Phylogeny and evolutionary patterns of South American octodontoid rodents

DIEGO H. VERZI, A. ITATÍ OLIVARES, and CECILIA C. MORGAN

Verzi, D.H., Olivares, A.I., and Morgan, C.C. 2014. Phylogeny and evolutionary patterns of South American octodontoid rodents. *Acta Palaeontologica Polonica* 59 (4): 757–769.

Octodontoidea is the most diverse clade of hystricognath rodents, and is richly recorded in South America since at least the Oligocene. A parsimony-based morphological phylogenetic analysis of a wide range of extant and extinct octodontoids recovered three major clades, here recognised as Echimyidae, Octodontidae, and Abrocomidae. Taxa previously assigned to Echimyidae or Octodontoidea incertae sedis are here interpreted for the first time as early representatives of Ctenomyinae (Octodontidae), Octodontinae or Abrocomidae. Based on our results, we estimate the divergence of octodontoid families and subfamilies to have occurred during the Late Oligocene, which is consistent with molecular estimates, but older than previous inferences based on the fossil record. Contrary to previous suggestions, we show the first appearances of modern members of Abrocomidae, Octodontinae and Ctenomyinae to be distinctly decoupled from the origin of these clades, with different stages in the evolutionary history of octodontoids seemingly following distinct phases of palaeoenvironmental change. Depending on the phylogenetic pattern, fossils from the stage of differentiation bear evolutionary information that may not be provided by crown groups, thus highlighting the unique and important contribution of fossils to our understanding of macroevolutionary patterns.

Key words: Mammalia, Rodentia, Hystricognathi, Octodontoidea, phylogeny, evolution, divergence dates, Cenozoic, South America.

Diego H. Verzi [dverzi@fcnym.unlp.edu.ar], A. Itatí Olivares [iolivares@fcnym.unlp.edu.ar], and Cecilia C. Morgan [cmorgan@fcnym.unlp.edu.ar], CONICET, Sección Mastozoología, Museo de La Plata, Paseo del Bosque s/n, La Plata B1900FWA, Argentina.

Received 9 November 2012, accepted 11 March 2013, available online 13 March 2013.

Introduction

Octodontoidea is the most diverse clade of hystricognath rodents (Woods and Kilpatrick 2005). In the Recent South American fauna, it includes the fossorial to subterranean Octodontidae (degus, coruros, and tuco-tucos), the terrestrial and scansorial Abrocomidae (chinchilla rats), and the arboreal, semiaquatic, and terrestrial to fossorial Echimyidae (spiny rats and coypus) (Redford and Eisenberg 1992; Eisenberg and Redford 1999; Emmons and Feer 1999). In particular, the families Echimyidae (including *Myocastor*, sometimes included in a family of its own; Table 1) and Octodontidae (including Ctenomyinae, sometimes considered a family in their own right; Table 1, and discussion in Verzi 2001) comprise more than 60% of the extant species of South American hystricognaths (Woods and Kilpatrick 2005; Upham and Patterson 2012) and have the richest fossil record of the entire suborder (McKenna and Bell 1997).

The abundant fossil record of octodontoids extends at least as far back as the Oligocene (Wood and Patterson 1959; Patterson and Wood 1982; Vucetich et al. 1999, 2010b) and possibly even the Eocene (Frailey and Campbell 2004; Antoine et al. 2012). While the monophyly of Octodontoidea is not disputed (Opazo 2005; Honeycutt 2009; Vilela et al. 2009; Upham and Patterson 2012), the phylogenetic relationships of most living and fossil octodontoids, and in particular those from the Oligocene–Middle Miocene, remain poorly understood (e.g., Patterson and Wood 1982; Vucetich and Kramarz 2003; Vucetich et al. 1999, 2010a). Most of these early octodontoids have been assigned to Echimyidae owing to their lophate, low-crowned molars (Carvalho and Salles 2004). The latter are retained by extant members of this family, which inhabit mainly forested areas in northern South America (Reig 1986). By contrast, Octodontidae and Abrocomidae are thought to have originated during the Late Miocene, based on the first appearance of species with simplified, hypsodont molars – which are characteristic of their extant representatives – in Argentina and Bolivia (Rovereto 1914; Reig 1989; McKenna and Bell 1997; Vucetich et al. 1999). However, this taxonomic arrangement has been disputed by several authors (Winge

1941; Wood and Patterson 1959; Patterson and Wood 1982; Verzi 2002; Verzi et al. 2011).

