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ORIGINAL PAPER

Contrasting Phylogenetic and Diversity Patterns in Octodontoid Rodents and a New Definition of the Family Abrocomidae

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Abstract Octodontoidea is the most species-rich clade among hystricomorph rodents. Based on a combined parsimony analysis of morphological and molecular data of extinct and extant species, we analyze the history of South American octodontoids and propose ages of divergence older than interpreted so far. Early Abrocomidae are recognized for the first time, and a new definition of the family is provided. Traditionally accepted fossil-based times of origin for the southern clades are reinterpreted as later stages of differentiation markedly uncoupled from the origin, differentiation implying specializations for open environments as shown in a morphospace of skull variation. Origin of crown groups is also strongly uncoupled from origin of clades as a consequence of extinction of deep lineages. In the resulting diversity pattern of modern southern clades of octodontoids, the combination of greater disparity, less content of evolutionary history, and lower taxonomic diversity, compared to their northern counterparts, appears at first counterintuitive. We propose that primary components of diversity derived from evolutionary transformation or anagenesis, on the one hand, and from cladogenesis and extinction, on the other, should not be considered associated, or at least not necessarily. Certain patterns of relationships between these distinct components could be driven by environmental dynamics. Like environments, octodontoid diversity would have been more stable in northern South America, whereas in the south, both strong adaptive change and extinction would have been triggered by emerging derived environments.

Keywords Rodentia · South American Octodontoidea · Abrocomidae · Phylogeny · Divergence times · Diversity patterns

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Introduction

Octodontoidea is the most diverse clade among both New World and Old World hystricomorph rodents (Woods and Kilpatrick 2005). In the recent South American fauna, it includes small to middle sized rat-like rodents of the families Abrocomidae, Echimyidae (including *Myocastor*, sometimes included in a family of its own), and Octodontidae (including Ctenomyinae) (Upham and Patterson 2012; Patton et al. 2015). The sister families Echimyidae and Octodontidae comprise more than 60 % of the extant species of South American Hystricomorpha (caviomorphs), and have the richest fossil record of the suborder (McKenna and Bell 1997). Echimyids have arboreal (tree rats, bamboo rats) or terrestrial to fossorial lifestyles (spiny rats), and they inhabit Amazonian, coastal, and Andean tropical forests in northern South America, and occasionally more open, xeric habitats in the Cerrado and Caatinga (Eisenberg and Redford 1999; Emmons and Feer 1999; Bonvicino et al. 2008; Emmons et al. 2015); the semiaquatic coypu *Myocastor* is an exceptional, large-sized representative widely distributed in southern South America. Octodontids are terrestrial to fossorial (degus, rock rats, viscacha rats) and subterranean rodents (coruros, tuco-tucos)

endemic to mesic and arid biomes of southern South America (Redford and Eisenberg 1992; Ojeda et al. 2013). The living abrocomids make up a less diversified clade, sister to echimyids-octodontids (Upham and Patterson 2012, in press). They comprise nine (or perhaps ten) living species classified in two genera, with terrestrial, scansorial (*Abrocoma*, chinchilla rats), and arboreal habits (*Cuscomys*, arboreal chinchilla-rats), and distributed in southern South America through the central Andes, in cloud forests, mesic environments, and Puna and Monte deserts (Glanz and Anderson 1990; Emmons 1999; Braun and Mares 2002; Taraborelli et al. 2011; Patton and Emmons 2015).

The fossil record of octodontoids is at least as early as late Oligocene (Wood and Patterson 1959; Patterson and Wood 1982; Vucetich et al. 2014) or may possibly reach even the middle-late Eocene (Frailey and Campbell 2004; Campbell et al. 2004; Antoine et al. 2012: 1323). The phylogenetic position of the ancient, pre-late Miocene representatives of this strongly diversified clade is controversial. The difficulties in interpreting early fossils arise firstly from the fact that they are usually poorly preserved. Even beyond this, a conceptual issue also creates controversy; ancient fossils may share few apomorphies with modern species even within restricted clades (see Briggs and Fortey 2005). The adoption of different criteria regarding the significance of this issue shapes the systematic, phylogenetic, and chronological delimitation of lineages, resulting in differing classification proposals for suprageneric taxa. Thus, there has been some consensus in assigning many of the early octodontoids to Echimyidae (e.g., Patterson and Wood 1982; Vucetich and Verzi 1991; Carvalho and Salles 2004), partly because the living species of this family have a conservative molar morphology that is at least superficially similar to that of ancient octodontoids (Reig 1986); in contrast, Abrocomidae and Octodontidae are frequently thought to have originated during the late Miocene, based on the first appearances during this lapse of species with hypsodont molars characteristic of their extant representatives (Simpson 1945; Vucetich et al. 1999; Arnal and Pérez 2013). Whereas in the case of Octodontidae alternative proposals exist that consider this family to be a group as old as the Echimyidae (Winge 1941; Wood and Patterson 1959; Patterson and Wood 1982), the Abrocomidae had not been until now recognized in the pre-late Miocene fossil record. The first ancient abrocomid, preceding the modern (late Miocene to Recent) †*Protabrocoma* and *Abrocoma*, has been recognized quite recently among fossils largely assigned to the conservative family Echimyidae (Verzi et al. 2014).

In this work we present results of a phylogenetic analysis of a comprehensive sample of South American extinct and extant octodontoid rodents, and revisit the evolutionary history of the Octodontoidea. In addition, we provide a new definition of the family Abrocomidae. First, we analyze the phylogenetic relationships of a wide sample of living and extinct octodontoids on the basis of morphological and molecular evidence. The topologies and datings obtained from these analyses are used to delimit both taxonomically and temporally the major octodontoid clades, in agreement with the recognition of stages of origin and differentiation of these clades. We review the phylogenetic diversity and morphological variation encompassed by each clade to assess how cladogenesis, extinction, and anagenesis play a part in establishing evolutionary patterns. We revise the hypothesis that southern octodontoids present differentiation stages uncoupled from the origin of clades (i.e., modernization; Verzi et al. 2014, 2015), and analyze possible causes of the occurrence of this pattern in the context of the palaeoclimatic history of the continent. We discuss the importance of the environment as a factor linking the diversity resulting from cladogenesis and extinction with that arisen from evolutionary transformation or anagenesis.

Materials and Methods

Phylogeny and Divergence Times

Phylogenetic relationships of extinct and extant octodontoids were examined through a combined parsimony analysis based on a dataset of 77 morphological characters (50 craniomandibular and 27 dental from 2252 specimens examined) and four marker sequences obtained from GenBank (Online Resources 1 and 2): growth hormone receptor (GHR, 814 bp; 189 parsimony-informative sites), recombination activating gene 1 (RAG1, 1072 bp; 89 parsimony-informative sites), von Willebrand factor (vWF, 1173 bp; 203 parsimony-informative sites), and mitochondrial subunit 12S (12S rRNA, 979 bp; 323 parsimony-informative sites) genes. The matrix of morphological characters was built following essentially Verzi et al. (2014), and new primary homologies were recorded, including a new proposal for homologies of lower molar crests. Genes were selected following Upham and Patterson (2012). Gene sequences were aligned using BioEdit 7.2.0 (Hall 1999) with the default values of gap opening and gap extension. The dataset of morphological traits was concatenated with the genes sequences, and extinct taxa were coded as missing for all molecular characters. This matrix contained a total of 72 taxa and 4216 characters (Online Resource 1); the sample of South American octodontoids included 36 of the 53 extinct genera and 28 of the 33 living genera; *Erethizon* (Erethizontoidea), *Cavia*, *Cuniculus*, *Dasyprocta*, *Hydrochoerus* (Cavioidea), and *Chinchilla* (Chinchilloidea) were included as outgroups. The parsimony analysis was conducted treating gaps as missing data in TNT 1.1 (Goloboff et al. 2008a, 2008b). The heuristic search consisted in 10,000 replicates of a Wagner tree with random addition sequence of taxa and followed by TBR

branch swapping. In addition, we performed an extra round of TBR on the optimal trees to increase the chance of finding all minimum-length topologies (Bertelli and Giannini 2005). Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (Coddington and Scharff 1994). The age of taxa for which no molecular datings were available was estimated through the modified Stratigraphic Manhattan Measure (MSM*, Pol and Norell 2001), which allows integration of phylogeny with temporal information from the fossil record.

Phylogenetic relationships and molecular dating of divergence times among living octodontoid genera were estimated through Bayesian inference methods implemented in BEAST 2.1.3 (Bouckaert et al. 2014). The four-gene matrix was analyzed considering each gene as a partition, so model parameters were estimated independently. The software jModelTest 2.1.5 (Darriba et al. 2012) was employed to determine the most appropriate model of sequence evolution for each gene; the best-fit model selected for all genes was general time-reversible plus among-site rate variation (GTR+G). The analyses were performed using Markov chain Monte Carlo (MCMC) simulations for 300,000,000 generations and a sample frequency of 5000. We ran two independent runs. We used a relaxed molecular clock model, which allows substitution rates to vary across branches according to an uncorrelated lognormal distribution (Drummond et al. 2006; Drummond and Rambaut 2007). The tree prior was set as Yule process. Convergence in the analyses was determined using the program Tracer 1.6 (Bouckaert et al. 2014). We computed the maximum credibility tree in TreeAnnotator 2.1.2 (Bouckaert et al. 2014), and the first 6000 sampled trees were excluded. Seven fossil calibrations were selected for the divergence analyses, with the selected extinct taxa located on the tree according to the results of the parsimony analysis (Online Resource 3). All calibrations were set as minimum dates (the most reliable date for the oldest levels bearing the indicative fossil; Benton and Donoghue 2007) using lognormal priors, which allows considering a soft bound for maximum dates. Calibrated nodes were constrained as monophyletic.

Morphological and Phylogenetic Diversity

We analyzed the shape variation of the skull in lateral view, which allows capturing shape changes in the orbit, rostrum, auditory bulla, and cranial vault. We used a sample of 174 specimens belonging to 44 species of 29 genera of the families Abrocomidae, Echimyidae, and Octodontidae (Verzi et al. 2015). This dataset included three sufficiently complete skull remains of the extinct †*Eucelophorus chapalmalensis*, †*Actenomys priscus*, and †*Prospaniomys priscus*. Two-dimensional coordinates were captured on digital images of the skull in left lateral view; for specimens where this side was damaged, the reflected image of the right side was used. A set of 20 landmarks and 19 semi-landmarks was chosen to capture skull morphology in detail (Online Resource 4). The x, y coordinates of landmarks and semi-landmarks were digitized using tpsDig version 2.12 (Rohlf 2008). Semi-landmarks were slid by means of the minimum Procrustes distance criterion (Bookstein et al. 2002; Perez et al. 2006) using tpsRelw 1.49 (Rohlf 2010). The resulting aligned Procrustes coordinates were averaged by genus and the consensus configurations were analyzed by Principal Components Analysis (PCA, also known as Relative Warps Analysis) in the software MorphoJ 1.05d (Klingenberg 2011). Shape changes were pictured by means of transformation grids. In order to visualize the phylogenetic relationships between the taxa included in this morphospace, the phylogeny obtained by Bayesian analysis was mapped onto the bivariate plot of the first two PC using the software MorphoJ 1.05d (Klingenberg 2011), which reconstructs the values for ancestral nodes by squared-change parsimony (Maddison 1991). Disparity was calculated after Foote (1993) from the landmark data of aligned specimens (i.e., the configurations that result after sliding semi-landmarks), using the Procrustes distance from the mean specimen (centroid) of each group to the average of all the groups as the distance metric. Disparity values and confidence intervals were calculated using the DisparityBox 7.14a module of the IMP714 package (Sheets 2012).

Phylogenetic diversity (PD), expressed as the total length of all the branches of the tree or a particular clade, was used as an estimate of evolutionary history contained in each familial clade (Purvis et al. 2000; von Euler 2001; Erwin 2008); PD was measured in units of time, i.e., million years (Ma), using the Total Branch Length estimate (TBL) of the Caper package for R version 0.5.2 (Omer et al. 2013) on the tree obtained by Bayesian analysis.

Morphology of Lower Molars and Nomenclature of Crests

We revisited the lower molar morphology of octodontoids and generated a new interpretation for the homologies of crests (Figs. 1, 2 and 3). We do not intend to impart greater importance to the phylogenetic information provided by molars, but consider it a necessary task because this issue is far yet from a consensus (see Patterson and Wood 1982; Carvalho and Salles 2004; Frailey and Campbell 2004; Candela and Rasia 2012; Antoine et al. 2012).

