



Main radiation events in Pan-Octodontoidea (Rodentia, Caviomorpha)

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Caviomorphs (South American hystricognaths) are recorded in the continent since the middle Eocene. The middle Eocene–early Oligocene is considered a key moment for their evolutionary history because by the early Oligocene they were differentiated into four superfamilies: Octodontoidea, Cavoidea, Chinchilloidea and Erethizontoidea. Due to their generalized dental patterns and abundance in the fossil record, Octodontoidea are interesting for analysing the origin and early history of caviomorphs. The phylogenetic relationships of the earliest octodontoids are studied herein. Results confirmed a basal caviomorph diversification in the middle Eocene (c. 45 Mya), with one lineage leading to Pan-Octodontoidea, and another leading to Erethizontoidea, Cavoidea and Chinchilloidea, which is not in accordance with analyses based on molecular data. Three major radiations were identified: the first one (late Eocene/early Oligocene?) occurred in low latitudes with the differentiation of Pan-Octodontoidea and the earliest crown-Octodontoidea. The second radiation (late Oligocene) was a large-scale South American event; in the southernmost part of the continent it is recognized as the first Patagonian octodontoid radiation, which provided the characteristic high morphological disparity of the superfamily. The third radiation (late Miocene) is characterized by the replacement of ‘old’ by ‘modern’ octodontoids; the nature of this third event needs to be studied in a broader taxonomic context.

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INTRODUCTION

The South American fossil record suggests that caviomorphs, those rodents endemic to South America, have been in the continent at least since the middle/late Eocene (Antoine *et al.*, 2012), and by the late Eocene – early Oligocene they were already differentiated into the four major clades recognized for living species (Frailey & Campbell, 2004; Vucetich *et al.*, 2010a, 2014a, 2015; Bertrand *et al.*, 2012): Octodontoidea (tuco-tucos, spiny rats, coypus), Cavoidea (agouties, cavies, capybaras), Erethizontoidea (porcupines) and Chinchilloidea (chinchillas, viscachas, pacaranas). Although the middle Eocene – early Oligocene caviomorph

record is poorly known, this interval is considered a key moment for the evolutionary history of this group. This is inferred from the rich subsequent record of the Deseadan South American Land Mammal Age (SALMA) (early–late Oligocene) (Kraglievich, 1932; Wood, 1949; Wood & Patterson, 1959; Hoffstetter & Lavocat, 1970; Lavocat, 1976; Mones & Castiglioni, 1979; Patterson & Wood, 1982; Vucetich, 1989; Vucetich & Ribeiro, 2003; Pérez & Vucetich, 2012b; Vucetich *et al.*, 2014a, 2015). Deseadan localities are known in high latitudes of Patagonia and lower latitudes of Uruguay, Bolivia, Brazil, and Peru (Fig. 1), exhibiting those of Patagonia the greatest taxonomic diversity. Recently, Vucetich *et al.* (2015) described new caviomorphs from Cabeza Blanca (Chubut Province, Argentina, Fig. 1), the richest rodent Palaeogene local fauna, and contributed to corroborate the hypothesis that states that Deseadan rodent

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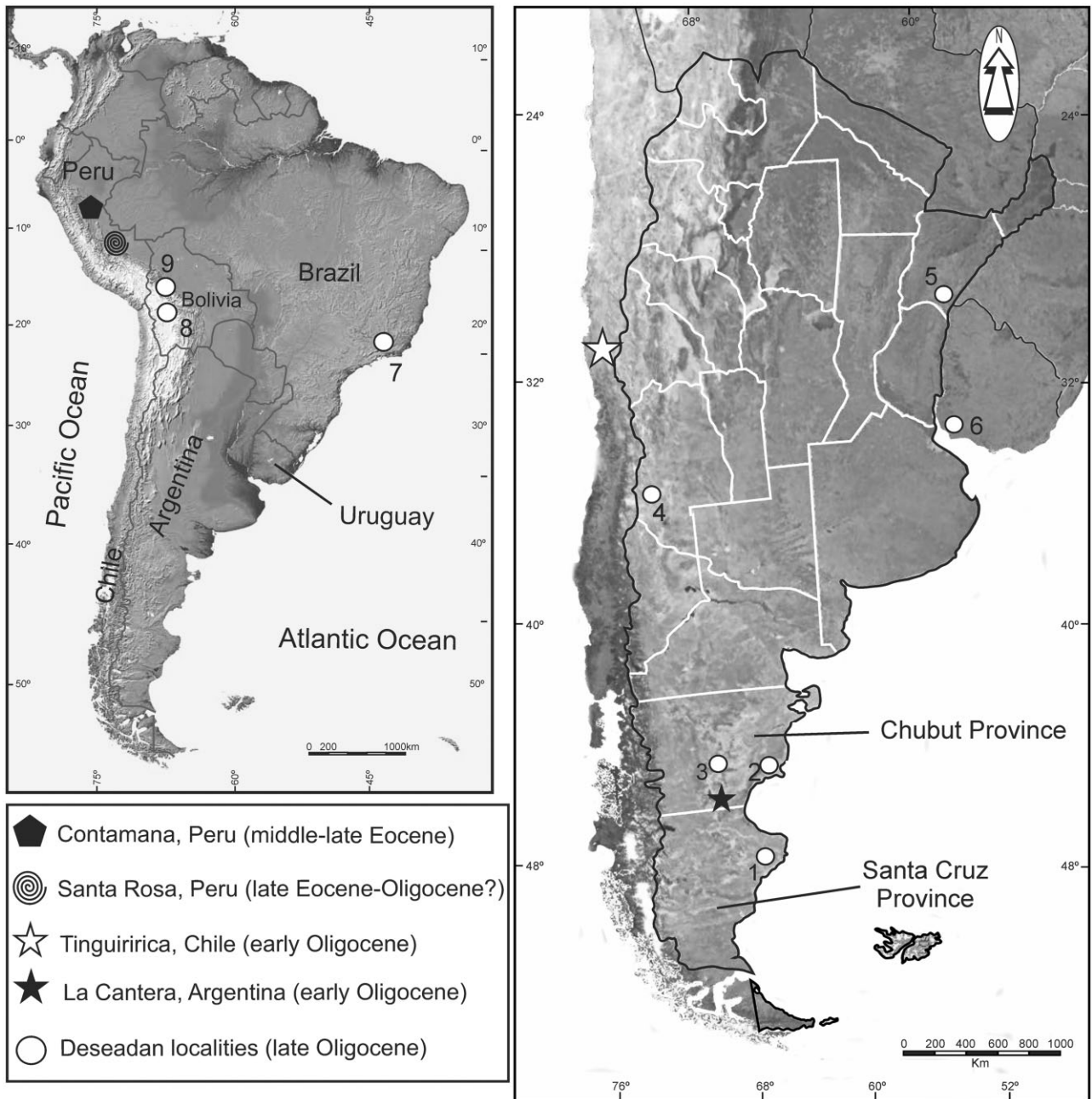


Figure 1. Location map showing the South American caviomorph fossil localities from the Eocene–Oligocene. Numbers refer to the South American Deseadan localities with rodents: 1, La Flecha; 2, Cabeza Blanca; 3, Scarrit Pocket; 4, Quebrada Fiera; 5, Arroyo Ávalos; 6, Nueva Palmira; 7, Taubate Basin; 8, Salla-Luribay Basin; 9, Lacayani.

diversity had been underestimated (Arnal, 2012; Pérez, Krause & Vucetich, 2012; Pérez & Pol, 2012).

Despite recent progress, the early evolutionary history of caviomorphs in general and within each superfamily in particular remains incompletely understood. Results provided by cladistic analyses with palaeontological data are in disagreement with molecular studies. Most analyses with molecular data suggest a

sister relationship of Octodontoidea with Chinchilloidea, and Caviioidea with Erethizontoidea (Huchon *et al.*, 2007; Blanga-Kanfi *et al.*, 2009; Fabre *et al.*, 2012, 2013; Upham & Patterson, 2012; Patterson & Upham, 2014). However, morphological cladistic analyses with fossils changed these systematic arrangements, proposing a complex early evolution of caviomorphs with an early differentiation of octodontoids and with many fossil

lineages not included into any of the four superfamilies (Antoine *et al.*, 2012; Arnal *et al.*, 2014; but see Verzi, Olivares & Morgan, 2014). Within caviomorph superfamilies, Octodontoidea is the most diverse from a morphological and taxonomic point of view, and also the most abundant group since the late Eocene – early Oligocene (Wood, 1949; Wood & Patterson, 1959; Hoffstetter & Lavocat, 1970; Patterson & Wood, 1982; Vucetich & Kramarz, 2003; Vucetich & Ribeiro, 2003; Frailey & Campbell, 2004; Vucetich & Vieytes, 2006; Vucetich *et al.*, 2010a, 2015, 2014a; Vucetich, Kramarz & Candela, 2010b; Arnal & Pérez, 2013; Arnal *et al.*, 2014; Arnal & Vucetich, 2015). Small to medium-sized taxa with low-crowned, lophodont to bunolophodont cheek teeth were described as octodontoids. Thus, they represent an interesting case for analysing their origin as well as the early evolutionary history of caviomorphs. It is clear that to elucidate the early evolutionary history of caviomorphs in general, and octodontoids in particular, palaeontological studies require an increased taxonomic sampling and new sources of morphological characters. In this context, the aim of this work is to study the phylogenetic relationships of the earliest octodontoids, including taxa recently described, to evaluate their relationships, history and main diversification events. Additionally, the phylogenetic hypothesis was combined against the stratigraphic information to study the time of origin and early diversification of octodontoids.

MATERIAL AND METHODS

Dental nomenclature follows Marivaux *et al.* (2002) and Candela & Rasia (2012) (Fig. 2).

