (uncertain in original data).

23. m1–m3, lingual opening of the metaflexid in little-worn teeth (= character 24 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

In *Eumysops* the metaflexid is more persistent than the mesoflexid, and is relatively more persistent than the metaflexid of *Thrichomys*. In *Pampamys*, the metaflexid is also more persistent than those of *Thrichomys* and *Euryzygomatomys* (Vucetich & Verzi, 1995: 194). Thus, *Eumysops* and *Pampamys* are re-scored as 1 (coded 0 and unknown, originally). *Euryzygomatomys* and *Thrichomys* are re-scored as 0 (unknown, in original data). *Myocastor* and *Tramyocastor* are re-scored as 1 and *Paramyocastor* is re-scored as 0. In *Myocastor* the depth of the metaflexid seems to be somewhat lesser than in *Phyllomys*, *Echimyis*, *Diplomys*, and *Makalata*. An intermediate state would be necessary to express the condition of *Myocastor* and possibly also that of *Eumysops* and *Pampamys* in future analyses of the group.

It is important to remark that in echimyids in general, the mesoflexid usually closes before the metaflexid, a condition that was described for fossil and living forms (Verzi *et al.*, 1994). A metaflexid that is more persistent than the mesoflexid is present in at least some living and extinct taxa, such as *Myocastor*, *Eumysops*, and *Pampamys*. Future analyses may have to consider the variation in the relative depth of the meso- and metaflexids within the same taxa. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

24. dp4–m3, anterolingual extension of hypoconid (= character 25 in analysis I and in Carvalho & Salles, 2004): (0) absent; (1) present.

*Maruchito trilophodonte* is re-scored as 1 (unknown in original data) because it shows an anterolingual extension of the hypoconid that makes contact with the hypolophid, exhibiting a forward obliquity of the hypoflexid (as in *Echimys semivillosus*, *Callistomys*, and *Phyllomys*). *Tramyocastor* and *Paramyocastor* are scored as 0. The remaining taxa are scored as described in Carvalho & Salles (2004: table 2).

25. Dp4–M3; ‘neoloph’ (= metaloph *sensu* Lavocat, 1976; character 26 in analysis I and in Carvalho & Salles, 2004): (0) present; (1) absent.

In caviomorphs the fourth loph (neoloph *sensu* Patterson & Wood, 1982) was homologized with the metaloph (Lavocat, 1976; Candela, 1999; Marivaux *et al.*, 2004). So, the term neoloph is used here in quotation marks.

*Eumysops* is re-scored as 0 (1 in original data). *Paramyocastor* and *Tramyocastor* are scored as 0. In these taxa the fourth loph is distinguished from the posteroloph or is assimilated to this latter condition as a consequence of tooth wear. This latter condition is expressed in a posteroloph that widens as wear progresses (see Candela *et al.*, 2007: fig. 4). The remaining taxa are scored as described in Carvalho & Salles (2004: table 2).

26. DP4–M3, ‘metaloph’ (mesolophule *sensu* Candela, 1999; Marivaux *et al.*, 2004; = character 27 in analysis I and in Carvalho & Salles, 2004): (0) present; (1) absent.

The third loph in the upper molars of caviomorphs was homologized with the metaloph by Patterson & Wood (1982) or with the mesolophule of the ‘Baluchimyinae’ by Candela (1999) and Marivaux *et al.* (2004). So, the term metaloph is used here in quotation marks. *Paramyocastor* and *Tramyocastor* are scored as 0. The remaining taxa are scored as described in Carvalho & Salles (2004: table 2).

27. DP4–M3, protoloph (= character 28 in analysis I and in Carvalho & Salles, 2004): (0) fully developed (from the labial margin to the contact with the mure); (1) restricted to the labial margin; (2) absent (ordered).

*Tramyocastor* and *Paramyocastor* are scored as 0. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

28. DP4–M3, labial opening of paraflexus in little-worn teeth (= character 29 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

*Myocastor* was re-scored as 0 (unknown in original data), like *Paramyocastor*.

*Tramyocastor* is scored as uncertain, because little-worn upper molars are not known for this genus.