Candela and Rasia (2012) exhaustively revised the crest homologies in octodontoids, especially Echimyidae, and on this basis Candela (2015) discussed the dental characters used in Verzi et al.'s (2014) phylogenetic analysis. In their proposal, efforts are put on detecting relationships between dental crests and cusps, a core criterion for determining homologies of lophs and lophids in rodent molars (Wood and Wilson 1936;

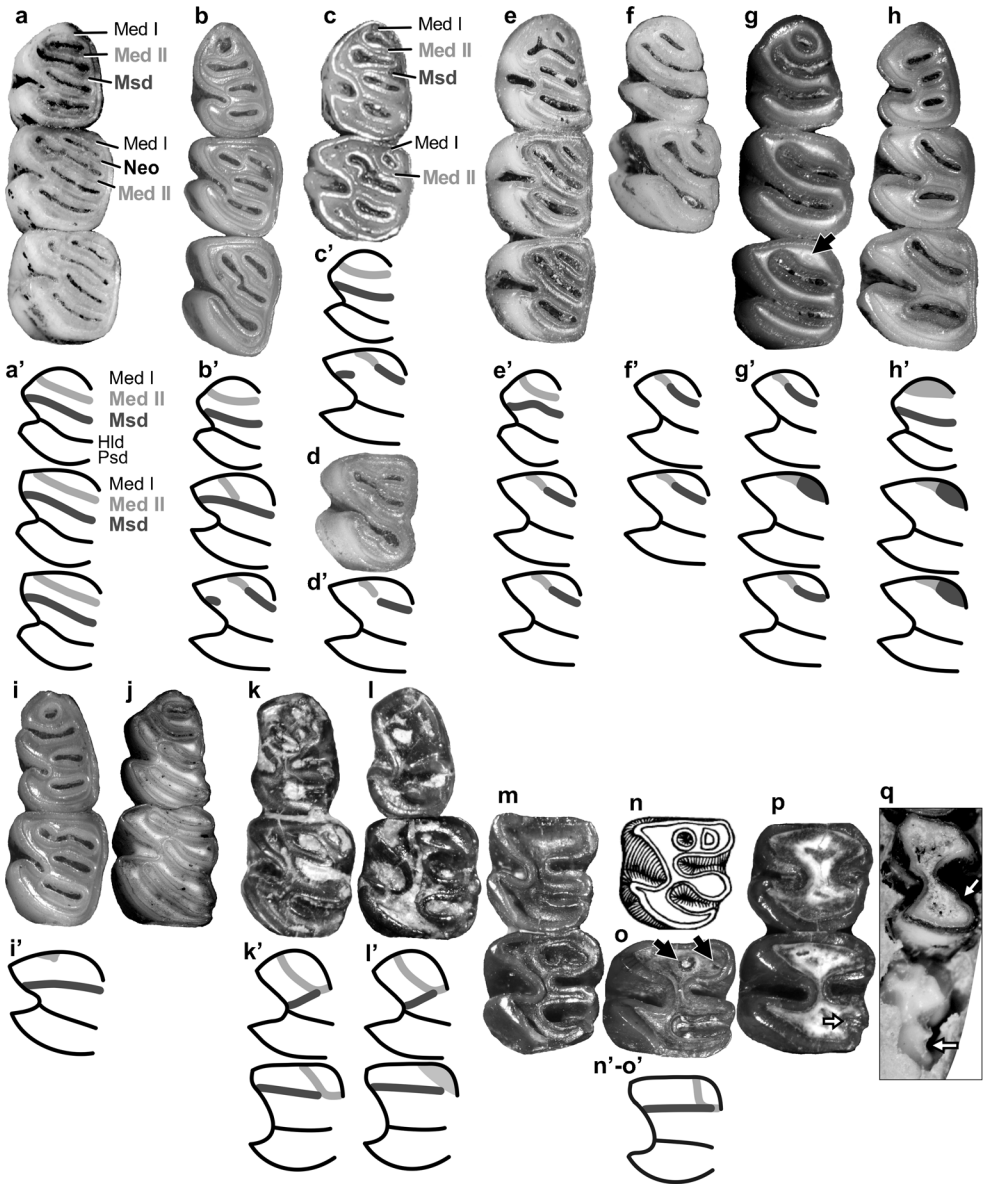

Fig. 1 Occlusal morphology of left Dp4-m2 (a,b,e,g,h), Dp4-m1 (c, f, i-l), m1-2 (m, p, q), m1 (o), and m2 (d, n), with corresponding schematic illustrations of crest homologies indicated by prime symbols. **a** *Hoplomys gymnurus* USP 2001; **b** and **i** *Proechimys cuvieri* UFRJ MN 20313; **c** *Lonchothrix emiliae* MN-UFRJ 4856; **d** *Proechimys roberti* MVZ 197578; **e** *Mesomys hispidus* MVZ 190653; **f** *Trinomys dimidiatus* UFRJ MN 62275; **g** *Trinomys elegans* UFRJ MN 43842; **h** *Proechimys poliopus* MLP 22.II.00.7, **j** *Myocastor coypus* MLP 20.XII.89.3; **k** †*Acarechimys minutus* MPM-PV 4223; **l** †*Acarechimys minutus* MPM-PV 4193; **m** †*Acaremys* (†*Sciamys principalis*) MLP 15–349; **n** †*Platypittamys brachyodon* (modified from Wood 1949: fig. 3d); **o** †*Acaremys* (including †*Sciamys*) MLP 84-III-8-83; **p** †*Acaremys* (including †*Sciamys*) MLP 84-III-8-43; **q** *Aconaemys porteri* UACH 2255 (inverted right molars in **b**, **d**, **e**, **f**, **h**, **k**, **p** and **q**). Interpretation of crest homologies according to Candela and Rasia (2012) and Candela (2015) is shown in **a** and **c**. Schematic illustrations show the interpretation used here. *Abbreviations*: *Hld* hypolophid; *Med I* metalophulid I; *Med II* metalophulid II; *Msd* mesolophid; *Neo* neolophid; *Psd* posterolophid. Not to scale

Marivaux et al. 2004). However, in most octodontoids the detection of cusps is not easy. Butler (1985) proposed that the molar morphology of caviomorphs is at an evolutionary grade in which the occlusal surface is a flattened grinding area adjusted to a single chewing movement, a simplification of the two-phase chewing of cuspidate molars. More recent findings have shown the existence of cuspidate patterns in early caviomorphs (Frailey and Campbell 2004; Antoine et al. 2012), at least in juvenile stages (see e.g., Vucetich and Verzi 1996; Vucetich and Kramarz 2003; Vucetich and Vieytes 2006). In any case, Butler's proposal seems to be the rule for modern octodontoids (from the late Miocene on) and even for adult individuals of earlier species.

Beyond their usefulness as landmarks, cusps and crests are structures that function, and thus undergo changes in position, size, or timing of development (Butler 1985; Frailey and

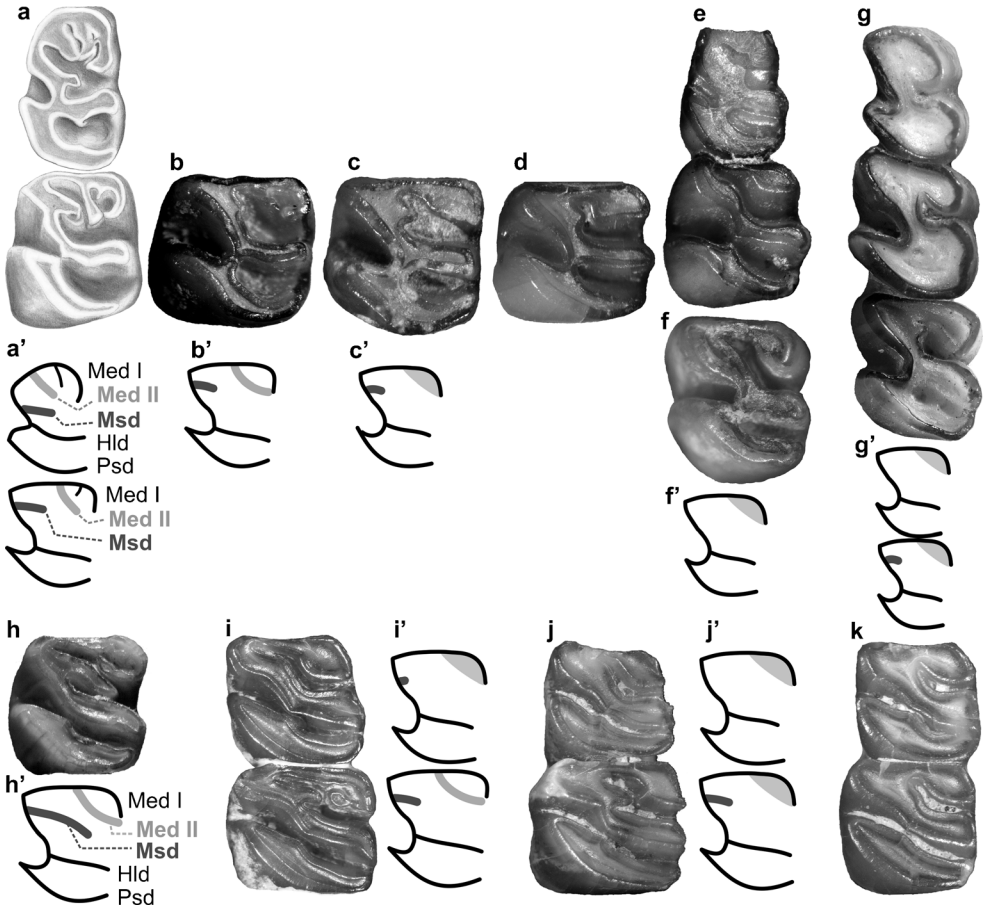

Fig. 2 Occlusal morphology of left lower molars, with corresponding schematic illustrations of crest homologies indicated by prime symbols. **a** Dp4-m1 of †*Sallamys quispea* (based on Shockey et al. 2009: fig. 5); **b** m1 of †*Sallamys pascuali* UATF-V 5010; **c** m2 of †*Sallamys pascuali* UATF-V 5009c; **d** m2 of †*Willidewu esteparius* MPEF 5031; **e** Dp4-m1 of †*Willidewu esteparius* MPEF 5024; **f** m2 of †*Chasichimys bonaerense* GUNLPam 5068; **g** Dp4-m2 of †*Chasichimys scagliai* MMP 481-M (holotype); **h** m1 of †*Protadelphomys* sp. MMP 949-M; **i** m1-2 of †*Protadelphomys latus* MPEF 90–166; **j** m1-2 of †*Protadelphomys latus* MPEF 90-391-4; **k** m1-2 of †*Protadelphomys latus* MPEF 90-391-1 (inverted right molars in **a**, **b**, **e**, **f**, **h**, **i**, **k**). Schematic illustrations show the interpretation used here. *Abbreviations*: *Hld* hypolophid; *Med I* metalophulid I; *Med II* metalophulid II; *Msd* mesolophid; *Psd* posterolophid. Not to scale

Campbell 2004: 98; Lazzari et al. 2015). Therefore, the search for possible correspondences between structures in molars must take into account that these are dynamic. At least in octodontoids, recognition of homologies requires interpreting changes in the relationships between crests and cusps (or the areas presumably occupied by the latter) or just between crests; many of these changes are recurrent and may be tracked with reasonable confidence.

Figure 1a' and c' show the interpretation followed here for the pentalophodont pattern of the Echimyidae *Hoplomys gymnurus* and the more simplified *Lonchothrix emiliae*, respectively, compared with the proposal of Candela and Rasia (2012) for the same taxa (Fig. 1a and c, respectively). Candela and Rasia (2012) interpreted the second and third crests of the pentalophodont molars as neolophid and metalophulid II, respectively (Fig. 1a), while in *Lonchothrix* the second crest is identified as metalophulid II (Fig. 1c). Their interpretation stems from prioritizing the assumed connection of 'metalophulid II' with the presumptive location of the metaconid. This proposal has a series of difficulties. First, it offers different interpretations for the same structures depending on whether they are recognized in premolars or molars. Second, penta- and tetralophodonty are assumed to be fixed, static morphologies without transitional stages between them. In addition, what Candela and Rasia (2012) interpreted as metaconid is not always solely this cusp, but in many cases represents an enlarged area formed by early ontogenetic fusion of crests (e.g., *Acarechimys minutus*, Fig. 1k, l; *Sallamys*, Fig. 2a-c; *Protadelphomys*, Fig. 2h-k). As a result, these authors offered different interpretations for morphologies that are essentially identical, such as those of Dp4 vs m1-2 of *Hoplomys* (Fig. 1a).