PHYLOGENETIC ANALYSIS

An enlarged version of the data matrix of Arnal *et al.* (2014) (see Appendix 1) was used, where a few minor changes have been made in the coding of taxa following personal observations of new specimens. Twenty-four caviomorph taxa were added (see Appendix 2). Based on the objectives of this work, the oldest octodontoids (Eocene? – Oligocene) not included in the previous analysis (Arnal *et al.*, 2014) were here included. Additionally, the taxon sampling of modern octodontoids was enlarged to include, at least, one representative of each family. As new outgroups, and to discuss in a broad sense the early evolutionary history of caviomorphs, we included the cephalomyid [fossil caviomorph family (late Oligocene – early Miocene) of uncertain relationships] *Cephalomys arcidens* and the oldest chinchilloids (*Eoviscaccia frassinettii* and *E. boliviana*) (see Appendix 2). Sixty-one characters were added: 48 skull characters were taken from Arnal (2012), with the remaining dental and mandibular characters included due to the extension of taxon sampling (Appendix 3). For euhypsodont cheek teeth (e.g. those of living Octodontidae) the presence/absence of cusps and some crests that are not evidenced in the simplified occlusal pattern are scored as ‘inapplicable’ as we cannot infer its absence or presence. Those crests whose presence can be inferred, e.g. the metalophulid I in lower molars, are scored as ‘present’ as the anterior wall of lower cheek teeth is formed by this crest in the *Ctenostrychia* Huchon, Catzeflis & Douzery (2000) lineage (Marivaux, Vianey-Liaud & Jaeger, 2004).

The data matrix was analysed using TNT 1.1 (Goloboff, Farris & Nixon, 2008a,b) followed by Tree Bisection Reconnection (TBR) branch swapping

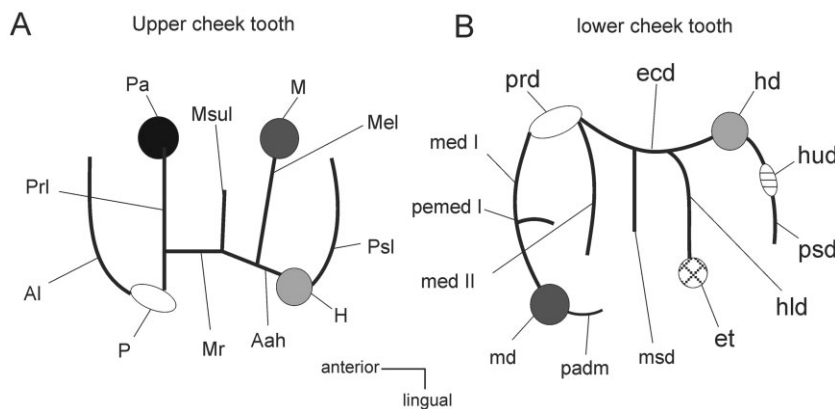


Figure 2. Dental terminology used in this paper. Upper tooth abbreviations: Aah, anterior arm of the hypocone; Al, anteroloph; H, hypocone; M, metacone; Mel, metaloph; Mr, mure; Msul, mesolophule; P, protocone; Pa, paracone; Prl, protoloph; Psl, posteroloph. Lower tooth abbreviations: ecd, ectolophid; et, entoconid; hd, hypoconid; hld, hypolophid; hud, hypoconulid; md, metaconid; med I, metalophulid I; med II, metalophulid II; msd, mesolophid; padm, posterior arm of the metaconid; pemed I, posterior extension of the metalophulid I; prd, protoconid; psd, posterolophid.

algorithm (holding ten trees per replicate). Equally weighed parsimony was used to minimize the number of postulated evolutionary transformations. Thirty characters were treated as ordered (Appendix 2). The robustness of the obtained most parsimonious trees (MPTs) was calculated with both absolute and relative Bremer support (Bremer, 1994; Goloboff & Farris, 2001).

The phylogenetic tree was calibrated against geological time based on the first occurrence of fossil taxa in the fossil record. For the age calibration we followed Fleagle *et al.* (2012) and Dunn *et al.* (2013) for the Oligocene – early Miocene, Deschamps *et al.* (2013 and literature therein) for the late Miocene – Pliocene, and Cione & Tonni (2005) for the Quaternary.

RESULTS

The cladistic analysis retrieved 939 MPTs of 699 steps found in 40 of the replicates, with consistency index (ci) = 0.323 (a low ci means a high degree of homoplasy) and retention index (ri) = 0.547 (a medium ri means relatively structured synapomorphies). The strict consensus shows a polytomy at the base of the cladogram caused by the alternative positions of *Changquin woodi* in the MPTs (Fig. 3A), which obscure the relationships of major groups of caviomorphs and octodontoids. *Changquin woodi* was described as an octodontoid by Vucetich *et al.* (2014a). Nevertheless, the analysis performed here does not resolve its phylogenetic and

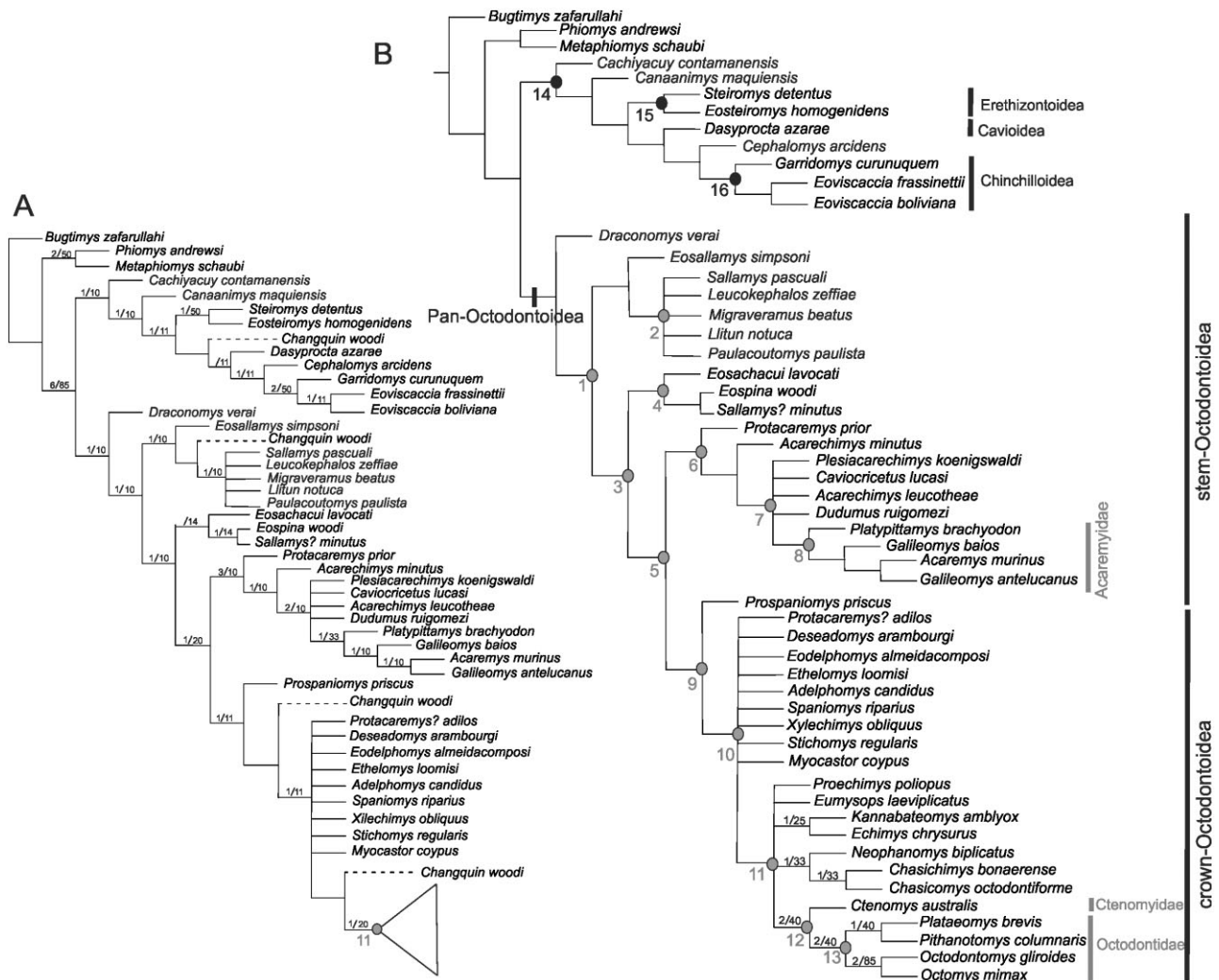


Figure 3. A, reduced consensus of 939 MPTs ($L = 699$ steps, $ci = 0.323$, $ri = 0.547$) showing the alternative position of *Changquin woodi*. Numbers above nodes separated by slash are absolute and relative Bremer support values (no number denotes 1). B, reduced consensus tree of the MPTs after the exclusion of *C. woodi*. Nodes referred to in the text are numbered (1–12). Grey bars indicate the families recognized within Pan-Octodontoidea. Black bars indicate caviomorph superfamilies.

systematic position. Hence, the discussion was based in a reduced consensus (Fig. 3B) pruning *Changquin* posterior to the analysis.

Branch support values were relatively low for all nodes. Many taxa are represented by fragmentary remains, e.g. isolated teeth (*Protacaremys?*, *Sallamys?*, *Eospina*, *Eosachacui*), or with unstable phylogenetic positions (*Changquin*) that led to low support in most nodes. When pruning *Changquin* from the analysis as previously explained, levels of support are as follows: nodes with the highest support are those delimiting caviomorphs (absolute and relative Bremer support 6 and 85, respectively), node 6 (absolute and relative Bremer support 3 and 10, respectively), and nodes 7, 12 and 13 of Figure 3B (absolute and relative Bremer support 2 and 40, respectively). Outside Pan-Octodontoidea, highest support is for node 16 (Chinchilloidea) (absolute and relative Bremer support 2 and 50, respectively) (Fig. 3B).