Here, we reevaluate the evolutionary history of octodontoids through a comprehensive phylogenetic analysis including a wide range of extant and extinct taxa. In addition, we provide a new set of intra-clade divergence time estimates based on the fossil record.

Institutional abbreviations.—IMCN-CM, Instituto y Museo de Ciencias Naturales, San Juan, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia", Mar del Plata, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

Other abbreviations.—MSM*, Stratigraphic Manhattan Measure; TBR, tree bisection reconnection; $t_{1–3}$, times of origin (t_1) and differentiation (t_2) of a clade, and of emergence of its crown group (t_3).

Material and methods

Our phylogenetic analysis is based on 73 cranio-mandibular and dental characters scored for 53 extant and extinct Octodontoid genera (SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/appXX-Verzi_etal_SOM.pdf). The character matrix was generated through first-hand revision of nearly 2000 specimens representing all of the South American octodontoid families and subfamilies, plus the extant Antillean *Capromys* (Capromyidae) (SOM 2). The extant cavioid *Dasyprocta* (Dasyproctidae) was used as outgroup. The informal name "†*Acaremys* group" is here used to refer to the closely related genera †*Sciamys* and †*Acaremys* (Scott 1905; Vucetich and Kramarz 2003), whose contents and independence remain in need of revision. We analysed our matrix using the "traditional search" option of TNT v. 1.1 (Goloboff et al. 2008a, b), using 10 000 random stepwise-addition replicates and tree bisection reconnection (TBR) branch swapping, saving 100 trees per replicate. In addition, we performed an extra round of TBR on the optimal trees to increase the chance of finding all topologies of minimum length (Bertelli and Giannini 2005). All characters were equally weighted and (except for character 49; SOM 1) treated as non-additive. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (Coddington and Scharff 1994). Branch support was calculated in the form of absolute and relative Bremer indices (Bremer 1994; Goloboff and Farris 2001).

The modified Stratigraphic Manhattan Measure (MSM*; Pol and Norell 2001) was used to assess the fit of the resulting phylogeny with the stratigraphic record. Minimum divergence date estimates for individual clades were based on the oldest, reliably dated fossil confidently assigned to either of the two lineages arising from each branching point (SOM 3) (Benton and Donoghue 2007). We calculated the MSM* both for the entire tree and for the two major octodontoid clades, which are similar in size and hence comparable (Pol et al. 2004).

Results

Phylogenetic relationships.—Our analysis resulted in three most parsimonious trees of 139 steps (CI = 0.65, RI = 0.88; SOM 1), and reveal three major clades (Fig. 1): extant Echimyidae (node A), as well as some of the extinct genera traditionally assigned to this family (Table 1); Octodontinae and Ctenomyinae (node J), plus a range of genera previously included in other taxa (Fig. 1, Table 1); and †*Spaniomys* and Abrocomidae (node T).

Node A (Echimyidae) has low support, but no character conflict (Fig. 1), and is diagnosed by (i) the lacrimal foramen opening into the maxilla (character state 10-1; Fig. 2); (ii) the presence of a continuous rim (without a suture) formed by the maxilla around the foramen into the lacrimal canal (character state 11-1); (iii) the lateral process of the supraoccipital extending ventrally below the level of the mastoid process (character state 38-1; Fig. 3); and (iv) the rotation of the distal portion of the paroccipital process, resulting in the posterolateral or posterior orientation of its external margin (character state 41-1). Within Echimyidae, there are two major subclades. The first of these (node I) includes the extant fossorial eumysopines *Carterodon*, *Clyomys*, and *Euryzygomatomys*, as well as the extinct †*Theridomysops* and †*Dicolpomys*, and is supported by details of the morphology of the zygomatic arch (character states 21-1, 24-1, and 25-1; not preserved in †*Theridomysops* and †*Dicolpomys*). The second subclade (node B) comprises the terrestrial spiny rats *Thrichomys*–†*Pampamys*–†*Eumysops* and *Hoplomys* + *Proechimys*–*Trinomys*, the semiaquatic coypu *Myocastor*, the spiny tree-rat *Mesomys*, and the arboreal echimyines-dactylomyines, all of which are united by the shape of their pterygoid fossae (character state 33-1).