We think that pentalophodonty, tetralophodonty, trilophodonty (and even more simplified morphologies) should not be interpreted as static patterns but as part of different transformation pathways that include transitional morphologies (Figs. 1, 2 and 3). In this sense, the morphology of lophate deciduous premolars is more stable than that of m1 and m2, the latter showing more frequent reduction and fusion of crests

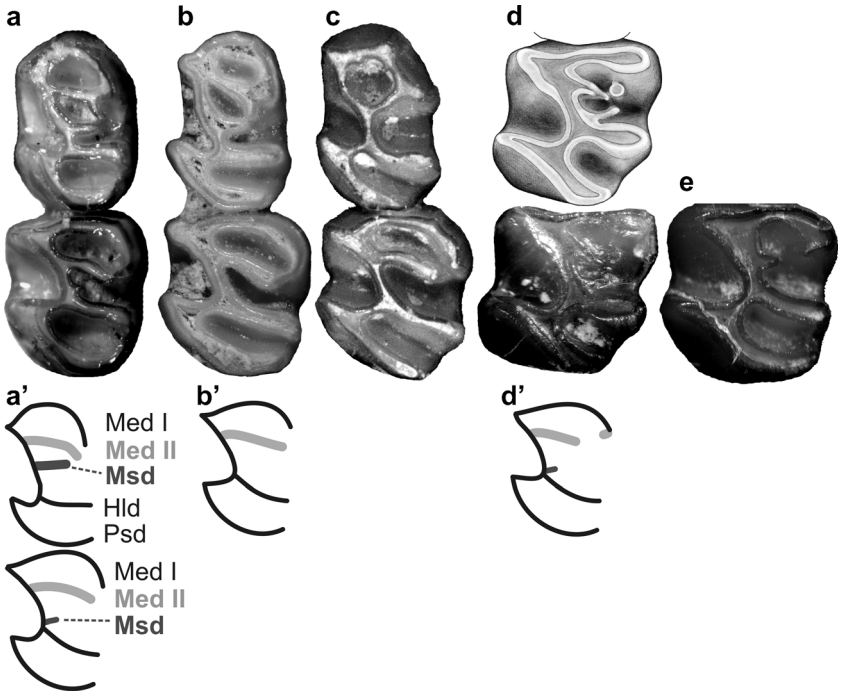

Fig. 3 Occlusal morphology of left lower molars, with corresponding schematic illustrations of crest homologies indicated by prime symbols. **a** Dp4-m1 of †*Protacaremys prior* MPEF 5652; **b** Dp4-m1 of †*Protacaremys prior* MPEF 7557; **c** Dp4-m1 of †*Prospaniomys priscus* MPEF 6447; **d** m2 of †*Caviocricetus lucasi* MPEF 5076; **e** m1 of †*Deseadomys arambourgi* MLP 93-XI-21-5 (inverted right molars in **a**, **c**, **d**). Schematic illustrations show the interpretation used here. *Abbreviations*: *Hld* hypolophid; *Med I* metalophulid I; *Med II* metalophulid II; *Msd* mesolophid; *Psd* posterolophid. Not to scale

at both ontogenetic and evolutionary scales (Frailey and Campbell 2004; Antoine et al. 2012; see Renvoisé and Montuire 2015). Taking this into account, and the fact that deciduous premolars and unreplaced molars share an embryological origin (see Luckett 1985: 233), the morphology of Dp4 may be useful to understand that of molars (Carvalho and Salles 2004). In Figs. 1, 2 and 3 it can be seen that the anterior portion of the molar becomes simplified by crest fusion and reduction (with the exception of *Hoplomys*, Fig. 1a). The transformation pathway in Fig. 1a-j shows how the root of metalophulid II becomes fused or even submerged into metalophulid I; subsequently, the origin of the mesolophid changes progressively by uniting to the root of metalophulid II (Fig. 1b-g). This gives rise to 'crest C' proposed by Carvalho and Salles (2004), with whose recognition we strongly agree beyond the different interpretation of its composition (see Fig. 1d and Carvalho and Salles 2004: Fig. 6). The disappearance of the fossettid that separates this mixed-origin crest from metalophulid I originates an anterior crest simple in appearance but with a composite origin involving the three above mentioned lophids (Fig. 1g and h). In the molars of Figs. 1k-o and 2, metalophulid II originates close to the lingual margin of metalophulid I. In Fig. 1k-o the mesolophid is a crest whose distal end joins metalophulid II or the distal thickening of the first crest corresponding to this lophid. The disappearance of the resulting anterior fossettids leads to the formation of an anterior lobe that is simple in appearance but of composite origin (Fig. 1m, p, q). Figure 2 shows molars in which the mesolophid is reduced to a short crest (Fig. 2h-h') or a little spur (even absent in some specimens). This spur was considered as the metalophulid II by Verzi et al. (2014), but later examination of unpublished material corresponding to †*Protadelphomys* sp. (Fig. 2h-h') in comparison with †*Sallamys quispea* (Fig. 2a-a') led us to revise this interpretation. In †*S. quispea* it is possible to track the identity of the above mentioned crests from Dp4 to m1; in m1, the short metalophulid II and mesolophid are aligned into a short anteroposterior stretch, as if driven by pressure exerted from behind on the anterior wall of the hypoflexid in a morphology such as that of the Dp4. In these genera, the first lophid becomes simple but its origin is also composite (Fig. 2b-b', c-c', i-k), as is also the case in †*Willidewu* and †*Chasichimys* (Fig. 2d-e and f-g, respectively).

Figure 3 shows another pattern, in which metalophulid II, as a complete or reduced crest, originates in the posterior protoconid area and the mesolophid is absent (a short-lived relic of the mesolophid was detected in the m1-2 of †*Caviocricetus* MLP 99-XII-10-1/3, MPEF 5076, Fig. 3d-d'; and †*Protacaremys* MPEF 5673 and 5652, Fig. 3a-a'; it is also present in †*Dudumus* MACN- Pv CH 2040, see Arnal et al. 2014: Fig. 3c). If metalophulid II remains separated, metalophulid I does not have any evidence of being a composite crest.

On the basis of available evidence, we have not been able to track a route of simplification for the trilophodont molar configuration of 'eumysopines,' 'echimyines,' 'dactylomyines,' or abrocomids.

Results

Phylogeny

The combined parsimony analysis of morphological and molecular data resulted in a single most parsimonious tree 3,572

steps long (CI=0.56, RI=0.59), which shows the existence of three main clades within Octodontoidea (Fig. 4). Most nodes are poorly supported, but show essentially little character conflict (high relative Bremer support values).

The clade at node A clusters the traditionally recognized Abrocomidae, i.e., euhypsodont representatives from late Miocene to Recent, with late Oligocene to middle Miocene genera previously assigned to other taxa of Octodontoidea (Fig. 5; Appendix). Morphological characters supporting this clade were the anteriorly oriented proximal portion of the nasolacrimal canal (character state 14–1; Fig. 6), the morphology of the lateral margin of the pterygoid fossa, on a level with its medial margin and extending posteriorly (character state 35–1), and the position of the anterior margin of the coronoid apophysis, which is lateral and ventral with respect to the alveolar margin of the molars (character state 50–1; Fig. 7). Within this clade, two subclades were recovered. The first (node E) comprises the extinct †*Caviocricetus*-†*Dudumus* and †*Protacaremys*-†"*Protacaremys*" *denisae*-†*Prospaniomys*-†*Deseadomys*. These taxa share the morphology of the origin of the masseteric crest, which is ventrally deflected from the notch for the tendon of the medial masseter muscle (character state 46–2), and the morphology of the anterior lobe of Dp4 (unknown in †*Deseadomys*; character-state 62–2; Fig. 3). †*Caviocricetus* and †*Dudumus* share the morphology and orientation of the mesolophule on DP4 (character state 53–1) and M1 (character state 56–1) (Verzi et al. 2014: Fig. 7a; Arnal et al. 2014: Fig. 4), while †*Protacaremys*-†"*P.*" *denisae*-†*Prospaniomys*-†*Deseadomys* are clustered by the morphology of the anterior side of metalophulid I and the protoconid area, the latter presenting an anterior concavity and a sharp labial end (character state 64–1; Fig. 3). The second subclade (node F) includes the extant chinchilla rats *Cuscomys*, *Abrocoma bennettii*, and *Abrocoma cinerea* complex as well as the extinct †*Protabrocoma* and †*Spaniomys*, and is supported by the shortened lower incisor (character state 51–1) and the shape of the contour of the hypolophid (character state 68–1). In modern abrocomids, the lower incisor is extremely short (character state 51–2).

The clade at node B groups the living Octodontidae and Echimyidae with late Oligocene (late Eocene-early Oligocene considering †*Eodelphomys*) - Pleistocene fossils. They share the metalophulid II of m1-2 originating from the metalophulid I (character state 65–1; Figs. 1 and 2).

The clade at node C groups the living Octodontidae with late Oligocene to Pliocene genera (Fig. 5; Appendix). Members of this clade share the ventral deflection of the masseteric crest posterior to the notch for the medial masseter muscle tendon (character state 46–1; Verzi et al. 2014: Fig. 4) and the Dp4 with an anterior rounded lobe (character state 62–1; Figs. 1k, l and 2a, g). Within this group, two major subclades include the traditionally recognized living and extinct Octodontinae and Ctenomyinae. The former (node G) includes crown octodontines and late Oligocene to late Miocene fossils, which share the mesolophule of M1 with its labial end joined to the medial wall of the metacone area (character state 56–1; Fig. 8a, c). The 'acaremyids' †*Galileomys*, †*Platypittamys*, and †*Acaremys* (including †*Sciamys*) are part of the lineage that leads to extant octodontines, with which they share the early formation of a complex lobe anterior to the hypo- and posterolophid in the lower molars (character-state 67–1; Fig. 1m-q); in living octodontids this may be seen in early ontogeny (*Aconaemys* FMNH 50752, 50754; UACH 2255, Fig. 1q). The grouping of †*Acaremys* (including †*Sciamys*) with traditional octodontines is supported by the para- and metaflexus closing markedly earlier than the mesoflexus, the parafossette generally smaller and more short-lived than the metafossette (character state 60–1; Fig. 8b-f). †*Plesiacarechimys*+†*Acarechimys minutissimus*-†*Neophanomys* form a clade external to 'acaremyids'- extant octodontines; these three genera share a short and posteriorly oriented mesolophule in DP4 and M1 (character states 53–1 and 55–1, respectively; Fig. 8a). The upper early Miocene †*Acarechimys minutus* forms a three-way polytomy with the mentioned clades (Fig. 4).

The clade Ctenomyinae (node H), sister to Octodontinae, is supported by the foramen into the nasolacrimal canal opening on the margin of the sphenopalatine fissure, oriented posteriorly toward the fissure and not visible laterally (character state 12–1; Fig. 9a-c), the auditory bulla extended posteriorly to the level of the root of the paroccipital process (character state 45–1; Verzi et al. 2014: Fig. 6), and the fusion of the mesolophule and posteroloph+metaloph into a lobe in molars with presence of paraflexus/fossette and mesoflexus (character state 58–1; Fig. 8g-k). The late Miocene †*Chasicomys* and †*Chasichimys* are part of the lineage that leads to the modern, euhypsodont ctenomyines, and the late Oligocene to early Miocene †*Sallamys*+†*Protadelphomys*-†*Willidewu* are sister to the latter.

The clade at node D comprises the extant Echimyidae and some of the extinct genera traditionally assigned to this family (Fig. 5; Appendix). It is diagnosed by the lacrimal foramen opening into the maxilla (character state 10–1; Fig. 6e), the presence of a continuous rim (without a suture) formed by the maxilla around the foramen into the nasolacrimal canal (character state 11–1), the lateral process of the supraoccipital extending ventrally below the level of the mastoid process (character state 39–1; Verzi et al. 2014: Fig. 3), and the rotated distal portion of the paroccipital process that results in the posterolateral or posterior orientation of its external margin (character state 42–1; Verzi et al. 2014: Fig. 3). As in previous analyses, two major subclades are recovered within Echimyidae. The first of these (node I) comprises the terrestrial spiny rats *Thrichomys*-†*Pampamys*-†*Eumysops* and *Hoplomys*-*Proechimys*+the semiaquatic coypu *Myocastor*, and a group of arboreal genera comprising spiny tree-rats