Results are in general agreement with previous proposals (Vucetich & Kramarz, 2003; Arnal & Pérez, 2013; Arnal *et al.*, 2014), but new evolutionary events can be observed as more taxa were included in the analyses. The reduced consensus shows a dichotomy event early in the South American rodent evolution with one lineage leading to the differentiation of Octodontoidea, and another leading to the origin of the remaining three caviomorph superfamilies (Erethizontoidea, Cavoidea and Chinchilloidea) (Fig. 3B). Pan-Octodontoidea (Fig. 2B) is characterized by four synapomorphies: metacone slightly lingual to paracone on upper molars (character 39[1]), crestiform metacone on M3 (character 50[2]), m3 smaller than m2 (character 100[1]) and a notch for the insertion of the medial masseteric muscle *pars infraorbitalis* (nmmpio) located at the middle of the mandible height (character 111[1]). Characters 100 and 111 are the only ones with relatively good distribution as they are shared with a few other taxa, but they could be scored only in a few species. *Draconomys verai* is the earliest divergent taxon (Fig. 3B) and is excluded from the rest of the clade by the absence of: a mesolophule slightly posterolabially orientated on upper molars (character 42[1]), M3 smaller than M2 (character 55[0]), a flexid on the anterior face of metalophulid I on p4 (character 70[0]) and an anterior border of the nmmpio of the mandible anterior to m1 (character 110[1]). The importance of characters 55 and 70 as indicators of relationships remains unknown because few M3 are known in the fossil record and most octodontoids retain the deciduous premolars (DP4/dp4) through life. Two groups diverge at the level of node 1 (Fig. 3B). The clade including (*Eosallamys* (*Sallamys* *Llitun Paulacoutomys Leucokephalos Migraveramus*)) is characterized by two synapomorphies: a strong anterior arm of the hypoconid on p4 (character 75[2]), a character shared only with

erethizontoids (*Eosteiomys homogenidens* and *Steiomys detentus*), and no posterolophid–entoconid connection on p4 (character 77[0]), a character shared with *Cachiyacui* and *Garridomys*. Node 2 (Fig. 3B) is supported by five synapomorphies: mesodont cheek teeth (character 3[1]), indistinct cusps (character 10[1]), entoconid anterior with respect to hypoconid (character 89[1]), presence of a posterior extension of metalophulid I (character 96[0]) and presence of an accessory cusp (character 97[0]) on m1–m3. This result also confirms the hypothesis of Vucetich *et al.* (2015) which stated that *Llitun*, *Leucokephalos* and *Migraveramus* are more closely related to each other than to other caviomorphs. These authors affirmed that these taxa were grouped by sharing a replacement of the premolars, and molarized p4 (with conspicuous metalophulid I, metalophulid II, hypolophid and posterolophid). Nevertheless, the phylogenetic analysis performed here shows that these characters are instead plesiomorphic as most caviomorphs replace the premolars, and have conspicuous metalophulid I and II on the p4 [the only taxa without metalophulid II on p4 are both erethizontoids (*Steiomys* and *Eosteiomys*) and *Garridomys*]; mesolophid on p4 is present in *Llitun*, *Dasyprocta*, erethizontoids and *Garridomys*, being well developed only in erethizontoids and *Dasyprocta*. Vucetich *et al.* (2015) proposed that this clade was characterized by having tetralophodont lower molars with a well-developed posterior arm of the metaconid and a posterior extension of metalophulid I. The tetralophodont morphology of lower cheek teeth is a general condition for South American rodents, so a conspicuous metalophulid II is a plesiomorphic character present in most caviomorphs. The posterior extension on metalophulid I appears as a synapomorphy of the clade restricted to node 2 (Fig. 3B), but its presence should be corroborated in more juvenile specimens of *Leucokephalos*. The posterior arm of the metaconid is a plesiomorphy absent in *Sallamys*, *Cephalomys* and most octodontoids.

Node 3 (Fig. 3B) is characterized by two synapomorphies: upper molars with absence of mesolophule (character 41[1]) and a metaloph lingually joined to the posteroloph (character 43[0]). Both characters have good distributions and have been previously proposed as Octodontoidea synapomorphies (Arnal *et al.*, 2014). Node 4 defines a clade formed by (*Eosacachui lavocati* (*Eospina woodi* *Sallamys? minutus*)) (Fig. 3B) supported by the presence of a long anterocingulum (character 19[1]) and absence of hypocone (character 26[0]) on P4, and paracone–metacone labially opposed (character 39 [0]) and absence of posteroloph–metacone connection (character 47 [0]) on upper molars. Node 5 (Fig. 3B) is characterized by the acquisition of mesodont cheek teeth (character 3[1]), retention of deciduous premolars (character 8[1]),

absence of metaloph on P4 (character 23[1]) and presence of a small mental foramen (character 107[0]). A further synapomorphy of this node is the presence of derived incisor enamel microstructure (character 104[2]), the only morphological character traditionally proposed as a synapomorphy of the Octodontoidea (Martin, 1992). Characters 3 and 23 were also proposed as synapomorphies of the superfamily (Arnal *et al.*, 2014). Retention of the deciduous premolars (character 8[1]) is only described for some octodontoids, but its evolution is still under study as the acaremyids [a fossil octodontoid family (see Vucetich & Kramarz, 2003; Arnal & Pérez, 2013; Arnal & Vucetich, 2015)] (node 7 of Fig. 3B) and *Deseadomys arambourgi* replaced this tooth as with most caviomorphs. An explanation could be that both taxa are actually more basal pan-octodontoids than the result yielded by this analysis, and consequently they are excluded from the clade defined at node 5 (Fig. 3B); alternatively, a repeated loss of the permanent premolar during the evolutionary history of pan-octodontoids or a reversion to the original dental replacement could have happened (less parsimonious for us). As previously proposed (Arnal *et al.*, 2014) a basal dichotomy is observed (node 5). One clade (defined at node 6) is formed by fossil taxa that lead to the differentiation of acaremyids, and another clade (defined at node 9) leads to the crown-Octodontoidea (Fig. 3B). Node 6 groups *Protacaremys*, *Acarechimys*, *Plesiacarechimys*, *Caviocricetus*, *Dudumus* and the Acaremyidae (*Platypittamys brachyodon* plus more derived taxa). This clade is characterized by hypocone lingually aligned to protocone on M1 and M2 (characters 45[1] and 46[1]), metacone reduced but distinct on M3 (character 50[1]) and laterally compressed lower incisors (character 101[0]). The Acaremyidae (node 8) (Fig. 3B) are here characterized by the replacement of deciduous premolars (character 8[0]), absence of mesolophule on M1–M3 (character 41[1]), presence of a spur of the posterior margin of metalophulid I on m1–m2 (character 96[0]), and nmmpio above the mid height in the mandible (character 111[0]). As proposed by Arnal & Pérez (2013) and Arnal & Vucetich (2015), *Platypittamys* is the earliest divergent acaremyid. Unlike the hypothesis of Vucetich *et al.* (2015), *Galileomys baios* is not directly related to *Galileomys antelucanus*, but it is an early acaremyid (*Acaremys murinus* and *G. antelucanus* are here recognized as sister taxa). Nevertheless, these relationships should be studied in a complete acaremyid context.

The lineage leading to crown-octodontoids (node 9) is characterized by having quadrangular M1 (character 56[0]), short posterolophid on m1–m2 (character 90[0]), hypoflexid transverse or opposed to the hypolophid or mesoflexid on m1–m3 (character 99[1]), small post-orbital processes (character 130[0]) and a poorly developed masseteric tuberosity (character 141[0])

in the skull. Nevertheless, most of these synapomorphies are reversals and the only true synapomorphy (small post-orbital processes) could be scored in only four taxa (*Prospaniomys*, *Myocastor*, *Ctenomys* and *Pithanotomys*). The earliest divergent taxon of this clade is *Prospaniomys priscus*. Node 10 (Fig. 3B) delimits Crown Octodontoidea (those caviomorphs originating from the last common ancestor of two or more extant caviomorphs); it is formed by a polytomy between *Protacaremys? adilos*, *Deseadomys*, *Eodelphomys*, *Ethelomys*, *Adelphomys*, *Stichomys*, *Spaniomys*, *Xylechimys*, *Myocastor* and octodontoids from the late Miocene – Recent (Fig. 3B). This clade is supported by 20 synapomorphies (see Appendix 3). The analysis yielded that *Protacaremys? adilos* is not closely related to the stem octodontoid *Protacaremys prior* (Fig. 3B). This Deseadan species is represented by an isolated right m2 and was originally described with doubts as *Protacaremys* owing to its tetralophodont morphology; however, the analysis performed here demonstrated that tetralophodont lower molars are plesiomorphic and are present in most caviomorphs. The systematic status of *Protacaremys? adilos* will remain dubious until more complete material is found. Some fossil taxa traditionally grouped in the subfamily ‘Adelphomyinae’ (Patterson & Pascual, 1968) are part of this polytomy (*Deseadomys*, *Ethelomys*, *Adelphomys*, *Stichomys* and *Xylechimys*). Nevertheless, the monophyly of this clade has been questioned (Arnal, 2012). In none of the 939 MPTs was *Ethelomys loomisi* grouped with *Deseadomys arambourgi*. So, the new combination proposed by Vucetich *et al.* (2015) is here corroborated. Node 11 is characterized by 19 synapomorphies (see Appendix 3). A remarkable result is the paraphyly of Echimyidae. In no MPTs does *Myocastor* cluster with the other three living ‘echimyids’ or with the fossil *Eumysops*. *Proechimys* and *Eumysops* show a different position within this clade. Node 12 is support by 11 synapomorphies (see Appendix 3) and groups Octodontidae and Ctenomyidae (Fig. 2B). *Neophanomys*, *Chasichimys bonaerense* and *Chasicomys octodontiforme* (late Miocene of Argentina) are excluded from this clade. *Neophanomys* was originally described as a Cavoidea (Rovereto, 1914), *Chasicomys octodontiforme* as an octodontid (Pascual, 1967) and *Chasichimys bonaerense* as an echimyid; nevertheless, their systematic position was subsequently changed (Verzi, 1999; Vucetich & Kramarz, 2003; Arnal & Pérez, 2013; Arnal *et al.*, 2014; Verzi *et al.*, 2014). In this work they are excluded from Octodontidae and Ctenomyidae, an hypothesis that is going to be tested in a complete octodontoid analysis. The monophyly of Octodontidae (node 13) is supported by five synapomorphies (see Appendix 3).