Within the second echimyid subclade (node B), *Myocastor* is sister to the arboreal *Mesomys* + echimyines–dactylomyines (node C), as indicated by the presence of a thick lower margin of the posterior process of the squamosal (character state 34-1) and a short lower incisor (character state 49-1). The clade comprising *Mesomys* + echimyines–dactylomyines (node D) is supported by the position of the sphenopalatine fissure posteroventral to the lacrimal foramen (character state 18-1), the presence of a wide maxilla dorsal to this fissure (character state 19-1), and the dorsal or anterodorsal orientation of the anterior margin of the alisphenoid (character state 30-1). Within this clade, the adelphomyine †*Maruchito* clusters with the echimyines *Echimys* + *Phyllomys* owing to the presence of a transversely oriented posteroflexus crossing the entire occlusal surface of M1–M2 (node E; character state 57-1). A further group (node F)

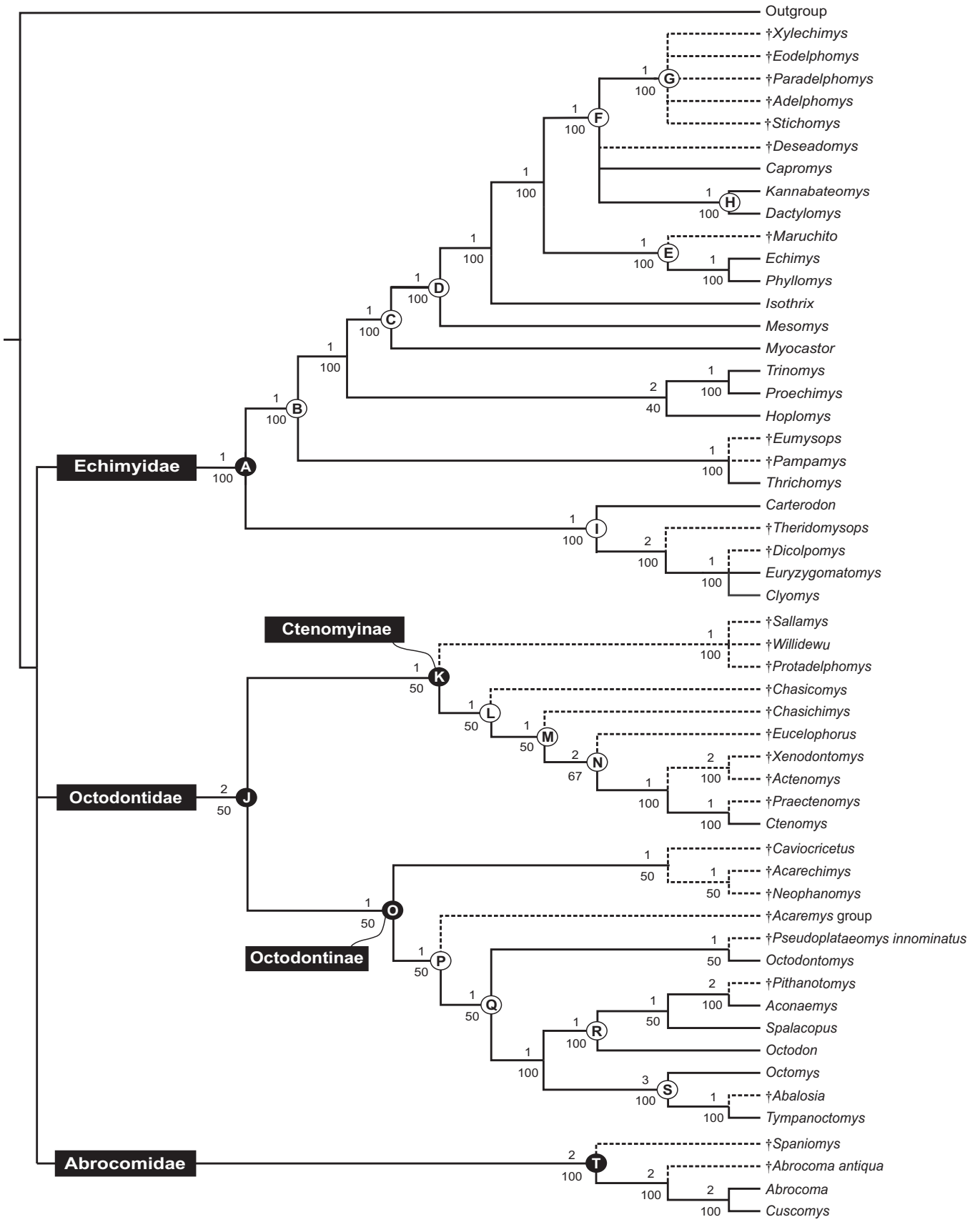

Fig. 1. Strict consensus of the three most parsimonious trees (139 steps; CI = 0.65, RI = 0.88) resulting from the phylogenetic analysis. Numbers above and below branches represent absolute and relative Bremer support, respectively. A to T represent nodes discussed in the text. Black background indicates major taxa and their corresponding nodes as recognised in this study (cf. Table 1). Dashed lines indicate extinct taxa.

Table 1. Taxonomic arrangements for studied taxa. Comments: 1, tentatively included; 2, including †*Sciamys*; 3, including *Pipanacoctomys*; 4, invalid synonym of *Thrichomys*; 5, including †*Abrocoma antiqua*; 6, including *Tympanoctomys*; 7, including *Aconaemys*.