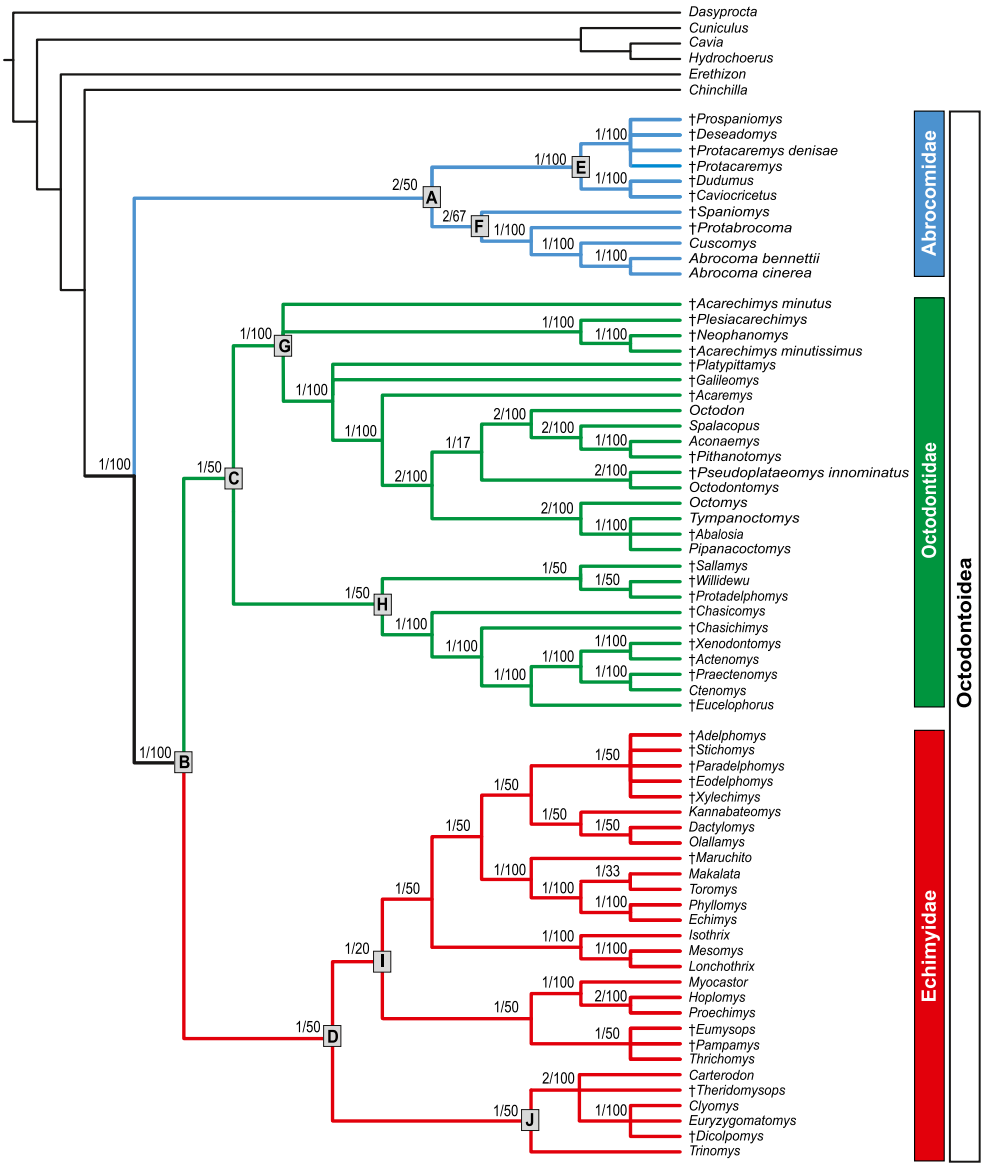

Fig. 4 Most parsimonious tree of a combined analysis of morphological and molecular data. Values of absolute/relative Bremer support are given above branches. A to J, nodes mentioned in the text

Mesomys-Lonchothrix+brush-tailed rat *Isothrix* and echimyines-dactylomyines. The middle Miocene †*Maruchito* clusters with extant echimyines, while the late Eocene-early Oligocene †*Eodelphomys* and the late Oligocene to early Miocene adelphomyines †*Adelphomys*-†*Paradelphomys*-†*Stichomys*-†*Xylechimys* cluster with the dactylomyines. The second subclade (node J) includes the extant terrestrial spiny rat *Trinomys* and the fossorial *Carterodon*, *Clyomys*, and *Euryzygomatomys* (euryzygomatomyines sensu Emmons 2005), as well as the extinct †*Theridomysops* and †*Dicolpomys*.

Paleontological Datings

The age and phylogenetic relationships of fossil octodontoids suggest a minimum late Oligocene age for the divergence between the main octodontoid clades (Fig. 10), i.e., abrocomids, crown echimyids, and the major octodontid lineages. Indeed, based on the evidence of †*Eodelphomys*, some of these splits may have occurred earlier; however, we purposely excluded †*Eodelphomys* from our date estimations owing to a lack of consensus regarding its proposed Eocene age (Frailey and Campbell 2004; MacFadden 2006; Antoine et al. 2012; Woodburne et al. 2014). The initial branching of differentiated, euhypsodont abrocomids, octodontines, and ctenomyines is recorded during the late Miocene, modern octodontines and especially abrocomids starting to diversify slightly earlier than modern ctenomyines. The desert-adapted octodontines and *Abrocoma* are first recorded at least as early as the latest Pliocene-early Pleistocene (Fig. 10). Also during the Pliocene, a recent branching event within ctenomyines gave rise to the lineage leading to the extant *Ctenomys*.

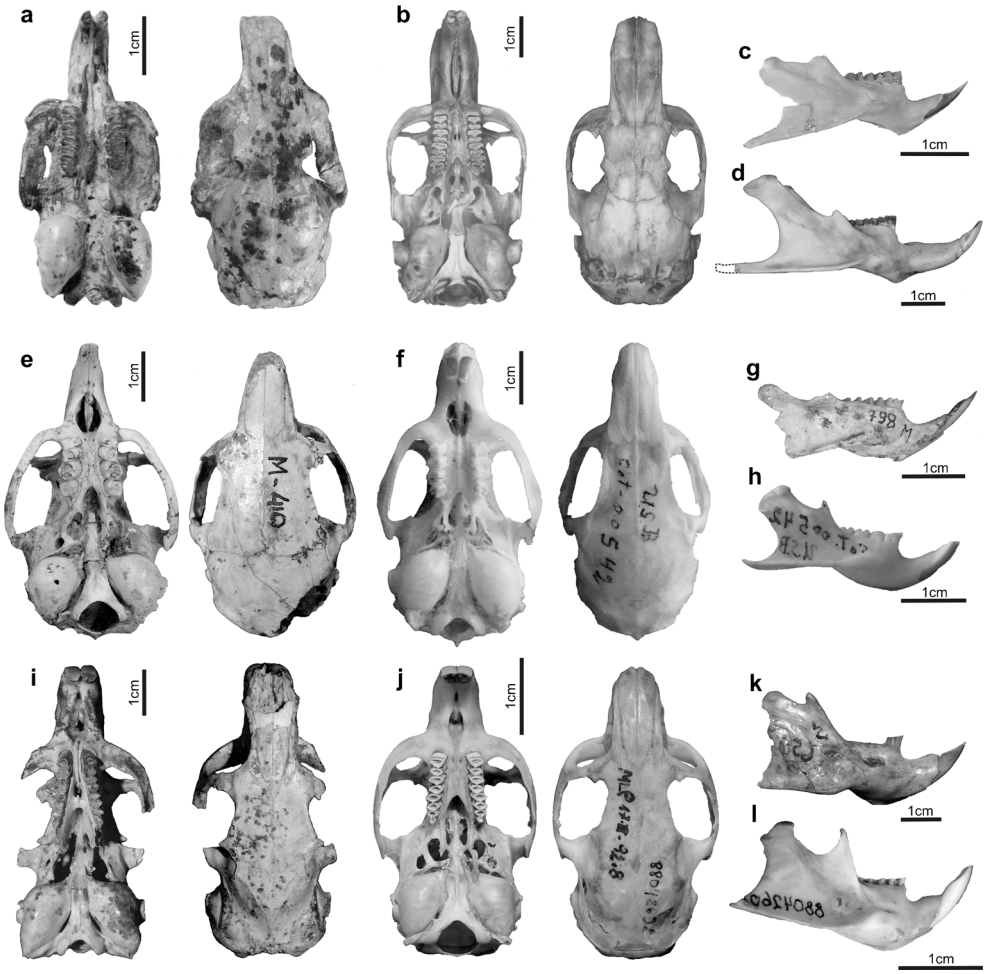

Fig. 5 General morphology of the skull (**a**, **b**, **e**, **f**, **i**, **j**) and mandible (**c**, **d**, **g**, **h**, **k**, **l**) of selected genera of the three families of Octodontoidea: **a** †*Prospaniomys priscus* MACN-Pv CH1913; **b** and **d** *Cuscomys ashaninka* MUSM 12715; **c** †*Prospaniomys* sp. MPEF 5039; **e** †*Eumysops gracilis* MMP 410-M; **f** and **h** *Thrichomys* sp. MMP 150; **g** †*E. gracilis* MMP 798-M; **i** †*Pithanotomys chapalmalensis* MMP 2132-M; **j** and **l** *Aconaemys sagei* MLP 17.II.92.8; **k** †*Pithanotomys chapalmalensis* MMP 650-S

Molecular Dating of Divergences

A time-scaled phylogeny for Octodontoidea was obtained through a relaxed molecular clock Bayesian analysis, setting seven fossil calibrations (Online Resource 3) based on Contamana and Tinguiririca rodents, and topology of the combined tree here obtained. The nodes of the inferred phylogeny were supported by >72 % posterior clade probabilities (PB), except for the nodes *Dactylomys-Olallamys* (64 % PB), *Myocastor-Hoplomys-Proechimys* (65 % PB) and *Echimys*/…/*Mesomys* (57 % PB).

The estimated age obtained for the divergence between Octodontoidea and Chinchilloidea is 41.7 Ma (95 % CI: 39.0–45.1 Ma). Within octodontoids, the initial divergence that separated abrocomids from echimyids-octodontids is dated at 34.1 Ma (95 % CI: 31.2–37.1 Ma), while the echimyids/octodontids split is estimated at 29.5 Ma (95 % CI: 27.3–32.0 Ma). The beginning of the diversification of crown echimyids, corresponding to the separation between their two major clades, is estimated to have occurred at 24.1 Ma (95 % CI: 22.2–26.3 Ma). The divergence octodontines/ctenomyines within octodontids is dated at 25.9 Ma (95 % CI: 25.0–27.4 Ma). Splits giving rise to genus-level lineages within the major clades are older in echimyids than in octodontids, with the only exception of *Clyomys-Euryzygomatomys* (Online Resource 3).

Cranial Shape Variation and Disparity

Figure 11 shows the skull shape variation of living octodontoid genera and the extinct †*Prospaniomys*, †*Actenomys*, and †*Eucelophorus* (see Materials and methods) as represented in the morphospace of the first two axes of a PCA of Procrustes coordinates. These first two principal components (PC) explained 61.53 % of the variation. Shape changes along PC1 (36.06 % of the variation) involved mainly the size of the auditory bulla (larger toward positive values), and to a lesser extent, the size of the orbit (smaller toward positive values). Along PC2 (25.47 % of the variation), the main changes involved rostrum shape (more elongated and procumbent toward positive values) and relative expansion of the cranial vault (higher vault toward negative values). As in a previous analysis (Verzi et al. 2015), the echimyids, and especially the forest-dwelling genera, occupied a comparatively restricted area, with most taxa having negative

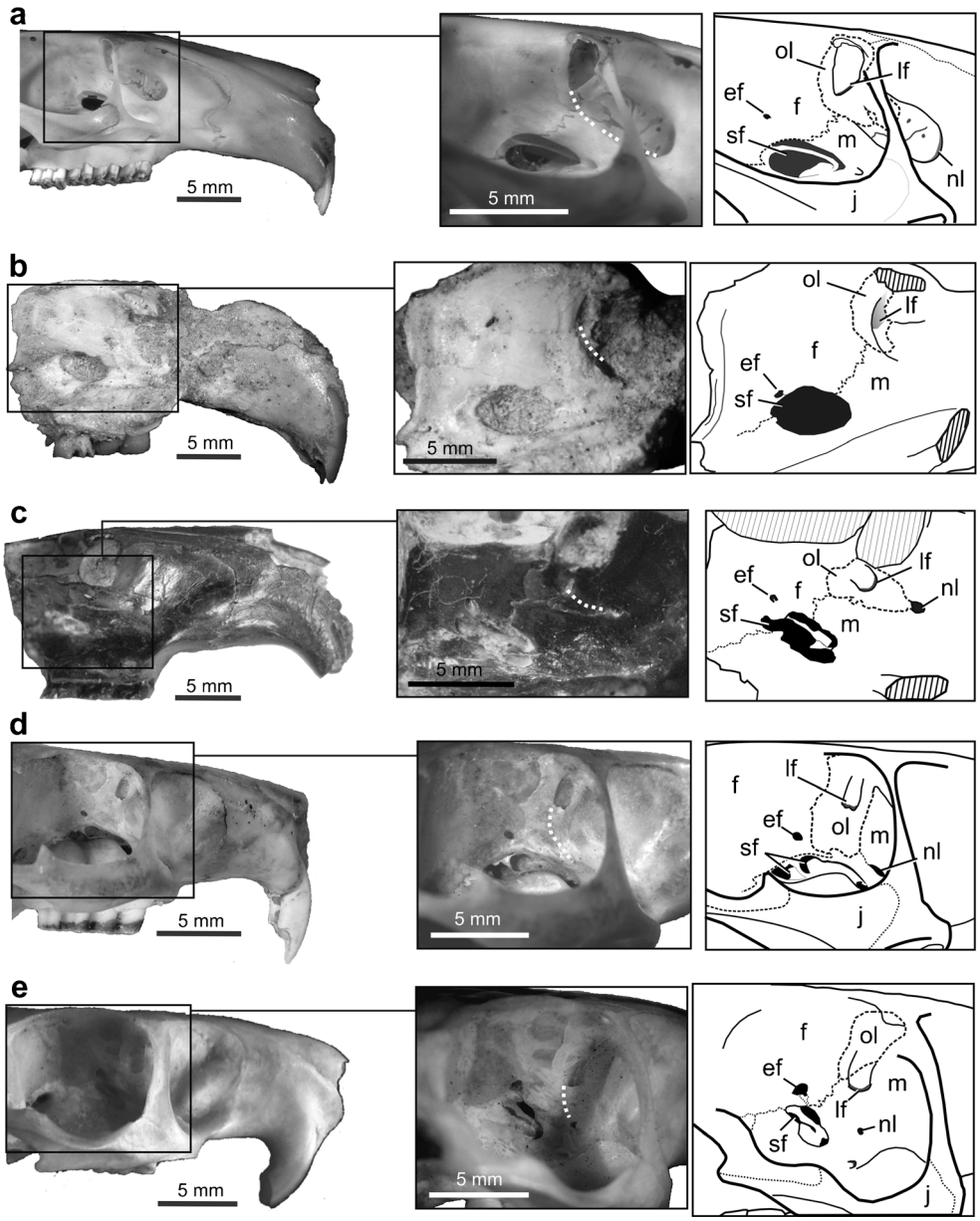

Fig. 6 Morphology of the orbital region: **a** *Abrocoma* sp. (*cinerea* complex) MLP 2038; **b** †*Prospaniomys priscus* MMP 952-M; **c** †*Spaniomys riparius* MACN-A 4184; **d** *Octodontomys gliroides* MLP 25.XI.98.1 (erroneously assigned to *Octomys* in Verzi et al. 2014: fig. 2a); **e** *Thrichomys* sp. MMP 150-USB542. Dotted line in photographs shows orientation of the nasolacrimal canal. *Abbreviations*: *ef* ethmoidal foramen; *f* frontal; *j* jugal; *lf* lacrimal foramen; *m* maxilla; *nl* foramen into nasolacrimal canal; *ol* orbital portion of lacrimal; *sf* sphenopalatine fissure