With regard to the origin of the remaining superfamilies, node 14 (Fig. 3B) is supported by five

synapomorphies: metaloph present and joined lingually to the posteroloph (character 13[1]) and strong mesostyle (character 15[2]) on DP4, P4 larger than or equal in size to M1 (character 17[0]), long anterocingulum (character 19[1]) and hypocone lingually aligned to protocone (character 27[1]) on P4. These are in general well-structured synapomorphies but should be studied in a broader cladistic context. The Contamana rodents, *Cachiyacuy* and *Canaanimys*, are the first two divergent taxa and are here considered stem caviomorphs. Erethizontoidea (node 15) is formed by *Eosteiomys homogenidens* and *Steiromys detentus* and are characterized by a paracone larger than metacone on M1–M3 (character 37[0]), metacone slightly lingual in relation to the paracone on M2 (character 39[1]), absence of metalophulid II (character 71[0]) and a strong anterior arm of the hypoconid (character 75[2]) on p4. *Garridomys curunuquem*, *Eoviscaccia frassinettii* and *E. boliviana* defined Chinchilloidea (node 16) and are characterized by the absence of mure on upper molars (character 48[0]), an anterior entoconid with respect to the hypoconid on m1–m3 (character 89[1]) and absence of the anterior arm of the hypoconid in unworn or little worn teeth (character 93[0]). It is noteworthy that elasmodonty (absence of mure on upper molars and absence of anterior arm of the hypoconid on lower molars) was previously proposed as a diagnostic feature for chinchilloids (Kramarz, Vucetich & Arnal, 2013). Cavioids are here represented only by the living *Dasyprocta*, whose autapomorphies are: mesolophule that reaches the labial side on P4 (character 22[2]), strong and high posterior arm of the paracone (character 38[2]), high anterior arm of the metacone (character 44[2]) and mesoflexus groove equal to metaflexus groove (character 53[1]) on upper molars, M2 longer than wide (character 57[2]), sub-equal talonid on p4 (character 78[0]), and on the mandible, small mental foramen dorso-anteriorly orientated and anteriorly to the lowest part of the diastema (characters 107[0], 108[2] and 109[0]). Except for cavioids (Pérez & Vucetich, 2012a, b; Vucetich *et al.*, 2014b) there are no comprehensive cladistic analyses for erethizontoids or chinchilloids including living and fossil forms. Therefore, the results obtained here concerning the relationships within and between superfamilies should be corroborated in broader cladistic contexts.

DISCUSSION AND CONCLUSIONS

The results of the analysis performed here confirmed the idea that a diversification event occurred early in the history of South American rodents, giving origin to one lineage leading to Pan-Octodontoidea, and another one (node 14) to Erethizontoidea, Cavioida and Chinchilloidea (Fig. 3) (Antoine *et al.*, 2012; Arnal *et al.*, 2014). In addition, there were also some caviomorphs

not included in any of these superfamilies (*Cachiyacuy*, *Canaanimys*) (Fig. 3B). Hence, these results differ from scenarios based on molecular evidence (Huchon *et al.*, 2007; Blanga-Kanfi *et al.*, 2009; Fabre *et al.*, 2012, 2013; Upham & Patterson, 2012; Patterson & Upham, 2014). As previously mentioned, the early evolutionary history of caviomorphs is still incompletely understood, in part because of the scanty cladistic analyses, but also because it is difficult to assign a taxonomic rank to the earliest caviomorphs that fits with the traditional taxonomic scheme (four caviomorph superfamilies and many families within them) owing to their generalized dental morphology (Vucetich & Kramarz, 2003; Vucetich *et al.*, 2010a; Antoine *et al.*, 2012; Bertrand *et al.*, 2012; Arnal *et al.*, 2014). For example, *Eosallamys*, *Eosachacui* and *Eospina* (late Eocene? of Peru), *Draconomys* (early Oligocene of Patagonia), *Sallamys* and *Migraveramus* (late Oligocene of Bolivia), and *Paulacoutomys* and *Sallamys? minutus* (late Oligocene of Brazil) were originally described as octodontoids (Patterson & Wood, 1982; Vucetich, Mazzoni & Pardiñas, 1993a; Vucetich & Ribeiro, 2003; Frailey & Campbell, 2004; Antoine *et al.*, 2012). But later, *Paulacoutomys* was considered an erethizontoid (Candela & Rasia, 2012) and based on cladistic analyses *Eosallamys*, *Draconomys* and *Sallamys* were excluded from the superfamily (Antoine *et al.*, 2012; Arnal *et al.*, 2014). Additionally, *Leucokephalos* and *Llitun* were described as *Caviomorpha incertae sedis* (Vucetich *et al.*, 2015). Taking these dilemmas into account, and based on de Queiroz (2007) we used a phylogenetic nomenclature and named the total clade Pan-Octodontoidea including *Draconomys verai* and all its descendants (Fig. 3B), as *Draconomys*, the clade formed by (*Eosallamys* (*Sallamys Leucokephalos Migraveramus Llitun Paulacoutomys*)), that of (*Eosachacui* (*Eospina Sallamys? minutus*)) and *Protacaremys* plus all its descendants are more closely related to living octodontoids than to any other living caviomorphs (Fig. 3B). Bertrand *et al.* (2012) proposed something similar for two other caviomorph families. We intend to use a phylogenetic definition that may be adjustable and flexible to future formal definitions, as the relationships of the stem and crown octodontoids may change in complete cladistic analyses (Simpson, 1945; Arnal *et al.*, 2014). The broader sense of Octodontoidea (Pan-Octodontoidea) used here changed the features that were proposed as characteristic of the superfamily. Characters previously proposed as synapomorphies of the superfamily characterized node 2 (i.e. absence of mesolophule and metaloph lingually joined to the posteroloph on upper molars (Arnal, 2012; Arnal *et al.*, 2014) and node 3 [i.e. mesodont cheek teeth and absence of metaloph on P4 (Arnal, 2012; Arnal *et al.*, 2014)] of Figure 3B. Nevertheless, the traditional morphological feature characterizing octodontoids [derived incisor enamel

microstructure in Martin (1992)] appears as an ambiguous synapomorphy in node 5. However, the incisor enamel microstructure of *Eospina*, *Eosachacui* and *Sallamys? minutus* (Fig. 3) is unknown.

The temporal data and the phylogenetic hypothesis provided here (Fig. 4) suggest that the basalmost event of diversification giving rise to both caviomorph lineages occurred during the middle Eocene (c. 45 Mya) (Fig. 4). Additionally, adaptive radiations (Schluter, 2000) occurred in the late Eocene (c. 40 Mya), in the uppermost part of the early Oligocene/lowermost part of the late Oligocene (c. 28 Mya), and in the late Miocene (c. 10 Mya) (Fig. 4). The first of these diversification events corresponds to the first South American rodent radiation which took place at low latitudes. The first caviomorphs arrived in the continent by the early Eocene (Vucetich *et al.*, 2010a; Antoine *et al.*, 2012). Some authors considered that after their arrival, primitive caviomorphs competed with and replaced different herbivore lineages (Simpson, 1980; Huchon & Douzery, 2001; Goin, Abello & Chornogubsky, 2010), an hypothesis that is partially supported by the fossil record (Goin *et al.*, 2010). It was during this first radiation event when the earliest stem and crown octodontoids differentiated (Figs 3B, 4). This event has not been previously proposed either for octodontoids or for the origin of the superfamily, as it is not evidenced by the fossil record, but it is indicated by ghost lineages observed in the results (Fig. 4). The early divergence time of crown octodontoids is given by the relatively derived phylogenetic position of the Peruvian *Eodelphomys* which pre-dates (perhaps by several million years) the massive appearance of most octodontoids in the fossil record (late Oligocene – early Miocene). This early origin of the superfamily is not in accordance with the age proposed by molecular analyses [Opazo, (2005) 20.6 ± 2.4 Mya; Fabre *et al.* (2013) 27.7–25.1 Mya; Upham & Patterson (2012) 28.9–24.8 Mya]. Accordingly, the evolutionary novelties that characterize the superfamily appeared in the late Eocene and lead to the differentiation of the most taxonomically and morphologically diverse group of caviomorphs. *Eosallamys*, *Eosachacui*, *Eospina* and *Eodelphomys* recorded in Santa Rosa (Peru) are representatives of this radiation. We are not able to make inferences about the origin and early differentiation of the remaining superfamilies because neither the earliest erethizontoid (*Eopululo*) nor the earliest cavioids (*Eoincamys*, *Eopicure* and *Eobranisamys*) from Santa Rosa (Peru) were included in this analysis.