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)
Octodontoidea **Echimyidae** †*Adelphomys* †*Deseadomys* †*Dicolpomys* †*Eodelphomys* †*Eumysops* †*Maruchito* †*Pampamys* †*Paradelphomys* †*Stichomys* †*Xylechimys* †*Theridomysops* *Capromys* [1] *Carterodon* *Clyomys* *Dactylomys* *Echimys* *Euryzygomatomys* *Hoplomys* *Isothrix* *Kannabateomys* *Mesomys* *Myocastor* *Phyllomys* *Proechimys* *Thrichomys* *Trinomys* **Octodontidae** **Ctenomyinae** †*Actenomys* †*Chasichimys* †*Chasicomys* †*Eucelophorus* †*Praectenomys* †*Protadelphomys* †*Sallamys* †*Willidewu* †*Xenodontomys* *Ctenomys* **Octodontinae** †*Abalosia* †*Acarechimys* †*Acaremys* group [2] †*Pithanotomys* †*P. innominatus* †*Neophanomys* †*Caviocricetus* *Aconaemys* *Octodon* *Octodontomys* *Octomys* *Spalacopus* *Tympanoctomys* [3] **Abrocomidae** †*Abrocoma antiqua* †*Spaniomys* *Abrocoma* *Cuscomys*	**Octodontoidea** **Echimyidae** **Dactylomyinae** *Dactylomys* *Kannabateomys* **Echimyinae** †*Adelphomys* †*Protadelphomys* †*Spaniomys* †*Stichomys* *Carterodon* *Cercomys* [4] *Clyomys* *Echimys* *Euryzygomatomys* *Hoplomys* *Isothrix* *Mesomys* *Proechimys* **Ctenomyidae** †*Actenomys* †*Eucelophorus* †*Xenodontomys* *Ctenomys* **Octodontidae** †*Pithanotomys* *Aconaemys* *Octodon* *Octodontomys* *Octomys* *Spalacopus* **Abrocomidae** *Abrocoma* †*Protabrocoma* [5] **Capromyidae** †*Eumysops* *Capromys* *Myocastor* **Erethizontoidea** **Erethizontidae** **Acaremyinae** †*Acaremys* †*Sciamys*	**Octodontoidea** **Echimyidae** **Adelphomyinae** †*Adelphomys* †*Deseadomys* †*Paradelphomys* †*Stichomys* †*Xylechimys* **Capromyinae** *Capromys* **Dactylomyinae** *Dactylomys* *Kannabateomys* **Echimyinae** *Echimys* *Isothrix* **Heteropsomyinae** †*Acarechimys* †*Chasichimys* †*Eumysops* †*Protadelphomys* [1] †*Sallamys* *Carterodon* *Cercomys* [4] *Clyomys* *Euryzygomatomys* *Hoplomys* *Mesomys* *Proechimys* **Myocastorinae** †*Spaniomys* *Myocastor* **Octodontidae** †*Acaremys* †*Pithanotomys* †*Sciamys* *Aconaemys* *Octodon* *Octodontomys* *Octomys* *Spalacopus* **Ctenomyinae** †*Actenomys* †*Eucelophorus* †*Xenodontomys* *Ctenomys* **Abrocomidae** *Abrocoma*	**Octodontoidea** **Echimyidae** **Adelphomyinae** †*Adelphomys* †*Deseadomys* †*Paradelphomys* †*Sallamys* †*Stichomys* †*Xylechimys* **Dactylomyinae** *Dactylomys* *Kannabateomys* **Echimyinae** †*Chasichimys* †*Eumysops* †*Protadelphomys* *Carterodon* *Clyomys* *Echimys* *Euryzygomatomys* *Hoplomys* *Isothrix* *Mesomys* *Proechimys* *Thrichomys* **Ctenomyidae** †*Actenomys* †*Dicolpomys* [1] †*Eucelophorus* †*Xenodontomys* *Ctenomys* **Octodontidae** †*Acaremys* †*Sciamys* *Aconaemys* *Octodon* *Octodontomys* *Octomys* [6] *Spalacopus* **Abrocomidae** *Abrocoma* †*Protabrocoma* [5] **Capromyidae** *Capromys* **Myocastoridae** †*Spaniomys* *Myocastor*	