PC1 values and negative or near-zero PC2 values; *Myocastor* was an exception, with a positive PC2 score. Octodontids were widely spread over much of the remaining morphospace, and included taxa with extreme values for both PC1 (the desert-adapted *Tympanoctomys* and *Pipanacoctomys*, with hypertrophied auditory bullae) and PC2 (the specialized subterranean †*Eucelophorus*, with procumbent rostrum). Abrocomids showed greater spread than the forest-dwelling echimyids along

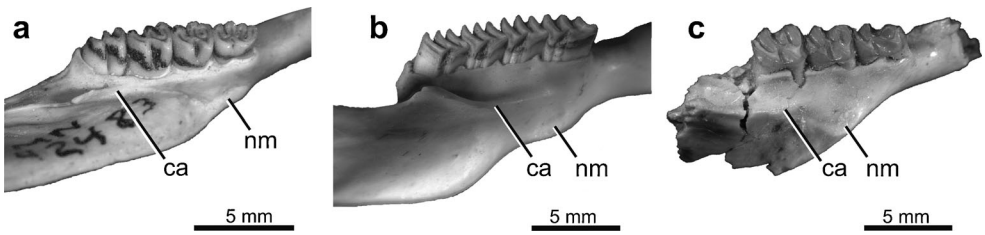

Fig. 7 Dorsolateral view of right hemimandible of abrocomids: **a** *Thrichomys laurentius* MN-UFRJ 42483; **b** *Abrocoma bennettii* MLP 2273; **c** †*Prospaniomys priscus* MPEF 7572 (inverted left hemimandible). *Abbreviations*: *ca* coronoid apophysis; *nm*, notch for the tendon of medial masseter muscle

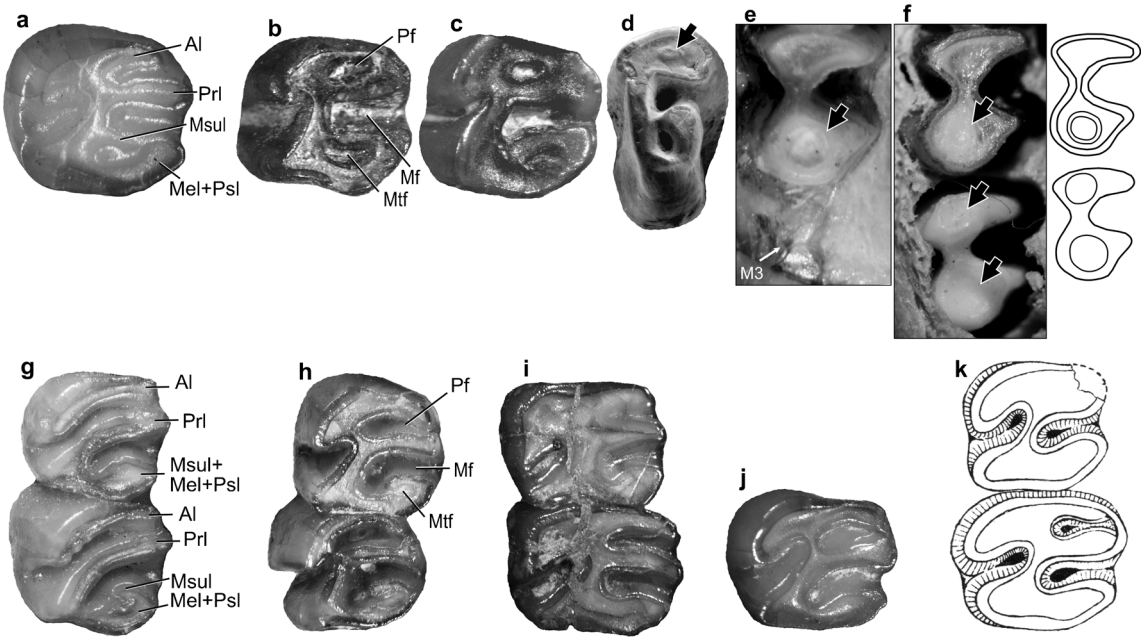

Fig. 8 Occlusal morphology of left upper molars. **a** M1 of †*Acarechimys minutissimus* MPEF 5065**;** **b** M1 of †*Acaremys* (including †*Sciamys*) MLP 15–122; **c** M1 of †*Acaremys* (including †*Sciamys*) MLP 15–197 (?); **d** M2 of *Octodontomys gliroides* MLP 12.VII.88.10; **e** M2 of *Aconaemys sagei* FMNH 50754; **f** M1-2 of *Aconaemys porteri* UACH 2255; **g** M1-2 of †*Protadelphomys latus* CFG 9; **h** M1-2 of †*Sallamys pascuali* UATF-V 5013; **i** M1-2 of †*Sallamys pascuali* UATF-V 5010; **j** M1 of †*Willidewu esteparius* MLP 90-II-13; **k** M1-2 of †*Chasicomys octodontiforme* MLP 55-IV-28-2 (from Pascual 1967; currently missing) (inverted right molars in **c**, **d**, **e**, **f**, **h**, **i**, **j**, **k**). Arrows indicate parafossette and/or metafossette. *Abbreviations*: *Al* anteroloph; *Mel* metaloph; *Mf* mesoflexus / mesofossette; *Msul* mesolophule; *Mtf* metaflexus/metafossette; *Pf* paraflexus/parafossette; *Prl* protoloph; *Psl* posteroloph. Not to scale

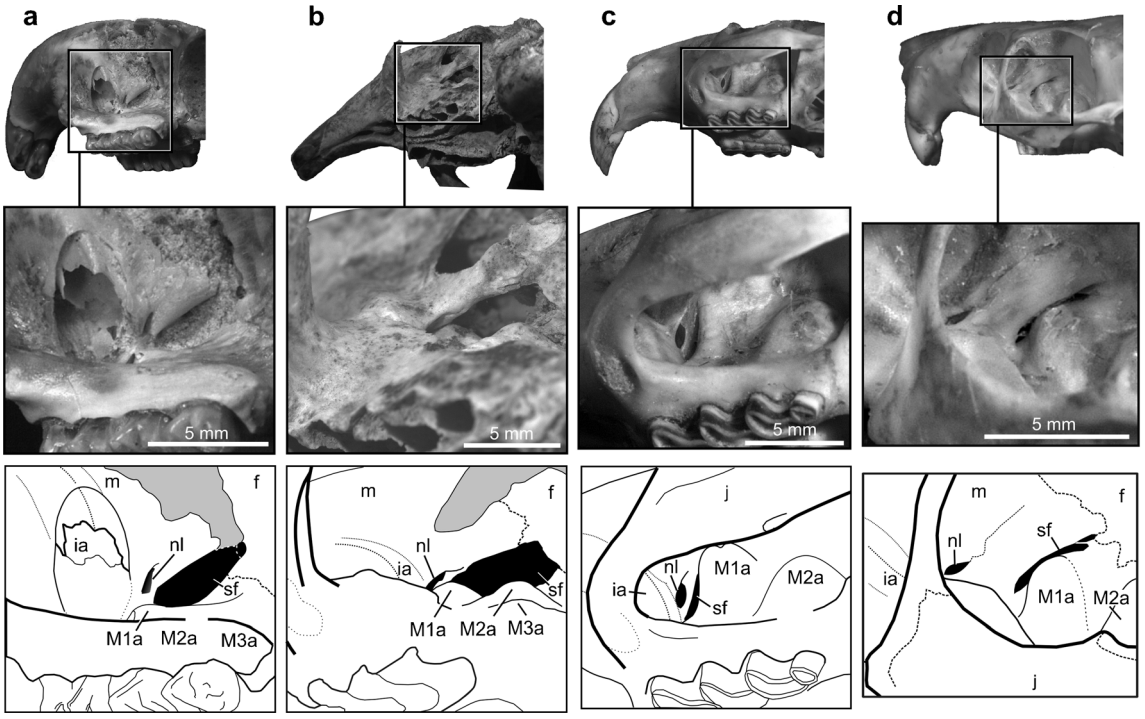

Fig. 9 Morphology of foramen into nasolacrimal canal: **a** †*Protadelphomys latus* field N° CF 025; **b** †*Actenomys priscus* MLP field N° H-1; **c** *Ctenomys maulinus* MLP 1.X.01.4; **d** *Octomys mimax* IMCN 024. *Abbreviations*: *f* frontal; *j* jugal; *ia* incisive alveolus; *m* maxilla; *M1a-M3a* alveolus of M1, M2 or M3, respectively; *nl* foramen into nasolacrimal canal; *sf* sphenopalatine fissure