A second caviomorph radiation is registered in the lowest part of the late Oligocene (c. 28 Mya). It had a great impact in pan-octodontoids because it provided the high morphological diversity observed in this group (Fig. 4). Unlike the first caviomorph radiation, this was a geographically extended event – with taxa

known from low (e.g. Bolivia, Brazil, Uruguay and northern Argentina) and high latitudes (five Patagonian localities) – and was characterized rather by the high number of species from Deseadan beds than by the number of ghost lineages (Fig. 4). This diversification event was related to the migration of rodents to high latitudes of the continent, the use of different ecological niches and the consequent phenotypical differentiation [e.g. environments with sparse trees and extensive open habitats (Bertrand *et al.*, 2012); global cooling resulting in the Patagonian Hinge (Goin *et al.*, 2010); opening of the landscape (Dunn *et al.*, 2015)]. In Patagonia the oldest caviomorphs were found in Gran Barranca (Chubut, Argentina) in a level known as ‘La Cantera’ (Vucetich *et al.*, 2010a) (Fig. 1) considered 30.77 and 30.62 Myr in age (Dunn *et al.*, 2013). Older Patagonian strata bearing mammals have been well studied but no caviomorphs have been found (Carlini, Ciancio & Scillato-Yané, 2010; Goin *et al.*, 2010). Hence, the arrival of rodents in central Patagonia is proposed for pre-La Cantera and post-La Cancha fauna’ (Tinguirirican of Gran Barranca) times, between 33.3 and 30.7 Mya (Vucetich *et al.*, 2010a). The posterior taxonomic and morphological differentiation in high latitudes of South America in post ‘La Cantera’ times (pre-Deseadan ages) (Fig. 4) is here recognized as the ‘first Patagonian octodontoid radiation’. This radiation event is coincident with the proposal of Upham & Patterson (2012) for the origin of the superfamily. By the early Miocene (Colhuehuapian, ‘Pinturan’ and Santacrucian SALMAs) pan-octodontoids were the most abundant caviomorphs in the fossil record and had the highest morphological disparity. Their acme occurred during the Colhuehuapian with 12 genera and 18 species. Their diversity decreased later, in the ‘Pinturan’ and Santacrucian being represented by 11 genera each of one and several nominal species. The taxa differentiated in this second radiation event are part of the stem-octodontoids (Fig. 4). By the middle Miocene the pan-octodontoid fossil record decreased notably (Vucetich *et al.*, 1993b; Vucetich & Vieytes, 2006; Arnal & Pérez, 2013) and by the late Miocene, when climatic conditions became increasingly rigorous in southern South America, most of the fossil stem and the oldest crown octodontoids became extinct (Fig. 4). A similar fossil record pattern is observed in the remaining caviomorph superfamilies, but what we observed in octodontoids is the replacement in the late Miocene of ‘old’ forms by ‘modern’ taxa with undoubtedly relationships with living forms (see below; Fig. 4). Based on a molecular cladistic analysis Fabre *et al.* (2012) detected a significant shift in diversification rate for living octodontoids in the Miocene (without specifying which part of the Miocene). However, they did not detect a similar shift at the base of Caviomorpha, despite their high diversity, and explained it as a consequence of the

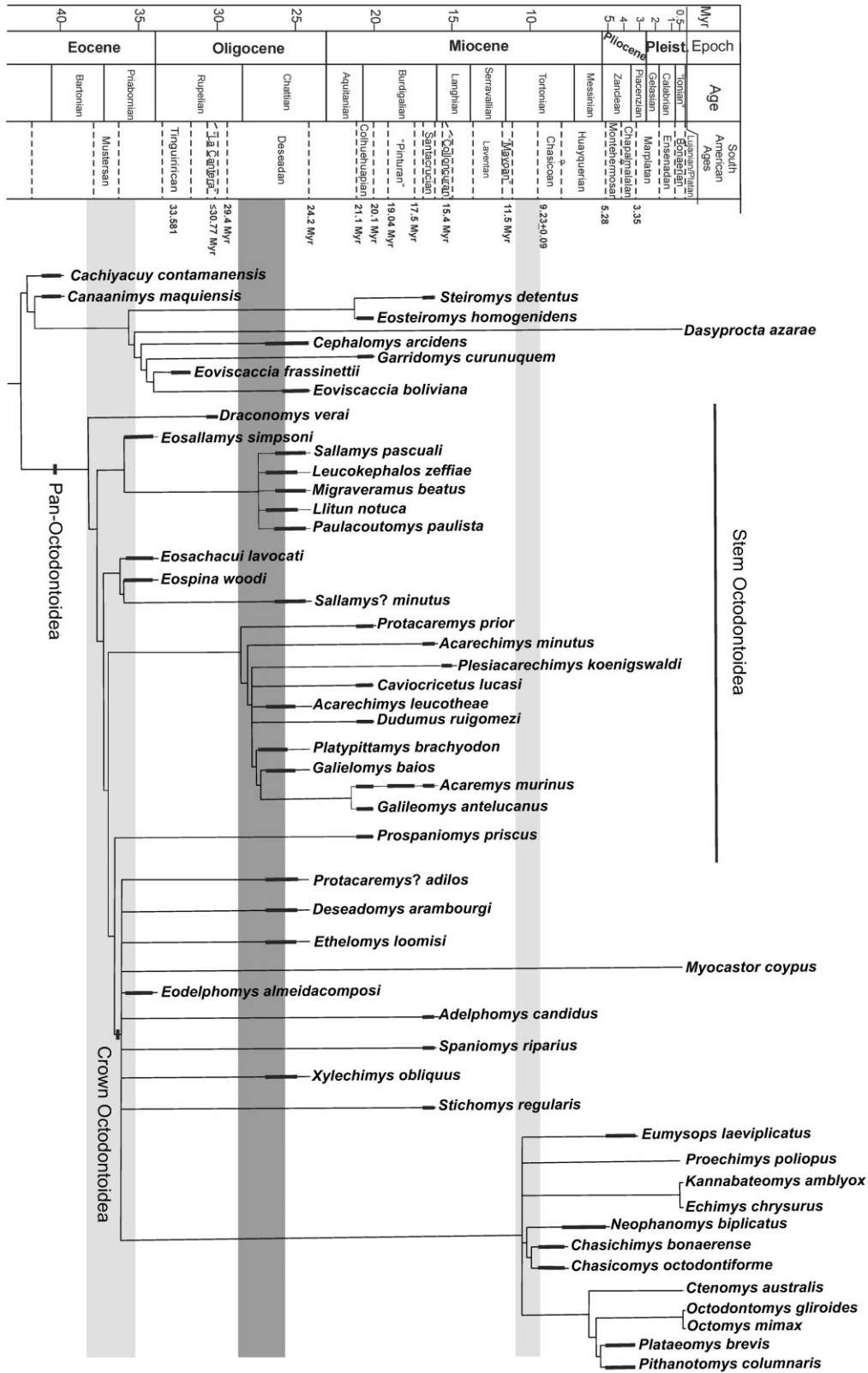


Figure 4. Phylogenetic hypothesis combined with the stratigraphic information. Thick branches mark the temporal extension of taxa based on its first occurrence in the fossil record. Grey horizontal bars show the three diversification events mentioned in the text; dark grey represents the first Patagonia radiation (second South American radiation event).

extinction of taxa of the earliest caviomorph radiations. Something similar could have happened with octodontoids, and the phylogenetic analysis with molecular data could have been unable to detect the first two diversification events in the superfamily reported here (late Eocene, *c.* 40 Mya and uppermost part of the early Oligocene/lowermost part of the late Oligocene, *c.* 28 Mya) as it is represented by extinct species with no direct relationships with the living ones.

The third radiation corresponds to the differentiation of those ‘modern’ octodontoids that are closely related to most living forms. It is inferred to have occurred in the late Miocene, agreeing with previous proposals (Vucetich, Verzi & Hartenberger, 1999; Honeycutt, Rowe & Gallardo, 2003) (Fig. 4). These octodontoids are characterized by having cheek teeth with a marked tendency to hypsodonty and a concomitant simplification of the molar pattern traditionally recognized as octodontids (e.g. *Chasichimys*, *Neophanomys*, *Plataeomys*, *Pithanotomys*), as well as others with protohypsodont cheek teeth with a simplified lophate occlusal pattern traditionally recognized as ‘echimyids’ (*Eumysops*, *Reigechimys* Verzi, Vucetich & Montalvo, 1994, and *Theridomysops* Vucetich, 1995). Our results do not agree with the monophyly and the time of differentiation of extant ‘echimyids’ (here represented by *Myocastor*, *Echimys*, *Kannabateomys* and *Proechimys*) proposed by molecular analyses (Honeycutt *et al.*, 2003; Upham & Patterson, 2012; Fabre *et al.*, 2013; Upham *et al.*, 2013). Nevertheless, this hypothesis needs to be evaluated in a broader ‘echimid’ context. Results from the analysis performed here reject the close relationship of the living *Myocastor coypus* with the remaining living ‘echimyids’; it would be more closely related to extinct taxa traditionally included in the subfamily ‘Adelphomyinae’ (Patterson & Pascual, 1968; Patterson & Wood, 1982; Kramarz, 2001). The monophyly of this clade should be confirmed in a complete octodontoid context. Meanwhile, names such as ‘echimyids’ should be used with caution especially when dealing with fossil species, explaining which taxa are included in the analysis. The monophyly of Octodontidae is here recovered, as well as its sister relationships with ctenomyids. We suggest a late Miocene origin for these families from an ‘echimid-like’ ancestor. Further analysis with a broader extant octodontoid sampling is necessary to understand this third radiation with other methods (molecular phylogenies using molecular clocks methods to estimate divergence ages).

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APPENDIX 2

List of taxa included in the cladistic analysis. Bold type indicates new taxa included in the analysis performed here.