**Octodontoidea** **Echimyidae** †*Acarechimys* †*Adelphomys* †*Chasichimys* †*Deseadomys* †*Paradelphomys* †*Protadelphomys* †*Sallamys* †*Spaniomys* †*Stichomys* †*Willidewu* †*Xylechimys* Vucetich et al. (2010) **Octodontoidea** †*Acarechimys* †*Caviocricetus* †*Protadelphomys* †*Sallamys* †*Willidewu* **Echimyidae** **Adelphomyinae** †*Adelphomys* †*Eodelphomys* [1] †*Maruchito* †*Paradelphomys* †*Spaniomys* †*Stichomys* †*Xylechimys* **Acaremyidae** †*Acaremys* †*Sciamys*	**Octodontoidea** †*Caviocricetus* †*Dicolpomys* [1] **Echimyidae** †*Maruchito* †*Willidewu* **Adelphomyinae** †*Adelphomys* †*Deseadomys* †*Paradelphomys* †*Stichomys* †*Xylechimys* **Dactylomyinae** *Dactylomys* *Kannabateomys* **Echimyinae** *Echimys* *Isothrix* **Heteropsomyinae** †*Acarechimys* †*Chasichimys* †*Eumysops* †*Pampamys* †*Protadelphomys* †*Sallamys* *Carterodon* *Clyomys* *Euryzygomatomys* *Hoplomys* *Mesomys* *Proechimys* *Thrichomys* **Myocastorinae** †*Spaniomys* *Myocastor* **Octodontidae** **Acaremyinae** †*Acaremys* †*Sciamys* **Octodontinae** †*Chasicomys* **Ctenomyini** †*Actenomys* †*Eucelophorus* †*Praectenomys* †*Xenodontomys* *Ctenomys* **Octodontini** †*Abalosia* *Octodon* *Octodontomys* *Octomys* *Pithanotomys* [7] *Spalacopus* *Tympanoctomys* **Capromyidae** *Capromys* **Chinchilloidea** **Abrocomidae** *Abrocoma* †*Protabrocoma* [5]	**Octodontoidea** †*Deseadomys* †*Sallamys* †*Sciamys* †*Willidewu* †*Xylechimys* **Echimyidae** †*Acarechimys* †*Adelphomys* †*Caviocricetus* †*Eumysops* †*Maruchito* †*Pampamys* †*Protadelphomys* †*Theridomysops* †*Spaniomys* †*Stichomys* *Carterodon* *Clyomys* *Echimys* *Euryzygomatomys* *Hoplomys* *Isothrix* *Mesomys* *Myocastor* *Phyllomys* *Proechimys* *Thrichomys* *Trinomys* **Dactylomyinae** †*Paradelphomys* *Dactylomys* *Kannabateomys*	**Octodontoidea** **Echimyidae** **Dactylomyinae** *Dactylomys* *Kannabateomys* **Echimyinae** *Echimys* *Isothrix* *Phyllomys* **Eumysopinae** *Carterodon* *Clyomys* *Euryzygomatomys* *Hoplomys* *Mesomys* *Proechimys* *Thrichomys* *Trinomys* **Ctenomyidae** *Ctenomys* **Octodontidae** *Aconaemys* *Octodon* *Octodontomys* *Octomys* *Pipanacoctomys* *Spalacopus* *Tympanoctomys* **Abrocomidae** *Abrocoma* *Cuscomys* **Capromyidae** *Capromys* **Myocastoridae** *Myocastor*