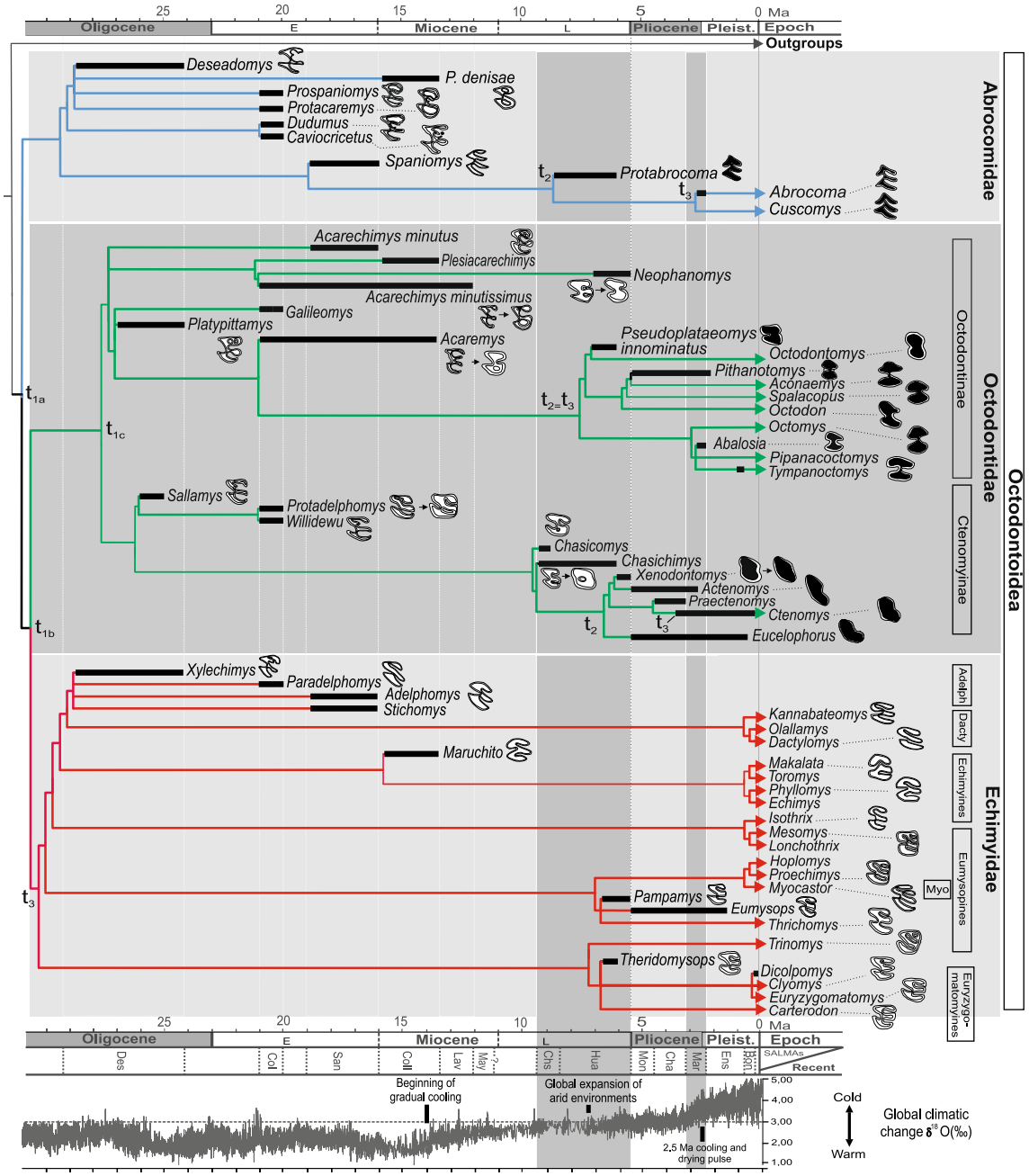

Fig. 10 Most parsimonious tree of octodontoids showing the temporal ranges of genera. Occlusal figures of the left m1 or m2 are illustrated next to the corresponding genus (when two figures are presented, the one to the right is ontogenetically more derived). Times of origin (t_1), morphological differentiation (t_2), and initial diversification of crown-group (t_3) are indicated; t_1 denotes the origin of lineages leading to abrocomids (t_{1a}), echimyids and octodontids (t_{1b}), and octodontines and ctenomyines (t_{1c}); the differentiation stage (t_2) is represented by the acquisition of euhypsodont molars (black occlusal figures). Dark grey background denotes differentiation times of the southern octodontoid clades (Chasicoan-Huayquerian), and the subsequent record of arid-adapted and desert-specialists among modern abrocomids and octodontines (Marplatan). We use informal names for echimyid subfamilies pending a review of their taxonomic status. Timescale after Gradstein et al. (2008); South American Land Mammal Ages boundaries after Madden et al. (1997), Zárate (2005), Folguera and Zárate (2009), Ré et al. (2010), Perkins et al. (2012), Deschamps et al. (2013), Dunn et al. (2013), Fernicola et al. (2014); isotopic curve after Zachos et al. (2008); global palaeoclimatic events after Vrba et al. (1995), Denton (1999), Zachos et al. (2001), Verzi and Quintana (2005), Tripati et al. (2009), and Pound et al. (2012). *Abbreviations*: *Adelph* adelphomyines; *Bon* Bonaerian; *Cha* Chapadmalalan; *Chs* Chasicoan; *Col* Colhuehuapian; *Coll* Colloncuran; *Dacty* dactylomyines; *Des* Deseadan; *Ens* Ensenadan; *Hua* Huayquerian; *Lav* Laventan; *Mar* Marplatan; *May* Mayoan; *Myo* myocastorines; *Mon* Montehermosan; *San* Santacrucian

PC1. The extant *Cuscomys* and *Abrocoma* had positive scores on both PCs (near zero for †*Prospaniomys*). †*Prospaniomys* was located close to mesic octodontids *Aconaemys*, *Octodon*, and *Spalacopus* (see Álvarez and Arnal 2015), whereas the arid-adapted *Abrocoma* sp. (*cinerea* complex) was nearer to the desert octodontids.

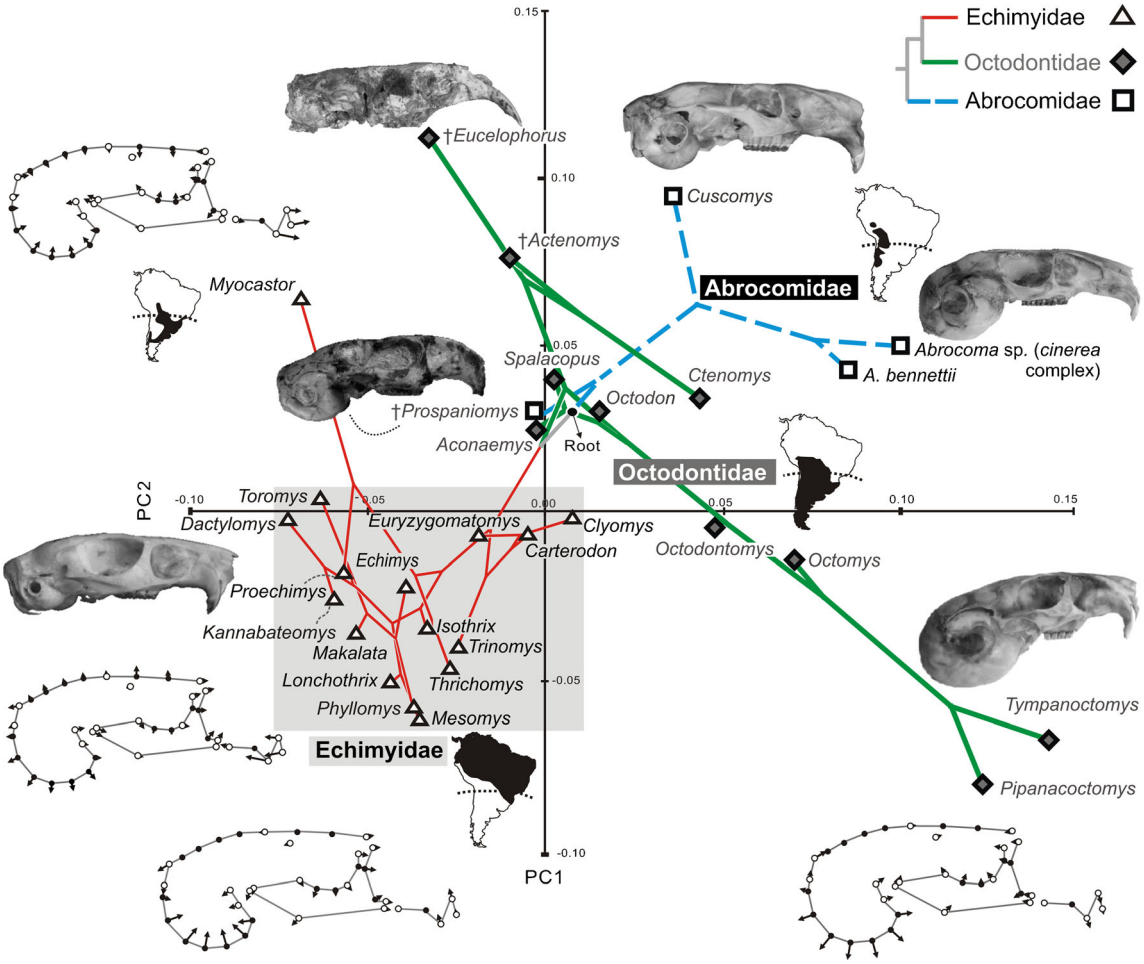

Fig. 11 Phylogenetic tree superimposed onto the plot of octodontoid genera in the morphospace defined by the first two principal components (PCs). The positions of internal nodes are reconstructed by squared-change parsimony using the tree topology obtained. Outline diagrams show shape change of the skull associated with each PC (*arrows*) from the consensus (*solid lines* and *circles*) to positive or negative scores. Maps show current distribution of the familial clades after Patton et al. (2015). Illustrated skulls not to scale. Empty *circles*, landmarks; *solid circles*, semilandmarks

Similarly to previous results (Verzi et al. 2015), and as anticipated by the relative dispersion of families in the morphospace, the values of the disparity index (Foote's F) calculated from this shape variation were markedly higher for octodontids than for echimyids. The disparity of abrocomids was intermediate, although also higher than that of echimyids. Table 1 presents these values along with those for phylogenetic diversity (PD) and taxonomic diversity at generic level (TD). Among the families analyzed, echimyids presented the lowest F values combined with markedly higher values of PD and TD.

Discussion

Delimitation of Higher Taxa

The clade at node A of Fig. 4 is recognized here as the family Abrocomidae. We include therein genera that were previously assigned to other octodontoid lineages, or considered to have uncertain affinities, along with the modern euhypsodont representatives (Appendix). Until the present, no fossil octodontoid with rooted molars had been assigned to this

Table 1 Generic richness (TD), phylogenetic diversity (PD), and disparity (F) of analyzed familial clades calculated from living / living+extinct genera included in the PCA; (t) total of living genera according to Woods and Kilpatrick (2005) and Emmons (2005)

Clade	TD (t)	PD	F
Echimyidae	16 (22)	267	0.0039
Abrocomidae	2 (2) / 3	36 / 56	0.0055 / 0.0080
Octodontidae	8 (9) / 10	97 / 109	0.0077 / 0.011

PD is used as an estimate of evolutionary history contained in each familial clade, and is expressed as the sum of branch lengths connecting all species within the clade (million years as obtained from the relaxed molecular clock Bayesian analysis, plus MSM* estimates for *Cuscomys* and fossils; MSM* value for *Carterodon* is here considered zero in accordance with paleontological results)

family and the early record of abrocomids was restricted to modern representatives belonging to the late Miocene genus †*Protabrocoma* (including †"*Abrocoma*" *antiqua*; Appendix). †*Deseadomys*, †*Protacaremys*, †*Prospaniomys*, and †*Spaniomys* were considered echimyids in the exhaustive reviews of Wood and Patterson (1959) and Patterson and Wood (1982) (see also Patterson and Pascual 1968). Arnal and Kramarz (2011) interpreted †*Prospaniomys* as an early offshoot of the Octodontidae lineage. Recent phylogenetic analyses showed that these genera, like †*Caviocricetus* and †*Dudumus*, could represent basal octodontoids not directly related to the origin of either Echimyidae or Octodontidae (Vucetich et al. 2014; Arnal et al. 2014; Arnal and Vucetich 2015). Alternatively, Verzi et al. (2014) included †*Spaniomys* within Abrocomidae. The results obtained here expand and support this alternative proposal through interpretation of the above mentioned pre-late Miocene octodontoids with rooted molars as ancient abrocomids.

The arrangement of the clades defined by nodes C and D is similar to the ones previously interpreted by us as Octodontidae and Echimyidae, respectively (Verzi et al. 2014, 2015), with the exception of the position of †*Caviocricetus* (previously included in Octodontidae) and †*Deseadomys arambourgi* (previously included in Echimyidae; cf. Fig. 4 and Verzi et al. 2014: Fig. 1). The name Octodontidae for node C and Octodontinae and Ctenomyinae for the subclades at nodes G and H, respectively (Fig. 4) are maintained here as in our previous proposal (Verzi et al. 2014, 2015). Nevertheless, we consider that a family-level assignment for these two subclades (Woods and Kilpatrick 2005; Patton et al. 2015) could be a suitable alternative given their extended history as independent lineages. Both Ctenomyinae and Octodontinae cluster traditional (euhypsodont) representatives of each subfamily along with genera that were previously classified as Echimyidae, as Octodontoidea with uncertain affinities, or as stem Octodontoidea (Appendix). In this arrangement, Octodontinae includes the 'acaremyids' †*Platypittamys* and †*Acaremys* (including †*Sciamys*) as in Wood and Patterson (1959; see also Winge 1941:190), as well as the more recently described 'acaremyid' †*Galileomys* (Vucetich and Kramarz 2003) and the taxa †*Plesiacarechimys*, †*Acarechimys minutus*, and †*Acarechimys minutissimus*. The topology of living Octodontinae is consistent with previous molecular phylogenies (Gallardo and Kirsch 2001; Honeycutt et al. 2003; Opazo 2005; Upham and Patterson 2012), and only the position of the mountain degu *Octodontomys* was unstable (cf. Fig. 4 and Online Resource 3; see also Upham and Patterson 2012: Figs. 3 and 4). Results by Arnal and Vucetich (2015) and Arnal et al. (2014) recovered the acaremyids and †*Plesiacarechimys* as more closely related to †*Dudumus* and †*Caviocricetus*, while Octodontidae was interpreted as a group more recently diverged from Echimyidae (see also Vucetich and Kramarz 2003; Frailey and Campbell 2004).

The relationship of †*Sallamys*+†*Protadelphomys*-†*Willidewu* with modern Ctenomyinae is here supported by two novel synapomorphies, one in the skull and another in the upper molars. This result markedly differs from those obtained by Vucetich et al. (2014), Arnal and Vucetich (2015), and Candela's (2015) reinterpretation of our previous analysis (Verzi et al. 2014).

Node D corresponds to Echimyidae in terms of the living fauna (Emmons et al. 2015), but excludes some of the late Oligocene to middle Miocene taxa previously referred to this family (Fig. 4; Appendix). The relationships among echimyids are mostly in agreement with previous molecular (Galewski et al. 2005; Upham and Patterson 2012, in press; Upham et al. 2013; Fabre et al. 2013, 2014; Loss et al. 2014), morphological (Emmons 2005; Olivares et al. 2012; Candela and Rasia 2012; Verzi et al. 2014), and combined phylogenies (Olivares and Verzi 2014; Verzi et al. 2015). Although with some differences, especially in the arrangement of the arboreal genera, these results are consistent in recovering two major subclades, one formed by the terrestrial spiny rat *Trinomys* plus the fossorial genera, and the other, by terrestrial and arboreal spiny rats, and the semiaquatic coypu (although see Candela and Rasia 2012). This information, together with recent phylogenies that have included the Caribbean capromyids (Fabre et al. 2014; Upham and Patterson in press) suggest the need for a profound revision of the status of Echimyidae subfamilies (see Olivares and Verzi 2014; Emmons et al. 2015).