The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

29. DP4–M3, labial opening of mesoflexus in little-worn teeth (= character 30 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

*Coendou* is re-scored as 0 (1 in the original data) because of the shallower mesoflexus than in echimyids such as *Phyllomys*, *Diplomys*, *Callistomys*, all of which are scored as 1 (see character 30 of Carvalho & Salles, 2004; table 2). *Myocastor* was re-scored as 0 (unknown originally), like *Paramyocastor*. *Tramyocastor* is scored as uncertain, because little-worn upper molars are not known for this genus. The remaining taxa were scored as described in Carvalho & Salles (2004).

30. DP4–M3, labial opening of metaflexus in little-worn teeth (= character 31 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

*Myocastor* was re-scored as 0 (uncertain in original data), like *Paramyocastor*.

*Tramyocastor* is scored as uncertain, because upper molars with very scarce and the degree of wear is not known. The remaining taxa were scored as described in Carvalho & Salles (2004).

31. DP4–M3, sulcus between protoloph and the protocone region in little-worn teeth (= character 32 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

*Paramyocastor* and *Tramyocastor* are 0. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

32. DP4–M3, sulcus between the lingual end of the protoloph and the posterior portion of the tooth in little-worn teeth (= character 33 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

*Tramyocastor* and *Paramyocastor* are scored as 0. The remaining taxa were scored as described in Carvalho & Salles (2004).

33. DP4–M3, sulcus between the hypocone region and the posteroloph in little-worn teeth (= character 34 in analysis I and in Carvalho & Salles, 2004): (0) absent (or quite shallow); (1) deep.

In at least two M3 of *Maruchito trilophodonte* (Vucetich *et al.*, 1993: fig. 7f–g) there is a sulcus between the hypocone and the posteroloph, so that there is a lingual opening of the metaflexus. Examination of these specimens indicates that this sulcus is shallow, and hence it would be quickly lost as wear proceeds. Therefore, *M. trilophodonte* was scored as 0 as in Carvalho & Salles (2004). *Myocastor*, *Paramyocastor* (e.g. Candela *et al.*, 2007: fig. 4c), and *Tramyocastor* are scored as 1 (*Myocastor* was scored originally as uncertain). These same taxa are also scored as 0, because the depth of

this sulcus is somewhat shallower than in echimyines. Results are the same when these taxa are scored 1 or 0.

*Myocastor*, *Paramyocastor*, and *Tramyocastor* would represent an intermediate condition for this character. In this study we prefer to maintain the same character states as in the original data, in order to conserve characters that are possibly not directly involved in the alternative hypotheses of primary homologies. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

34. Substitution of deciduous premolars (= character 35 in analysis I and in Carvalho & Salles, 2004): (0) substitution occurs; (1) the deciduous premolar is retained in adults.

*Theridomysops* is re-scored as 1. It is a non-informative character in this sample. However, we prefer to maintain this character to facilitate the comparison concerning homology hypotheses between analyses I and II and the analysis of Carvalho & Salles (2004).

35. Number of roots in upper molar teeth (= character 36 in analysis I and in Carvalho & Salles, 2004): (0) three, a lingual root and two labial roots; (1) four roots.

*Tramyocastor* and *Paramyocastor* are scored as 0. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

36. Unilateral hypsodonty in upper molariform teeth (= character 37 in analysis I and in Carvalho & Salles, 2004): (0) absent; (1) present.

*Tramyocastor* and *Paramyocastor* are scored as 1. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

37. Enamel microstructure of incisors (= character 38 in analysis I and in Carvalho & Salles, 2004): (0) parallel with acute multiserial; (1) rectangular multiserial.

*Tramyocastor* and *Paramyocastor* are scored as uncertain. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

38. Upper tooth rows (= character 39 in analysis I and in Carvalho & Salles, 2004): (0) parallel; (1) converging anteriorly.

*Eumysops* is re-scored as 0 (unknown in original data), because this genus shows upper tooth rows slightly convergent anteriorly. Parallel or slightly convergent anteriorly tooth rows are considered as the same character state. *Paramyocastor* was scored as 0, because this genus shows slightly convergent tooth rows, much less than *Myocastor* and *Tramyocastor*, both scored as 1.