Taxa	Location	Age (SALMA)	
Baluchimyinae	<i>Bugtimys zafarullahi</i>	Pakistan (Balochistan, Bugti Hills, Bugti Member, Chitarwata Fm)	early Oligocene
Phiomyidae	<i>Phiomys andrewsi</i>	Egypt (Jebel Qatrani Fm)	early Oligocene
	<i>Metaphiomys schaubi</i>	Egypt (upper sequence of the Jebel Qatrani Fm)	late Eocene – early Oligocene
Basal Caviomorpha	<i>Cachiyacuy contamanensis</i>	Peru, Contamana (top of the Yahuarango Fm)	middle Eocene
	<i>Canaanymys maquiensis</i>	Peru, Contamana (top of the Yahuarango Fm)	middle Eocene
Erethizontoidea	<i>Eosteiomys homogenidensis</i>	Argentina, Gran Barranca and Bryn Gwyn, Chubut Province (Sarmiento Fm)	early Miocene (Colhuehuapian)
	<i>Steiomys detentus</i>	Argentina, Santa Cruz Province (Santa Cruz Fm)	early Miocene (Santacrucian)
Cavioidea	<i>Dasyprocta azarae</i>	Brazil, Paraguay, and Argentina	recent
Chinchilloidea	<i>Eoviscaccia frassinetti</i>	Chile, Tinguiririca	early Oligocene
	<i>Eoviscaccia boliviana</i>	Bolivia, Lacayani	late Oligocene (Deseadan)
	<i>Garridomys curunuquem</i>	Argentina, Neuquén Province (Cerro Bandera Fm)	early Miocene (Colhuehuapian)
Cephalomyidae	<i>Cephalomys arcidens</i>	Argentina (Cabeza Blanca and La Flecha localities) and Bolivia (Lacayani)	late Oligocene (Deseadan)
Pan-Octodontoidea	<i>Eodelphomys almeidacomposi</i>	Peru, Santa Rosa (Yarahuangó Fm?)	late Eocene? /early Oligocene?
	<i>Eosallamys simpsoni</i>	Peru, Santa Rosa (Yarahuangó Fm?)	late Eocene? – early Oligocene?
	<i>Eosachacui lavocati</i>	Peru, Santa Rosa (Yahuarango Fm?)	late Eocene? /early Oligocene?
	<i>Eospina woodi</i>	Peru, Santa Rosa (Yahuarango Fm?)	late Eocene? /early Oligocene?
	<i>Draconomys verai</i>	Gran Barranca, Chubut Province, Argentina (Sarmiento Fm)	early Oligocene
	<i>Sallamys? minutus</i>	Brazil, Sao Paulo (Tremembé Fm)	late Oligocene (Deseadan)
	<i>Paulacoutomys paulista</i>	Brazil, Sao Paulo (Tremembé Fm)	late Oligocene (Deseadan)
	<i>Acarechimys leucotheae</i>	Argentina, Cabeza Blanca, Chubut Province (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Migraveramus beatus</i>	Bolivia (Salla- Luribay Basin)	late Oligocene (Deseadan)
	<i>Sallamys pascuali</i>	Bolivia (Salla- Luribay Basin)	late Oligocene (Deseadan)
	<i>Leucokephalos zeffiae</i>	Argentina, Cabeza Blanca, Chubut Province, (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Llitun notuca</i>	Argentina, Cabeza Blanca, Chubut Province, (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Changquin woodi</i>	Argentina, Scarrit Pocket, Chubut Province (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Deseadomys arambourgi</i>	Argentina, Cabeza Blanca and La Flecha, Chubut Province (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Ethelomys loomisi</i>	Argentina, Cabeza Blanca, Chubut (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Protacaremys? adilos</i>	Cabeza Blanca, Chubut Province, Argentina (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Xylechimys obliquus</i>	Argentina, Laguna de los Machos, Chubut Province (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Caviocricetus lucasi</i>	Argentina, Bryn Gwyn, Chubut Province (Sarmiento Fm)	early Miocene (Colhuehuapian)
	<i>Dudumus ruigomezi</i>	Argentina, Bryn Gwyn, Chubut Province (Sarmiento Fm)	early Miocene (Colhuehuapian)
	<i>Prospaniomys priscus</i>	Argentina, Gran Barranca, Pampa de Gan Gan, Chubut Province (Sarmiento Fm)	early Miocene (Colhuehuapian)
	<i>Protacaremys prior</i>	Argentina, Gran Barranca and Bryn Gwyn, Chubut Province (Sarmiento Fm)	early Miocene (Colhuehuapian)
	<i>Acarechimys minutus</i>	Argentina, Santa Cruz (Santa Cruz Fm)	early Miocene (Santacrucian)
	<i>Adelphomys candidus</i>	Argentina, Santa Cruz (Santa Cruz Fm)	early Miocene (Santacrucian)
	<i>Spaniomys riparius</i>	Argentina, Santa Cruz (Santa Cruz Fm)	early Miocene (Santacrucian)
	<i>Stichomys regularis</i>	Argentina, Santa Cruz (Santa Cruz Fm)	early Miocene (Santacrucian)
	<i>Plesiacaarechimys koenigsvaldi</i>	Argentina, Neuquén (Collon Curá Fm)	middle Miocene (Colloncuran)
	<i>Chasicomys bonaerense</i>	Argentina, Buenos Aires (Chasicó Fm)	late Miocene (Chasicooan)
	<i>Chasicomys octodontiforme</i>	Argentina, Buenos Aires (Chasicó Fm)	late Miocene (Chasicooan)
	<i>Neophanomys biplicatus</i>	Argentina, Catamarca, Mendoza, and La Pampa Provinces	late Miocene (Chasicooan)
	<i>Eumysops laeviplicatus</i>	Argentina, Buenos Aires Province (Monte Hermoso, Irene Fm)	early Pliocene (Chasicooan)
	<i>Kannabateomys amblyox</i>	E Brazil, Paraguay, NE Argentina	Recent
	<i>Myocastor coypus</i>	S Brazil, Paraguay, Uruguay, Bolivia, Argentina, Chile	Recent
	<i>Proechimys poliopus</i>	NW Venezuela, Colombia, and	Recent
Acaremyidae	<i>Acaremys murinus</i>	Argentina, Chubut and Santa Cruz Provinces (Sarmiento, Pinturas, and Santa Cruz Fm)	early Miocene (Colhuehuapian, Pinturan, and Santacrucian)
	<i>Galileomys antelucanus</i>	Argentina, Gran Barranca, Chubut Province (Sarmiento Fm)	early Miocene (Colhuehuapian)
	<i>Galileomys baios</i>	Argentina, Cabeza Blanca, Chubut (Sarmiento Fm)	late Oligocene (Deseadan)
	<i>Platypittamys brachyodon</i>	Argentina, Scarrit Pocket, Chubut Province (Sarmiento Fm)	late Oligocene (Deseadan)
Ctenomyidae	<i>Ctenomys australis</i>	E Argentina	Recent
Octodontidae	<i>Piathanotomys columnaris</i>	Buenos Aires Province	Pliocene
	<i>Plataeomys brevis</i>	Buenos Aires Province	Pliocene
	<i>Octodontomys gliroides</i>	Chile, Bolivia, and Argentina	Recent
	<i>Octomys mimax</i>	Argentina, Catamarca, La Rioja, San Juan, and Mendoza Provinces	Recent

APPENDIX 3

List of characters of the data matrix. We cite the source of characters taken from the literature, using an asterisk to signify some modifications of the original analysis. The following characters are treated as ordered: 3, 14, 15, 22, 31, 38, 44, 52, 54, 55, 59, 61, 67, 69, 75, 80, 83, 84, 99, 103, 104, 107, 109, 113, 118, 119, 128, 148, 161 and 164

TOOTH CHARACTERS

- (1) P3/DP3: present (0), absent (1).
- (2) Cingula: present (0), absent (1).
- (3) Crown height: brachyodont (0), mesodont (1), protohypsodont (2), euhypsodont (3).
- (4) Roots number on upper molars: three (0), four (1).
- (5) Tooth row: straight (0), convex (1).
- (6) Tooth rows: parallel (0), anteriorly slightly convergent (1), anteriorly very convergent (2), anteriorly slightly divergent (3).
- (7) Crest thickness in occlusal view: more slender than flexi/ids (0), equal or broader than flexi/ids (1).
- (8) Deciduous premolars (Marivaux *et al.*, 2004): replacement (0), retention (1).
- (9) Terraced occlusal surface: present (0), absent (1).
- (10) Cusp differentiation: yes, labial cusps of upper molars and lingual cusps of lower molars wider than their associated crests (0), no, cusps indistinct, entirely submerged in their associated crests (1).
- (11) Enamel on upper molars: complete and uniformly distributed (0), complete and not uniformly distributed (1), interrupted on the labial side (2), interrupted on the posterior wall of the posterior lobe (3).
- (12) Mesolophule on DP4: present (0), absent (1).
- (13) Metaloph on DP4: present and joined lingually to the anterior arm of the hypocone (0), present and joined lingually to the posteroloph (1), indistinct, probably fused to the posteroloph (2), connected to the metaconule (3).
- (14) Anterior arm of the metacone on DP4 (Antoine *et al.*, 2012): absent (0), weakly pronounced (1), high (2).
- (15) Mesostyle on DP4 (Antoine *et al.*, 2012): indistinct or absent (0), moderate (1), strong (2).
- (16) Hypocone on DP4 (Antoine *et al.*, 2012)*: small (0), moderate (as large as the protocone) (1).
- (17) Size of P4 respect M1 (Marivaux *et al.*, 2004)*: P4 > or = M1 (0), P4 < M1 (1).
- (18) Crown outline of P4 (Antoine *et al.*, 2012)*: transverse (0), oval (1), heart shape (2), quadrangular (3), reversed heart shape (4), subtriangular (5).
- (19) Anterocingulum on P4 (Antoine *et al.*, 2012)*: small, short (0), long (1).
- (20) Anterocingulum on P4 (Antoine *et al.*, 2012): low (0), high (anteroloph) (1).
- (21) Anterocingulum (or anteroloph) – paracone connection (Antoine *et al.*, 2012): absent (0), present (via a parastyle or not) (1).
- (22) Mesolophule on P4 (Antoine *et al.*, 2012): absent (0), short (1), reaches the buccal side (2).
- (23) Metaloph on P4: present (0), absent (1).
- (24) Metaloph on P4 (Antoine *et al.*, 2012)*: connected to the metaconule (0), connected to the anterior arm of the hypocone (1), connected to the posteroloph (2).
- (25) Metacone on P4 (Antoine *et al.*, 2012)*: small (0), strong (1).
- (26) Hypocone on P4: absent (0), present (1).
- (27) Hypocone on P4: labial to protocone (0), lingually aligned to protocone (1).
- (28) Anterior arm of the hypocone on P4 (Antoine *et al.*, 2012): absent (0), present (1).
- (29) Posteroloph – metacone connection on P4 (Antoine *et al.*, 2012): absent (0), present (1).
- (30) Hypoflexus on P4: absent (0), present (1).
- (31) Hypoflexus on P4: as a superficial lingual groove (0), as a moderately deep lingual groove separating protocone and hypocone, less penetrating than in molars (1), very deep, as in molars (2).
- (32) Division of the mesofossette into two fossettes on P4: absent (0), present (1).
- (33) Eight dental patterns in upper molars: absent (0), present (1).
- (34) Crest obliquity on M1–M3: transversal to the anteroposterior axis of the teeth (0), anterolabially-posterolingually oblique (1). All crests should be oblique to consider character state 1.
- (35) Anteroloph on M1–M3 (Antoine *et al.*, 2012)*: moderately high (0), high (1).
- (36) Anteroloph on M1–M3: short, not reaching the paracone (0), reaches the paracone (1), long, reaches the labial border of the crown but not connected to the paracone (2).
- (37) Paracone on M1–M3: larger than metacone (0), equal to metacone (1).
- (38) Posterior arm of the paracone (Antoine *et al.*, 2012): absent (0), weakly pronounced (1), strong and high (2).
- (39) Paracone – metacone position on M2 (Antoine *et al.*, 2012): mesiodistally opposed (0), metacone slightly lingual (1).
- (40) Anterolingual angle of the tooth on M1–M3: rounded or forming an obtuse angle (0), forming a right angle (1).
- (41) Mesolophule on M1–M3: present (0), absent (1).
- (42) Direction of the mesolophule (Antoine *et al.*, 2012)*: straight (transverse) (0), slightly oblique (posterolabially orientated) (1).