Differences between the results obtained here and those from other recent phylogenetic analyses of fossil octodontoids (Arnal and Pérez 2013; Arnal et al. 2014; Vucetich et al. 2014; Arnal and Vucetich 2015) could be due in large part to the disparate representation of living species in the samples considered. Arnal and Pérez (2013: 129) interpreted Octodontidae as a group of modern (late Miocene) origin derived from an allegedly paraphyletic grouping "Echimyidae" represented by †*Eumysops* and †*Stichomys*; the octodontid *Octomys mimax* was the only living species included in this analysis. In later proposals that included the living echimyids *Echimys* and *Kannabateomys*, Arnal and Vucetich (2015) and Arnal et al. (2014) supported the grouping of †*Eumysops* and †*Stichomys* with this family, and considered Echimyidae as sister to Octodontidae. In these proposals, the interpretation of †*Caviocricetus*, †*Dudumus*, †*Deseadomys*, †*Prospaniomys*, and †*Protacaremys* as part of a temporally extended and diverse stem Octodontoidea does not consider the Abrocomidae among the lineages of Octodontoidea; in that context, these genera actually represent stem members of Echimyidae-Octodontidae (rather than of Octodontoidea), which is equivalent to the position of Abrocomidae among living taxa (Upham and Patterson 2012; Fabre et al. 2013). Another possible source of discrepancies with alternative proposals lies in the differential use of

craniomandibular and dental characters (cf. Carvalho and Salles 2004; Arnal et al. 2014: appendix 2; Verzi et al. 2014: SOM1; Online Resource 1 in this work).

The Reinterpretation of Lower Molar Morphology

Interpreting the patterns of simplification of lophate lower molars from the frequently more complete and stable morphology of the Dp4 provides a result equivalent to the proposal of Lavocat for the posterior crests of upper molars (Lavocat 1974: 58–59, Fig. 1; 1976; see also Vucetich and Verzi 1994: Fig. 3; Antoine et al. 2012: supplementary data). This fresh outlook on the patterns of change of lower molars leads to the recognition of a mesolophid in octodontoids and even caviomorphs (but see Patterson and Wood 1982; Marivaux et al. 2004; Frailey and Campbell 2004; Candela and Rasia 2012). By extension of this approach, the lower molars of the earliest caviomorphs from Contamana †*Cachiyacuy* and †*Canaanimys* would already show reduction of anterior crests, and the second crest would more likely be the mesolophid than the metalophulid II as originally interpreted (Antoine et al. 2012). If this were the case, the implied loss of metalophulid II supposes that a route of transformation of the lower molars (different from those detected among octodontoids) was already established quite early on.

Timescale of Evolutionary Stages in Major Clades

Underlying the alternative proposals for the phylogenetic relationships of octodontoids, there are important differences regarding the interpretation of the time of origin of living higher taxa. The first records of modern Abrocomidae, with euhypsodont molars whose morphology is similar to that of the living forms, have been interpreted as evidence of a late Miocene origin of this family (e.g., Reig 1986; Vucetich et al. 1999; Arnal and Pérez 2013). The interpretation of the origin of Octodontidae, and especially Ctenomyinae (or Ctenomyidae), has followed a similar path. As an exception, Winge (1941) and Wood and Patterson (1959) proposed an older origin for octodontines, but no similar hypothesis was ever proposed for Abrocomidae or Ctenomyinae (although see Landry 1957: 51). We think that the use of dental morphology as key source of primary homologies in the fossil record has created a bias toward the above mentioned acceptance of a modern origin for Abrocomidae and Octodontidae, and has simultaneously promoted the inclusion of early octodontoids within Echimyidae, a family whose extant species retain lophate, rooted molars (Appendix; Fig. 10).

Three successive stages can be recognized in the evolutionary history of any clade, referred to as t_1, t_2, and t_3 by Hennig (1965: Fig. 4): t_1, its origin by separation from its sister clade; t_2, its morphological differentiation by acquisition of the apomorphies that characterize its extant members; t_3, the origin of the last common ancestor of these living representatives. The time when a clade splits from its sister clade (t_1) and that of acquisition of its main diagnostic apomorphies (t_2) are often decoupled, resulting in the existence of stem members that have split before t_2 and share few "non-key" apomorphies with their corresponding crown-group (Steiper and Young 2008). However, the difficulty of separating the earliest representatives of two diverging lineages does not negate the validity of the branching point as the origin of the resulting clades (Briggs and Fortey 2005: 100). Thus, the interpretation of the origin of a group on the basis of the recognition of the main diagnostic characters present in its living representatives should be assumed to be the product of an operational restriction rather than the reflection of an actual pattern; efforts focused on the recognition of plesiomorphic basal stems are indispensable to interpret the deep history of a lineage. Following this last criterion, we use a total-clade definition (i.e., including stems and crown members; Briggs and Fortey 2005) for the familial and subfamilial clades (Figs. 4 and 10).

Abrocomids with modern dental morphology like the one that characterizes living species are recognized in the fossil record since the late Miocene (Fig. 10). Although with chronological differences, octodontines and ctenomyines also acquire their modern dental characters during the late Miocene, thus implying strong uncoupling between the stages of origin and morphological differentiation in these three clades. This differentiation stage coincides with the time of origin of the crown group in octodontines, whereas it takes place before the origin of the crown group in ctenomyines (Verzi et al. 2014). Based on the position of †*Protabrocoma* as sister of the living abrocomid genera, the stage of modernization is also earlier than the origin of the crown group in this family (see also datings of the *Abrocoma-Cuscomys* split in Upham and Patterson in press).

The molecular clock analysis, using a restricted sample of living species (Online Resource 3), suggests divergence times mostly older than interpreted so far (Leite and Patton 2002; Honeycutt et al. 2003; Galewski et al. 2005; Opazo 2005; Rowe et al. 2010; Upham and Patterson 2012, in press; Fabre et al. 2013, 2014; Upham et al. 2013; Voloch et al. 2013). According to these results, the origin of octodontoids would have taken place during the middle Eocene, near the time represented by the most ancient South American rodent fauna (from Yahuarango Formation, Contamana, Peru) as suggested by Antoine et al. (2012) and Arnal et al. (2014). The divergence between the lineage that led to abrocomids and the common ancestor of echimyids-octodontids would have occurred near the Eocene-Oligocene boundary, while the origin of the echimyid and octodontid lineages is early Oligocene in age. The initial diversification of the respective crown-groups of octodontids and echimyids would have taken place during the late Oligocene. It is noteworthy that the lineages leading to

minor living clades of echimyids, i.e., echimyines, dactylomyines, arboreal spiny-rats, and spiny rats including *Myocastor*, would have branched off as early as the late Oligocene-early Miocene. Moreover, most of the divergences between echimyid lineages leading to living genera are markedly older than expected, as anticipated by Lara et al. (1996: 410) and Da Silva and Patton (1998), and supported by recent results (Upham and Patterson 2012, in press; Upham et al. 2013; Fabre et al. 2013, 2014). These divergences are in general markedly older than the ones that separate the lineages leading to living octodontid genera.

Phylogenetic and Diversity Patterns as the Outcome of Differential Responses to Palaeoenvironmental Changes

As mentioned, the stage of differentiation is strongly decoupled from the origin in the southern octodontoid clades, i.e., octodontines, ctenomyines, and abrocomids. This is in clear contrast with the phylogenetic structure of echimyids (Fig. 10) in which a stage of modernization distinct from the origin of the clade is not recognizable in any of their major subclades. These distinctly different evolutionary patterns would have resulted from different responses to Cenozoic environmental changes (Pascual 1967; Verzi 2002; Verzi et al. 2014, 2015). A deepening of the global Cenozoic cooling and drying trend (Denton 1999; Zachos et al. 2001; Tripati et al. 2009), partially combined with local diastrophism corresponding to Andean orogeny, gave rise to increasingly open and arid biomes in southern South America since the late Miocene (Pascual and Ortiz Jaureguizar 1990; Palazzesi and Barreda 2007; Le Roux 2012; Quattrocchio et al. 2013; Palazzesi et al. 2014). The stages of southern differentiation in abrocomids, octodontines, and ctenomyines show a hierarchy that follows that of these paleoenvironmental changes. The appearance of euhypsodont lineages, and extinction of those with primitive molars, marks the beginning of the stage of modernization of these clades during the late Miocene. The subsequent appearance in the fossil record of arid-adapted and desert-specialists among hypsodont abrocomids and octodontines coincides with a profound global cooling and drying event around 2.5 Ma, near the Plio-Pleistocene boundary (Fig. 5; Verzi 2001; Verzi and Quintana 2005 and references therein). As a result of this pattern, modern southern octodontoids show wide morphological disparity involving specializations to arid and desert habitats (*Abrocoma*, *Pipanacoctomys*, *Tympanoctomys*) and the subterranean ecotope (*Spalacopus*, *Ctenomys*, and the extreme †*Eucelophorus*) (Table 1, Fig. 11).

In contrast to this pattern, echimyids went extinct in the southern part of their geographical range during the late Miocene-Pleistocene (with the exception of the peculiar *Myocastor*). Given that the presence of echimyids in southern South America has always represented an impoverished marginal sample of its astonishing diversity in the northern tropical areas, it suggests that the evolutionary response to paleoenvironmental changes by this clade would have been fidelity to their original habitats (Verzi et al. 2014, 2015). Because taxa which track "original" habitats (in this case at least as a passive response, i.e., through local extinction) are expected to be morphologically more conservative than those that adapt to new environments (Raia et al. 2012), this could explain the morphological similarity detected among anciently diverged lineages of echimyids (Table 1 and Fig. 11) and the related absence of differentiation stages as perceptible events decoupled from the origin of the clade.

The phylogenetic structure of southern abrocomids, octodontines, and ctenomyines also differs markedly from that of echimyids with regards to the topology of the origin of the crown group (t_3) in relation to that of the corresponding clade (t_1, Fig. 10). In the southern clades, the initial diversification of the respective crown-groups is strongly uncoupled from the origin of the clades. In echimyids, in contrast, the origin of the crown-group of the family or of its two major subclades is not uncoupled from the origin of the respective clades, not even in the case of the larger subclade (comprising terrestrial, arboreal, and semiaquatic representatives) that includes early fossils. The decoupling between t_1 and t_3 observed in southern octodontoids is the result of the phylogenetic structure of extinction. In these groups, as opposed to echimyids, extinction eliminated deep clades bringing about a marked loss of evolutionary history (cf. Fig. 10 and Erwin 2008: Fig. 1); since the late Miocene onwards, extinction affected some of the euhypsodont genera and all the lineages with rooted molars (Vucetich and Verzi 1999). As a result, living abrocomids and octodontids are restricted to only late-diverged, euhypsodont representatives.

The question remains why the modernization of octodontoids took place latest among southern caviomorphs, given that chinchilloids were already becoming differentiated in the early Oligocene (see Bertrand et al. 2012) and cavioids in the early Miocene (Pérez and Pol 2012); even, octodontoids are unique among living South American hystricomorphs in retaining a rat-like appearance (i.e., a body plan without major modifications; e.g., Redford and Eisenberg 1992: pl. 17; Eisenberg and Redford 1999: pl. 13).

Environmental Dynamics as a Diversity-Driving Factor

The understanding of biological diversity is a central goal in evolutionary and ecological theories. The processes and factors that generate and control species richness, and its patterns of spatial and temporal distribution, are among the most revisited (e.g., Wiens and Donoghue 2004; Jablonski et al. 2006; Weir and Schluter 2007; Mittelbach et al. 2007;

Benton 2009; Buckley et al. 2010; Rull 2011; Davies et al. 2011; Rabosky et al. 2012). A positive correlation of species richness with morphological diversity (e.g., Ricklefs 2004), as expected in certain ecological and evolutionary scenarios (Eldredge and Gould 1972; Eldredge 1996; Schluter 2000), or with phylogenetic and functional diversity (the latter being a proxy for morphological diversity) is not the rule. Cladogenetic richness (from populations to species) seems not be linearly related with evolutionary dynamics of other components of diversity. On the contrary, there is a growing body of evidence of the uncoupling between these components (e.g., Fortey et al. 1996; Adams et al. 2009; Safi et al. 2011; Blankers et al. 2013; Ruta et al. 2013).

Given that evolutionary transformation, i.e., anagenesis underlying adaptation, requires cohesion of the evolving lineage (Futuyma 1987) rather than the contingent perturbation of such cohesion that underlies cladogenesis and extinction, adaptation and changes in cladogenetic richness (as two primary components of diversity) should not be expected to be coupled, or at least not necessarily (see Szalay 1999: 52).