39. Rostrum (= character 40 in analysis I and in Carvalho & Salles, 2004): (0) short and wide; (1) longer and narrower.

*Eumysops* is re-scored as 0 (unknown in original data). *Paramyocastor* is scored as uncertain. *Tramyocastor* is scored as 0. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

40. Anterior projection of the premaxillary bone (= character 41 in analysis I and in Carvalho & Salles, 2004): (0) small; (1) well developed; (2) very well developed, with the dorsal portion of the premaxillary bone presenting a well-marked anteromesial expansion in the region of nasal openings. (Ordered.)

*Eumysops* is re-scored as 1 (uncertain in the original data). *Tramyocastor* and *Paramyocastor* were scored as uncertain. The remaining taxa were scored as described in Carvalho & Salles (2004).

41. Canal of the infraorbital nerve in the infraorbital foramen (= character 42 in analysis I and in Carvalho & Salles, 2004): (0) absent; (1) present.

*Tramyocastor* and *Paramyocastor* are scored as uncertain. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

42. Sphenopalatine foramen (= character 43 in analysis I and in Carvalho & Salles, 2004): (0) well developed; (1) small.

*Tramyocastor* and *Paramyocastor* are scored as uncertain. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

43. Inferior zygomatic root (= character 44 in analysis I and in Carvalho & Salles, 2004): (0) short; (1) long.

*Eumysops* is re-scored as 0 (uncertain in original data). *Tramyocastor* and *Paramyocastor* are scored as uncertain. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

44. Placement of the inferior zygomatic root in relation to the ventral surface of the rostrum (= character 45 in analysis I and in Carvalho & Salles, 2004): (0) at the same level; (1) inferior zygomatic root ventrally exposed.

*Eumysops* is re-scored as 0, and *Paramyocastor* and *Tramyocastor* are scored as uncertain. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

45. Placement of the inferior zygomatic root in relation to the palatal region (= character 46 in analysis I and in Carvalho & Salles, 2004): (0) at the same level; (1) inferior zygomatic root more dorsally placed (palatal region projected ventrally).

*Eumysops* is re-scored as 0 (uncertain in original data). *Tramyocastor* and *Paramyocastor* are scored as 1. In available specimens of these extinct genera the inferior zygomatic root is not completely preserved, but the placement of the preserved portion

indicates that it is dorsal with respect to the palatal region, showing a similar condition to that of *Myocastor coypus*.

46. Palatal grooves posterior to the incisive foramen (= character 47 in analysis I and in Carvalho & Salles, 2004): (0) well developed; (1) poorly developed.

*Eumysops* is re-scored as 0 (uncertain in original data). *Paramyocastor* and *Tramyocastor* are scored as uncertain. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

47. Contact between the ectotympanic and the squamosal (= character 48 in analysis I and in Carvalho & Salles, 2004): (0) contact along the entire dorsal margin of the ectotympanic, generally forming an overhang; (1) partial contact, restricted to the posterior portion of the dorsal margin of the ectotympanic, thus presenting a cleft between the ectotympanic and the squamosal.

*Eumysops* is re-scored as 0, showing a similar condition to that of *Thrichomys*. *Paramyocastor* and

*Tramyocastor* are scored as uncertain. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

48. Palatine foramen (= character 49 in analysis I and in Carvalho & Salles, 2004): (0) well developed; (1) small or absent.

*Eumysops* is re-scored as 1. *Tramyocastor* and *Paramyocastor* are scored as uncertain. The remaining taxa were scored as described in Carvalho & Salles (2004; table 2).

49. Sphenopalatine vacuities (= character 50 in analysis I and in Carvalho & Salles, 2004): (0) absent; (1) well developed.

*Eumysops* is re-scored as 1. *Myocastor* is re-scored as 0. *Tramyocastor* and *Paramyocastor* are scored as uncertain. The remaining taxa are scored as described in Carvalho & Salles (2004; table 2).

50. Relative length of m3 with respect to m2 length (= character 51 in analysis I): (0) subequal to m2; (1) longer than m2.

*Myocastor* and *Tramyocastor* are scored as 1. *Paramyocastor* is scored as 0.