- (43) Metaloph on M1–M3: lingually joined to the anterior arm of the hypocone (0), lingually joined to the posteroloph (1), indistinct, probably fused to the posteroloph (2), lingually joined to the mesolophule (3).
- (44) Anterior arm of the metacone (Marivaux *et al.*, 2004)*: absent (0), weakly pronounced (1), high (2).
- (45) Hypocone on M1: labial to protocone (0), lingually aligned to protocone (1).
- (46) Hypocone on M2: labial to protocone (0), lingually aligned to protocone (1).
- (47) Posteroloph – metacone connection (Antoine *et al.*, 2012): absent (0), present (1).
- (48) Mure (Marivaux *et al.*, 2004)*: absent (0), present (1).
- (49) Mure connection (Antoine *et al.*, 2012): on the protoloph (central to the tooth) (0), on the protoloph more lingually (1).
- (50) Metacone size on M3 (Antoine *et al.*, 2012): distinct cusp (as large as the paracone) (0), reduced but distinct (1), crestiform (2).
- (51) Hypocone position in relation to the protocone on M3 (Antoine *et al.*, 2012)*: more labial (0), strongly more labial (1), at the same level (2).
- (52) Hypoflexus orientation on M1–M3: anteriorly oblique (0), slightly anteriorly oblique or transverse to the anteroposterior axis of the tooth (1), posteriorly oblique (2).
- (53) Mesoflexus groove respect metaflexus groove in M1–M2: mesoflexus groove deeper than metaflexus groove (0), mesoflexus groove equal than metaflexus groove (1).
- (54) Size of M1/M2 (Antoine *et al.*, 2012)*: M1 < M2 (0), M1 = M2 (1), M1 > M2 (2).
- (55) Size of M3/M2 (Antoine *et al.*, 2012): M3 < M2 (0), M3 = M2 (1), M3 > M2 (2).
- (56) M1 length/width proportions (Antoine *et al.*, 2012)*: length = width (0), length < width (1), length > width (2).
- (57) M2 length/width proportions (Antoine *et al.*, 2012)*: length = width (0), length < width (1), length > width (2).
- (58) Upper incisors: laterally compressed (0), laterally no compressed (1).
- Laterally compressed when anteroposterior diameter/transverse diameter ≥ 1.5 .
- (59) Posterior arm of the metaconid (metastylar fold) on dp4 (Marivaux *et al.*, 2004): absent (0), weak and low (1), well developed and high (2).
- (60) Anteroconid on dp4 (Marivaux *et al.*, 2004): present (0), absent (1).
- (61) Metaconid position with respect to protoconid on dp4: anterior (0), aligned (1), posterior (2).
- (62) Metalophulid I on dp4: present (0), absent (1).
- (63) Metalophulid II on dp4: present (0), absent (1).
- (64) Metalophulid II on dp4: conspicuous (0), reduced (1).
- (65) Mesolophid on dp4: present (0), absent (1).
- (66) Mesolophid on dp4: conspicuous (0), reduced (1).
- (67) Ectolophid on dp4 (Marivaux *et al.*, 2004)*: absent (0), mesially interrupted (unconnected to the protoconid) (1), complete (connected to the protoconid) (2).
- (68) Metaconid position with respect to protoconid on p4: anterior (0), aligned (1).
- (69) Posterior arm of the metaconid (metastylar fold) on p4 (Marivaux *et al.*, 2004)*: absent (0), weak and low (1), well-developed, high, and long (2).
- (70) Flexid on anterior aspect of metalophulid I on p4 (Vucetich & Kramarz, 2003): present (0), absent (1).
- (71) Metalophulid II on p4: absent (0), present (1).
- (72) Mesolophid on p4: absent (0), present (1).
- (73) Mesolophid on p4 (Antoine *et al.*, 2012): short (0), long, reaches the lingual side (1).
- (74) Hypolophid on p4 (Marivaux *et al.*, 2004): absent (0), present (1).
- (75) Anterior arm of the hypoconid on p4 (Antoine *et al.*, 2012): absent (0), thin (1), strong (2).
- (76) Hypoconulid on p4 (Antoine *et al.*, 2012): minute to absent (0), moderate (1).
- (77) Posterolophid – entoconid connection (Antoine *et al.*, 2012): absent (0), present (1).
- (78) Talonid on p4 (Marivaux *et al.*, 2004)*: sub-equal (0), wider than the trigonid (1).
- (79) Size of p4/m1 (Marivaux *et al.*, 2004)*: p4 > or = m1 (0), p4 < m1 (1).
- (80) Proportion of p4 (Antoine *et al.*, 2012)*: length clearly > width (0), length > width (1), length > or = width (2).
- (81) Enamel on lower molars: complete and uniformly distributed (0), complete and not uniformly distributed (1), interrupted on the anterior face and anterior face of hypoflexid (2).
- (82) Eight occlusal patterns on upper molars: absent (0), present (1).
- (83) Anterofossettid and metafossettid on m1–m3: persistent (0), ephemeral (1), absent (2). Fossettids are considered ephemeral when they are lost in juvenile-adult specimens.
- (84) Metaconid position respect protoconid on m1–m3: anterior (0), aligned (1), posterior (2).
- (85) Metalophulid II on m1–m2: present (0), absent (1).
- (86) Metalophulid II on m1–m2: complete (0), reduced (1).
- (87) Metalophulid II connection (Antoine *et al.*, 2012)*: anterolabially to the metaconid (0), posterolingually to the metaconid, on the posterior arm of the metaconid (1), posterolingually to the

- metaconid, on the mesostylid (2), do not contact neither (3), to the anterior projection of metalophulid I (4).
- (88) Metalophular spur (Antoine *et al.*, 2012)*: absent (0), short (1).
- (89) Entoconid position respect hypoconid on m1–m3: aligned (0), anterior (1).
- (90) Posterolophid on m1–m2: short (0), long (1).
- (91) Posterolophid – entoconid connection (Antoine *et al.*, 2012): absent (0), present (1).
- (92) Crest obliquity on m1–m3: transversal to the anteroposterior axis of the teeth (0), anterolabially – posterolingually oblique (1). All crests should be oblique to consider character state 1.
- (93) Anterior arm of the hypoconid: absent in unworn or little worn teeth (0), present in all stages (1).
- (94) Mesiodistal pinch of the hypoconid (Antoine *et al.*, 2012): absent (0), present (1).
- (95) Hypoconulid on m1–m3: recognizable (0), indistinct (1).
- (96) Spur of the posterior margin of metalophulid I on m1–m2: present (0), absent (1).
- (97) Accessory cusp posterior to metalophulid I on m1–m2: present (0), absent (1).
- (98) Posterior arm of metaconid on m1–m2: present (0), absent (1).
- (99) Hypoflexid orientation on m1–m3: posteriorly oblique, or opposed to the metaflexid or hypolophid (0), transverse or opposed to the hypolophid or mesoflexid (1) anteriorly oblique or opposed to the anteroflexid (2).
- (100) Size of m3/m2 (Marivaux *et al.*, 2004): m3 = m2 (0), m3 < m2 (1).
- (101) Lower incisors: laterally compressed (0), laterally no compressed (1).

Laterally compressed when antero-posterior diameter is at least 1.5 the width.

- (102) Labial side of lower incisors: curve (0), forming a right lingual border and a curved labial one (1), plane (2).
- (103) Lower incisors: long, passing beneath m3 (0), the base reaching m3 (1), short, the base does not reaches m3 (2).
- (104) Lower incisors enamel microstructure (Vucetich & Vieytes, 2006): multiserial HSB with acute IPM (0), multiserial HSB with transitional IPM (1), multiserial HSB with rectangular IPM (2).

MANDIBLE CHARACTERS

- (105) Diastema length: shorter than the p4(dp4)–m1 distance (0), equal or larger than the p4(dp4)–m1 distance (1).
- (106) Mental foramen: present (0), absent (1).