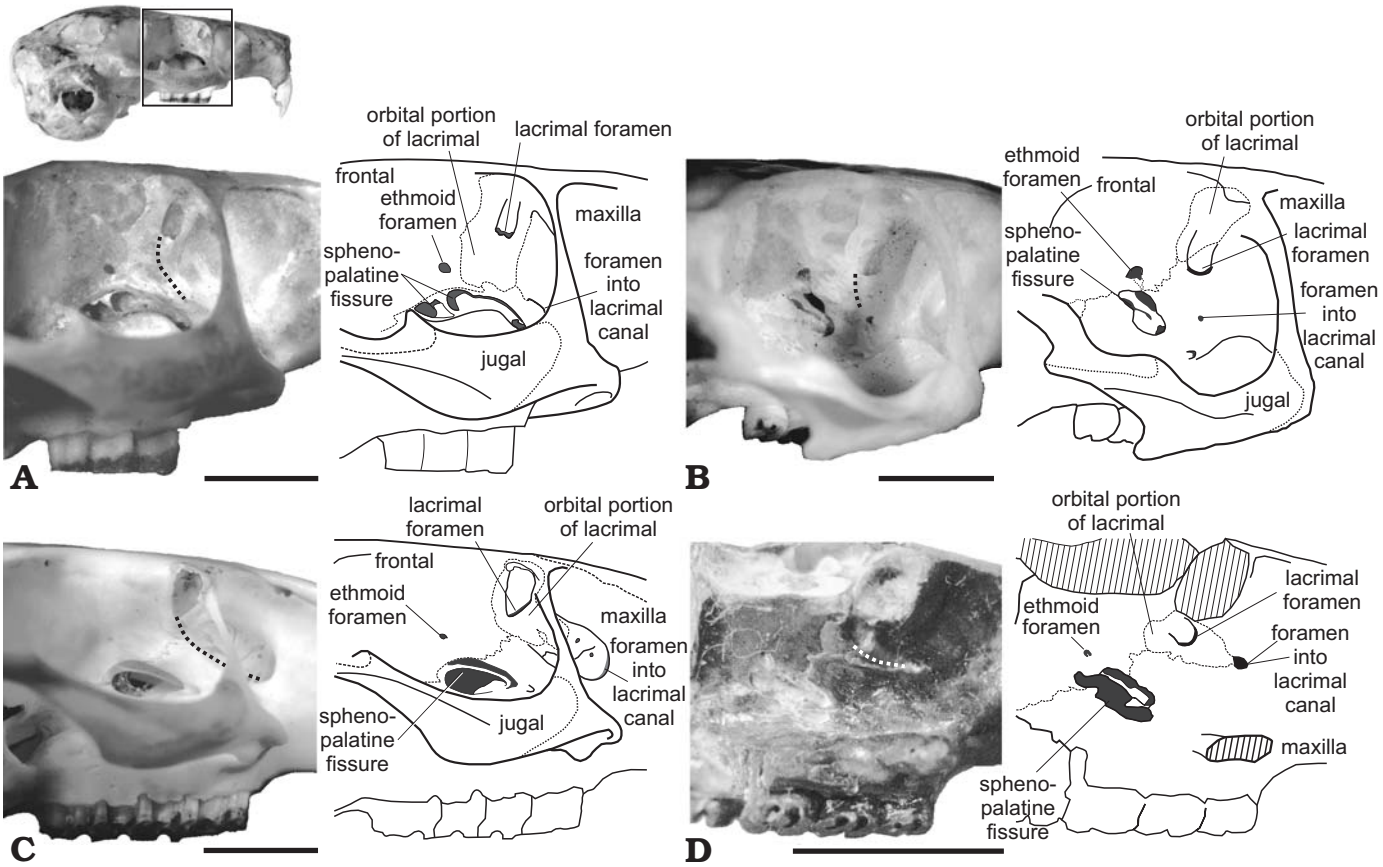

Fig. 2. Morphology of the orbital region of octodontoids in lateral view. **A**. *Octomys mimax* Thomas, 1920, Recent, IMCN-CM 24. **B**. *Thrichomys* sp., Recent, MMP 150-USB542. **C**. *Abrocoma* sp., Recent, MLP 2038. **D**. †*Spaniomys* sp. from the Santa Cruz Formation, late Early Miocene, southern Argentina, MACN-A 4184. Dotted line in photographs shows the orientation of the nasolacrimal canal. Scale bars 5 mm.