As described above, the distinctive evolutionary patterns of the southern and northern octodontoid clades include, in the former, both morphological transformation implied in the adaptation to derived emerging environments, and extinction of deep lineages causing strong loss of evolutionary history (see von Euler 2001; Erwin 2008). As a result, the living southern clades show greater disparity as well as less content of evolutionary history and lower taxonomic diversity, which could be considered at first as a counterintuitive pattern. We consider that such a pattern is channelled by environmental dynamics. Rainforests occurred in South America up to high latitudes during the Eocene (Burnham and Johnson 2004), and whereas the long-term global Cenozoic cooling (Denton 1999; Zachos et al. 2001, 2008) caused their retraction toward lower latitudes (Barreda and Palazzesi 2007; Quattrocchio et al. 2013; Palazzesi et al. 2014), their current condition in northern South America has remained essentially stable throughout the Cenozoic (Colinvaux and De Oliveira 2001). Conversely, in the south of the continent, the deepening Tertiary cooling and drying trend combined with local diastrophism gave rise to the development of new, derived open biomes (Pascual and Ortiz Jaureguizar 1990; Palazzesi and Barreda 2007; Barreda and Palazzesi 2007; Le Roux 2012; Quattrocchio et al. 2013; Palazzesi et al. 2014). As in the case of the environments, the dynamics of octodontoid diversity would have been more stable in the tropical habitats of northern South America. Meanwhile, both strong adaptation and extinction are expected evolutionary responses to changes generating new environments in the south. These differential dynamics of diversity probably occurred during much of the Tertiary, before the late Miocene, but the exploration of this issue is hindered by the fragmentary nature of the fossil record, especially in northern South America (MacFadden 2006; Antoine et al. 2013). Beyond this, we consider that such dynamics are not necessarily linked to latitude, but to the stability vs. mutability of environments on a temporal scale (Sheldon 1996; Verzi et al. 2015).

The importance of the environment to catalyze and channel evolutionary change has been thoroughly stated by Vrba for the fossil record in a rich body of theory (Vrba 1992, 1995, 2004, 2005). In this proposal, coordination between the diversity resulting from cladogenesis, extinction and distribution drift, and evolutionary transformation (represented in Vrba's proposal by a heterochronic change axis; see Vrba 2004, 2005) is given essentially by the environment. However, both in this theoretical paleontological context, as in ecological approaches, the contribution of the anagenetic component has received relatively little attention (Verzi et al. 2015). In this sense, as part of the efforts aimed at understanding the history of biological diversity, it is necessary to analyze evolutionary transformation in its environmental context along with cladogenesis and extinction (Sheldon 1996).

The evolutionary stages of a clade provide information regarding the dynamics of cladogenetic and anagenetic components of diversity. The times of origin of a clade and of its crown-group represent cladogenesis and extinction, i.e., changes in diversity irrespective of transformation or anagenesis; in contrast, the lapse between the time of origin of a clade and its differentiation stage implies evolutionary transformation in lineages (in this case, morphological change) a priori irrespective of cladogenetic diversification. Fossils provide key information on these stages, which highlights the involvement of paleontology to macroevolutionary interpretations.

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Appendix

Table 2 Taxonomic arrangements for studied taxa

This study	Simpson 1945	Wood 1955; Patterson and Pascual 1968; Patterson and Wood 1982	Woods 1984	Vucetich and Verzi 1991	McKenna and Bell 1997	Carvalho and Salles 2004	Woods and Kilpatrick 2005	Vucetich et al. 2010	Arnal and Vucetich 2015
Octodontoidea	Octodontoidea	Octodontoidea	Octodontoidea	Octodontoidea	Octodontoidea	Octodontoidea	Octodontoidea	Octodontoidea	Octodontoidea
Echimyidae	Echimyidae	Echimyidae	Echimyidae	Echimyidae	†*Caviocricetus*	†*Deseadomys*	Echimyidae	†*Acarechimys*	†*Acarechimys*
†*Adelphomys*	Dactylomyinae	Adelphomyinae	Adelphomyinae	†*Acarechimys*	†*Dicolpomys* [9]	†*Platypittamys*	Dactylomyinae	†*Caviocricetus*	†*Caviocricetus*
†*Dicolpomys*	*Dactylomys*	†*Adelphomys*	†*Adelphomys*	†*Adelphomys*	Echimyidae	†*Sallamys*	*Dactylomys*	†*Prospaniomys*	†*Dudumus*
†*Eodelphomys*	*Kannabateomys*	†*Deseadomys*	†*Deseadomys*	†*Chasichimys*	†*Maruchito*	†*Sciamys*	*Kannabateomys*	†*Protadelphomys*	†*Plesiacarechimys*
†*Eumysops*	*Olallamys*[7]	†*Paradelphomys*	†*Paradelphomys*	†*Deseadomys*	†*Willidewu*	†*Willidewu*	*Olallamys*	†*Sallamys*	†*Prospaniomys*
†*Maruchito*	Echimyinae	†*Stichomys*	†*Sallamys*	†*Paradelphomys*	Adelphomyinae	†*Xylechimys*	Echimyinae	†*Willidewu*	†*Protacaremys*
†*Pampamys*	†*Adelphomys*	†*Xylechimys*	†*Stichomys*	†*Platypittamys*	†*Adelphomys*	Echimyidae	*Echimys*	Echimyidae	Acaremyidae
†*Paradelphomys*	†*Prospaniomys*	Dactylomyinae	†*Xylechimys*	†*Prospaniomys*	†*Deseadomys*	†*Acarechimys*	*Isothrix*	Adelphomyinae	†*Acaremys*
†*Stichomys*	†*Protadelphomys*	*Dactylomys*	Dactylomyinae	†*Protacaremys*	†*Paradelphomys*	†*Adelphomys*	*Makalata*	†*Adelphomys*	†*Galileomys*
†*Xylechimys*	†*Spaniomys*	*Kannabateomys*	*Dactylomys*	†*Protadelphomys*	†*Stichomys*	†*Caviocricetus*	*Phyllomys*	†*Eodelphomys* [9]	†*Platypittamys*
†*Theridomysops*	†*Stichomys*	*Olallamys*[7]	*Kannabateomys*	†*Sallamys*	†*Xylechimys*	†*Eumysops*	Eumysopinae	†*Maruchito*	†*Sciamys*
Carterodon	*Carterodon*	Echimyinae	*Thrinacodus*	†*Spaniomys*	Dactylomyinae	†*Maruchito*	*Carterodon*	†*Paradelphomys*	Echimyidae
Clyomys	*Cercomys* [8]	*Echimys*	Echimyinae	†*Stichomys*	*Dactylomys*	†*Pampamys*	*Clyomys*	†*Protacaremys*	†*Adelphomys*
Dactylomys	*Clyomys*	*Isothrix*	†*Chasichimys*	†*Willidewu*	*Kannabateomys*	†*Prospaniomys*	*Euryzygomatomys*	†*Spaniomys*	†*Stichomys*
Echimys	*Echimys*	Heteropsomyinae	†*Eumysops*	†*Xylechimys*	*Olallamys*	†*Protacaremys*	*Hoplomys*	†*Stichomys*	†*Eumysops*
Euryzygomatomys	*Euryzygomatomys*	†*Acarechimys*	†*Pattersomys*		Echimyinae	†*Protadelphomys*	*Lonchothrix*	†*Xylechimys*	*Echimys*
Hoplomys	*Hoplomys*	†*Chasichimys*	†*Protadelphomys*		*Echimys*	†*Theridomysops*	*Mesomys*	*Olallamys*	*Kannabateomys*
Isothrix	*Isothrix*	†*Eumysops*	*Carterodon*		*Isothrix*	†*Spaniomys*	*Proechimys*	Acaremyidae	Octodontidae
Kannabateomys	*Lonchothrix*	†*Protacaremys*	*Clyomys*		*Makalata*	†*Stichomys*	*Thrichomys*	†*Acaremys*	†*Chasichimys*
Lonchothrix	*Mesomys*	†*Protadelphomys*[9]	*Echimys*		Heteropsomyinae	*Carterodon*	*Trinomys*	†*Sciamys*	†*Chasicomys*
Makalata	*Proechimys*	†*Sallamys*	*Euryzygomatomys*		†*Acarechimys*	*Clyomys*	Ctenomyidae		†*Neophanomys*
Mesomys	Ctenomyidae	*Carterodon*	*Hoplomys*		†*Chasichimys*	*Echimys*	*Ctenomys*		*Octodontomys*
Myocastor	†*Actenomys*	*Cercomys* [8]	*Isothrix*		†*Eumysops*	*Euryzygomatomys*	Octodontidae		*Octomys*
Olallamys	†*Eucelophorus*	*Clyomys*	*Lonchothrix*		†*Pampamys*	*Hoplomys*	*Aconaemys*		
Phyllomys	†*Megactenomys*	*Euryzygomatomys*	*Makalata*		†*Pattersomys*	*Isothrix*	*Octodon*		
Proechimys	†*Xenodontomys*	*Hoplomys*	*Mesomys*		†*Protacaremys*	*Lonchothrix*	*Octodontomys*		
Thrichomys	*Ctenomys*	*Lonchotrix*	*Proechimys*		†*Protadelphomys*	*Makalata*	*Octomys*		
Toromys	Octodontidae	*Mesomys*	*Thrichomys*		†*Sallamys*	*Mesomys*	*Pipanacoctomys*		
Trinomys	†*Pithanotomys*	*Proechimys*	Myocastoridae		*Carterodon*	*Myocastor*	*Spalacopus*		
Octodontidae	*Aconaemys*	Myocastorinae	†*Prospaniomys*		*Clyomys*	*Phyllomys*	*Tympanoctomys*		
Ctenomyinae	*Octodon*	†*Prospaniomys*	†*Spaniomys*		*Euryzygomatomys*	*Proechimys*	Abrocomidae		
†*Chasichimys*[1]	*Octodontomys*	†*Spaniomys*	*Myocastor*		*Hoplomys*	*Thrichomys*	*Abrocoma*		
†*Chasicomys*	*Octomys*	*Myocastor*	Ctenomyidae		*Lonchothrix*	*Trinomys*	*Cuscomys*		
†*Protadelphomys*	*Spalacopus*	Octodontidae	†*Dicolpomys* [10]		*Mesomys*	Dactylomyinae	Myocastoridae		
†*Sallamys*	Abrocomidae	†*Acaremys*	†*Actenomys*		*Proechimys*	†*Paradelphomys*	*Myocastor*		
†*Willidewu*	†*Protabrocoma*	†*Platypittamys*	†*Eucelophorus*		*Thrichomys*	*Dactylomys*			
†*Xenodontomys*[2]	*Abrocoma*	†*Sciamys*	†*Proctenomys*		Myocastorinae	*Kannabateomys*			
†*Actenomys*	Capromyidae	†*Pithanotomys*	†*Xenodontomys*		†*Prospaniomys*	*Olallamys*			

Table 2 (continued)

This study	Simpson 1945	Wood 1955; Patterson and Pascual 1968; Patterson and Wood 1982	Woods 1984	Vucetich and Verzi 1991	McKenna and Bell 1997	Carvalho and Salles 2004	Woods and Kilpatrick 2005	Vucetich et al. 2010	Arnal and Vucetich 2015
†*Eucelophorus* †*Praectenomys* *Ctenomys*(3) Octodontinae †*Acarechimys* †*Acaremys*(4) †*Galileomys* †*Neophanomys* †*Platypittamys*(5) †*Plesiacarechimys* †*Abalosia* †*Pithanotomys* †*P. innominatus* *Aconaemys* *Octodon* *Octodontomys* *Octomys* *Pipanacoctomys* *Spalacopus* *Tympanoctomys* Abrocomidae †*Caviocricetus* †*Dudumus* †*Deseadomys* †*Prospaniomys* †*Protacaremys* †'*Protacaremys*' *denisae* †*Spaniomys* †*Protabrocoma*(6) *Abrocoma* *Cuscomys*	†*Eumysops* *Myocastor* Erethizontoidea Erethizontidae Acaremyinae †*Acaremys* †*Protacaremys* †*Sciamys*	*Aconaemys* *Octodon* *Octodontomys* *Octomys* *Spalacopus* Ctenomyinae †*Actenomys* †*Eucelophorus* †*Megactenomys* †*Xenodontomys* *Ctenomys* Abrocomidae *Abrocoma* †*Protabrocoma*	*Ctenomys* Octodontidae †*Acaremys* †*Platypittamys* †*Sciamys* *Aconaemys* *Octodon* *Octodontomys* *Octomys* (11) *Spalacopus* Abrocomidae †*Protabrocoma* *Abrocoma*		†*Spaniomys* *Myocastor* Octodontidae Acaremyinae †*Acaremys* †*Platypittamys* †*Sciamys* Octodontinae †*Chasicomys* Ctenomyini †*Actenomys* †*Eucelophorus* †*Megactenomys* †*Praectenomys* †*Xenodontomys* *Ctenomys*(12) Octodontini †*Abalosia* *Octodon* *Octodontomys* *Octomys* *Pithanotomys* (13) *Spalacopus* *Tympanoctomys* Chinchilloidea Abrocomidae †*Protabrocoma* *Abrocoma*				

1 Including †*Pattersomys*; **2** Including †*Proctenomys*; **3** Including †*Megactenomys* and †*Paractenomys*; **4** Including †*Sciamys*; **5** Including †*Galileomys baios*; **6** Including †*Abrocoma antiqua*; **7** As *Thrinacodus*; **8** Invalid synonym of *Thrichomys*; **9** Tentatively included; **10** Included here or in Octodontidae; **11** Including *Tympanoctomys*; **12** Including †*Paractenomys*; **13** Including *Aconaemys*.

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