- (107) Development of the mental foramen: small (0), conspicuous (1), large (2).
- (108) Orientation of the mental foramen: externally orientated (0), anteriorly orientated (1), dorso-anteriorly orientated (2).
- (109) Position of the mental foramen: anterior to the lowest part of the diastema (0), at the lowest part of the diastema (1), beneath p4/dp4 (2).
- (110) Position of the anterior border of notch for the masseter muscle pars infraorbitalis (nmmpio): beneath m1 (0), anterior to m1 (1).
- (111) Position of the nmmpio respect mandible high: above the mid high (0), at the middle of the mandible high (1).
- (112) Origin of the masseteric crest: includes the nmmpio (0), does not include the nmmpio (1).
- (113) Depth of the anterior portion of the masseteric fossa (Candela, 2000): shallow or flat (0), moderately deep (1), deep (2), very deep (3).
- (114) Anterior margin of the coronoid process: convex (0), straight (1), concave (2).
- (115) Mandibular notch: conspicuous (0), poorly developed or absent (1).
- (116) Height of the coronoid process with respect to the mandibular condyle: same high (0), ventral to the condyle (1).
- (117) Height of the mandibular condyle: higher than the occlusal surface (0), as the occlusal surface (1).
- (118) Posterior border of the mandibular symphysis: anterior to the premolars (0), at the level of the premolars (1), posterior to the premolars (2). It is measured with the tooth row horizontal.

SKULL CHARACTERS

- (119) Posterior extension of the premaxillaries related to nasals: shorter (0), equal (1), longer (2).
- (120) Frontal extension between nasals and premaxillaries: absent (0), present (1).
- (121) Nasals shape: parallel lateral margins (0), lateral margins wider anteriorly (1).
- (122) Incisor included into the rostral masseteric fossa: no (0), yes (1).
- (123) Incisor foramina: length (0), short (1). They are considered long when its length is equal or larger than the half of the length of the diastema.
- (124) Incisor foramina shape: laterally narrow (0), anteriorly narrow (1), posteriorly narrow (2), both extremes acute (3). They are considered narrow when they are equally wide along the length of the foramina.
- (125) Premaxillary-maxillary suture: at the posterior border of the incisor foramina (0), at the middle length of the incisor foramina (1), posterior to the incisor foramina (2).

- (126) Diastemal ridges: absent (0), present (1).
- (127) Diastemal ridges: poorly developed (0), conspicuous (1).
- (128) Frontals: wider anteriorly than posteriorly (0), straight lateral margins (1), narrower anteriorly than posteriorly (2), concave lateral margins (3).
- (129) Post-orbital process: absent (0), present (1).
- (130) Post-orbital process: small (0), conspicuous (1).
- (131) Conformation of the post-orbital process: build only by the frontal (0), build by the frontal and parietal (1).
- (132) Post-orbital constriction: absent (0), present (1).
- (133) Post-orbital constriction: small (0), conspicuous (1).
- (134) Position of the zygomatic dorsal root (ZDR): anterior to M1 (0), at the level of M1 or M1–M2 (1).
- (135) Exposition of the lacrimal onto the vertical or ZDR: little exposed (0), conspicuous (1), no exposed (2).
- (136) Ventral root of the zygomatic arch (ZVR): similar anteroposterior and dorsoventral diameters (0), anteroposterior diameter twice dorsoventral or more (1).
- (137) ZVR with respect to the palatal level: at the same level (0), ZVR dorsal (1).
- (138) ZDR with respect to ZVR: aligned (0), posterior (1).
- (139) Groove for the infraorbitalis nerve within the infraorbital foramen: absent (0), present (1).
- (140) Groove for the passage of the infraorbitalis nerve within the infraorbital foramen: present with a small lateral rim (0), present with a large lateral rim (1).
- (141) Masseteric tuberosity (for the insertion of the masseteric superficial muscle): poorly developed (0), well developed (1).
- (142) Paraorbital process: present (0), absent (1).
- (143) Paraorbital process: build by the jugal and squamosal (0), build by the squamosal (1), build by the jugal (2).
- (144) Jugal fossa: present (0), absent (1).
- (145) Depth of the jugal fossa: superficial (0), deep (1).
- (146) High of the jugal fossa: low (0), high (1).
- (147) Length of the jugal fossa: antero posteriorly short (0), antero posteriorly long (1). It is considered long when its length is equal or longer than the length of the horizontal ramus of the zygoma.
- (148) Ethmoidal foramen: at the level of M3 (0), at the level of M2–M3 (1), at the level of the M2–M1 (2), at the level of the M2 (3).
- (149) Sphenopalatine foramen: anterior to the M1 (0), at the level of M1 (1), posterior to M1 (2), groove located at the DP4–M1 level (3), groove located at the M1–M2 level (4).
- (150) Posterior palatine foramina: between palatines and maxillaries at the M1 (0), into the maxillary at the level of the premolar (1), into the maxillary at the level of M1 (2).
- (151) Posterior palatine foramina: small (0), conspicuous (1).
- (152) Posterior nares: at the level of M3 (0), at the level of M2 (1).
- (153) Spheno-palatine vacuities: absent (0), present (1).
- (154) Spheno-palatine vacuities: small (0), conspicuous (1).
- (155) Buccinator and masticatory foramina: separated (0), fused (1).
- (156) Oval foramen: bounded by the alisphenoid (0), bounded posteriorly by the tympanic bulla (1), bounded by the alisphenoid and pterygoids (2).
- (157) Ventral extension of the lateral process of the supraoccipital: exceeds the dorsal border of the bulla (0), extends until the dorsal border of the bulla (1), do not reach the dorsal border of the bulla (2).
- (158) Parietals on the skull roof: reach or are close to the occiput (0), retracted and not near the occiput (1).
- (159) Dorsal extension of the mastoid exposure: do not exceed the dorsal border of the bulla (0), exceeds the dorsal border of the bulla (1), mastoid exposed on the skull roof (2).
- (160) Mastoid exposure on the occiput: absent (0), present (1).
- (161) Shape of the mastoid exposure: concave (0), plane (1), convex (2).
- (162) Dorsal exposition of the petrosal: absent (0), present (1).
- (163) Epitympanic sinus: small (0), conspicuous (1).
- (164) Hypotympanic recess: small (0), inflated (1), hypertrophied (2).
- (165) Accessory foramen below MAE: absent (0), present (1).
- (166) Accessory foramen below MAE: small (0), conspicuous (1).
- (167) Paraoccipital process: ventrally orientated with its tip separated from the bulla and well developed (0), ventrally orientated, with its tip fused to the bulla (1), short, laterally orientated and completely fused to the bulla (2), short, ventrally orientated and completely fused to the bulla (3).

APPENDIX 4

LIST OF SYNAPOMORPHIES MENTIONED IN THE TEXT
 Node 9: Anteriorly slightly convergent tooth rows (character 6[1]), crests equal or broader than flexi/ids (character 7[1]), cusps indistinct, entirely submerged in their associated crests (character 10[1]), long anteroloph that

is not connected to the paracone (character 36[2]), paracone – metacone antero-posteriorly opposed on M2 (character 39[0]), absence of mesolophid on dp4 (character 65[1]), metalophulid II antero-labially connected to the metaconid (character 87[0]) and absence of posterior arm of metaconid (character 98[1]) on m1–m2, base of lower incisors reaches m3 (character 103[1]), anterior border of the nmmpio beneath m1 (character 110[0]), incisor included into the rostral masseteric fossa (character 122[1]), zygomatic dorsal root (ZDR) located at M1 or M1–M2 (character 134[1]), little exposed lacrimal onto the vertical or ZDR (character 135[0]), antero-posterior diameter of the ventral root of the zygomatic arch twice dorso-ventral diameter (character 136[1]), ZVR dorsal respect the palatal level (character 137[1]), posterior palatine foramina into the maxillaries at the level of M1 (character 150[2]), plane mastoid exposure (character 161 [0]), small epitympanic sinuses (character 163 [0]), small hypotimpanic recess (character 164 [0]), and absence of accessory foramen below MAE (character 165 [0]).

Node 10: Protohypsodont cheek teeth (character 3[2]), hypocone lingually aligned to protocone on M1 (character 45[1]), hypocone labial to the protocone on M3 (character 51[0]), M1 = M2 in size (character 54[1]), absence of metalophulid II on m1–m2 (character 85[1]), metalophulid II not contacting the metaconid (character 87[3]), entoconid anterior to hypoconid (character 89[1]) and long posterolophid on m1–m3 (character 90[1]), transverse crests on lower cheek teeth (character 92[0]), long lower incisors (character 103[0]), absence of mental foramen (character 106[1]), anteri-

or border of the nmmpio anterior to m1 (character 110[1]), moderately deep anterior portion of the masseteric fossa in the mandible (character 113[1]), convex anterior margin of the coronoid process (character 114[0]), long incisor foramina (character 123[0]), absence of post-orbital process (character 129[0]), small post-orbital constriction (character 133[0]), high jugal fossa (character 146[1]), and posterior palatine foramina between palatines and maxillaries bones at the level of M1 (character 150[0]) on the skull.

Node 11 (Octodontidae Ctenomyidae): euhypsodont cheek teeth (character 3[3]), presence of posteroloph – metacone connection on upper molars (character 46[1]), absence of anterofossettid and metafossettid on lower molariforms (character 83[2]), on the mandible origin of the masseteric crest does not include the nmmpio (character 112[1]), on the skull nasals with lateral margins wider anteriorly (character 121[1]), well developed masseteric tuberosity (character 141[1]), sphenopalatine groove located at the level of DP4-M1 (character 149[3]), presence of mastoid exposure on the occiput (character 160[1]), convex mastoid exposure (character 161[2]), presence of dorsal exposition of the petrosal (character 162[1]), paraoccipital process short, laterally orientated and completely fused to the bulla (character 167[2]).

Node 12 (Octodontidae): presence of figureeight dental pattern in upper and lower molars (character 82[1]), nmmpio above the mid high of the mandible (character 111[0]), poorly developed or absent mandibular notch (character 115[1]), hypotimpanic recess inflated (character 164[1]).