is formed by *Capromys*, †*Deseadomys*, dactylomyines, and the adelphomyine assemblage †*Adelphomys*–†*Stichomys*–†*Eodelphomys*–†*Paradelphomys*–†*Xylechimys* (node G), and supported by the subvertical orientation of the lateral crest of the mandible (character state 48-1; Fig. 4). In two of the three most parsimonious trees (SOM 1), the extant hutia *Capromys* clusters with the dactylomyines *Dactylomys* + *Kannabateomys*, based on the close juxtaposition of the margins of the maxillary fossae (character state 4-1) and the lateral margins of the incisive foramina (character state 5-1).

Node J (Octodontidae) is poorly supported and based on (i) the paroccipital process terminating dorsal to the level of the ventral portion of the auditory bulla (character state 39-1; Fig. 3); (ii) a ventrally deflected origin of the masseteric crest of the mandible (character state 45-1; Fig. 4); (iii) the formation of a lobe by the anterior lophids of Dp4 (character state 60-1); and (iv) the presence of a reduced metalophulid II on m1–2 (character state 68-1; Fig. 5). Within this broader clade, the grouping of †*Protadelphomys*–†*Willidewu*–†*Sallamys*, †*Chasicomys* and †*Chasichimys* with traditional ctenomyines (node K) is supported by the absence of the mesolophid on m1–2 (character state 67-1; Fig. 5) and the mastoid bulla terminating posterior to the level of the root of the paroccipital process (character state 44-1; Fig. 6). †*Chasichimys* shares with traditional ctenomyines a high basal portion (lacking flexids) of the molar crown (node M; character state 70-1). The latter, including the extant tuco-tuco *Ctenomys* (node N), are united by molars with a simplified occlusal morphology (character states 59-3 and 69-2).

Next to Ctenomyinae, †*Caviocricetus* + †*Acarechimys*–†*Neophanomys*, the †*Acaremys* group and traditional octodontines form a clade (node O) supported by the connection of the labial end of the mesolophule to the medial wall of the metacone on M1 (character state 54-1, not comparable for traditional octodontines; Fig. 7). The †*Acaremys* group is sister to traditional octodontines, and shares with them figure-eight shaped adult m1–2 (node P; character state 69-1). The traditional octodontines (node Q) includes fossorial and subterranean genera, and are supported by the presence of a premaxillary septum with divergent posterior ends (character state 1-1). Within this clade, *Octodontomys* + †*Pseudoplataeomys innominatus* forms the sister group to the remaining genera. The desert-specialists *Octomys* + †*Abalosia*–*Tympanoctomys* are united in a strongly supported clade (node S) diagnosed by the presence of an apophysis on the posterior portion of the maxilla posterior to the M3 alveolus (character state 27-2), a narrow posterior process of the squamosal reaching the posterior margin of epitympanic recess (character state 36-1), and the orientation of both the tip of the lateral process of the supraoccipital (character state 37-1) and the

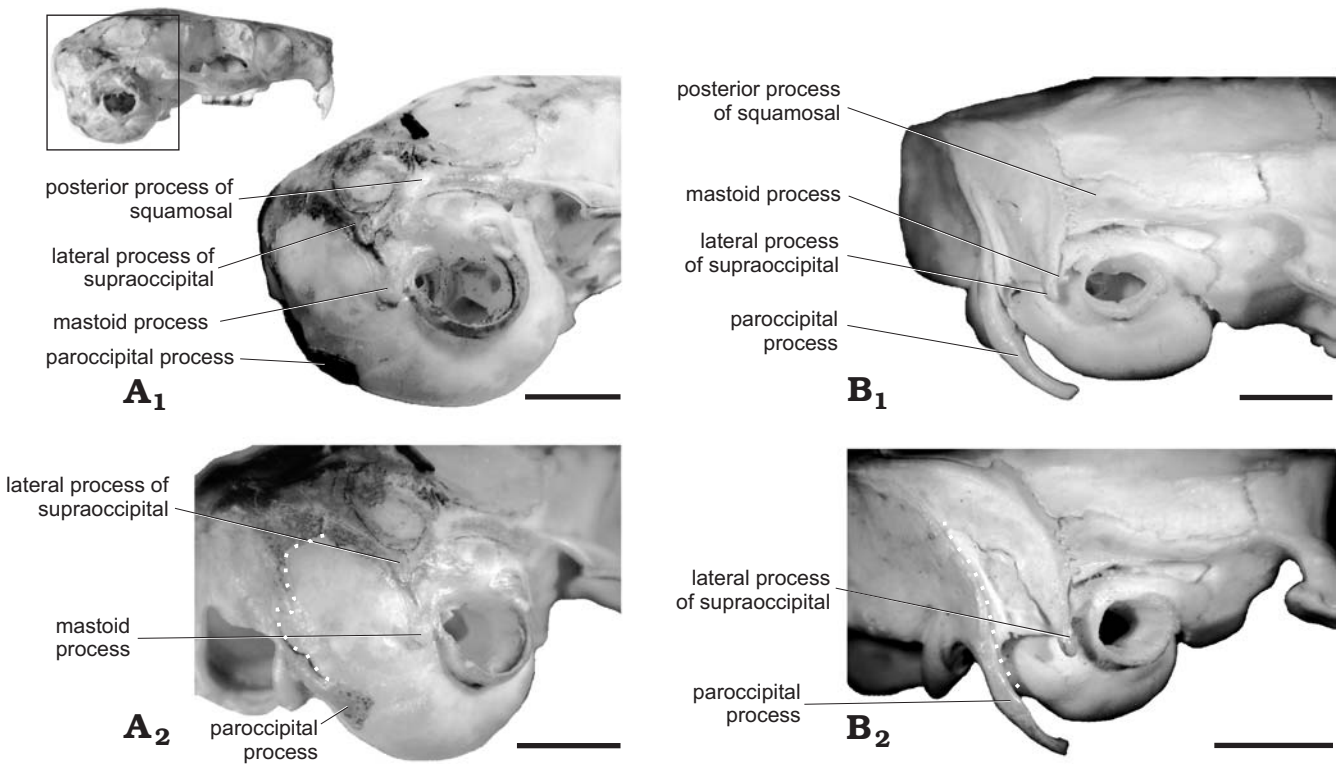

Fig. 3. Lateral (A_1, B_1) and posterolateral (A_2, B_2) views of the temporal region of Recent octodontoids. **A**. *Octomys mimax* Thomas, 1920, IMCN-CM 24. **B**. *Proechimys poliopus* Osgood, 1914, MLP 22.II.00.7. Dotted line indicates the margin of the supraoccipital. Scale bars 5 mm.

root of the paroccipital process (character state 43-1). The mesic-adapted *Octodon* + *Spalacopus* + *Aconaemys*–†*Pithanotomys* share the presence of an alisphenoid contacting the maxilla anteriorly (node R; character state 29-1). †*Pithanotomys* is sister to the rock rat *Aconaemys*, as indicated by a dorsally projecting jugal in the antorbital zygomatic bar (character state 20-1), and a pointed anterior face of Dp4 with well-defined secondary folds (character-state 58-1).

Finally, node T (†*Spaniomys* + Abrocomidae) is well-supported, and based on the contribution of the lacrimal to the posterior border of the foramen into the nasolacrimal canal (character state 12-1), a subhorizontally oriented nasolacrimal canal (character state 13-1; Fig. 2), a shortened lower incisor (character state 49-1), and anteriorly concave lophids on m1–3 (character state 63-1). The extinct abrocomid †*Abrocoma antiqua* is sister to the extant chinchilla rats *Abrocoma* + *Cuscomys*, with which it shares an extremely short lower incisor (character state 49-2), as well as a pointed anterior face of Dp4 with weak or no secondary folds (character state 58-3).

Divergence times.—The overall fit of our phylogenetic hypotheses with the stratigraphic record is low (MSM* score of 0.07 for the three optimal trees), implying the existence of substantial ghost lineages. We obtained similarly low values for echimyids (MSM*: 0.11–0.12), in which most extant lineages are inferred to originate in the Oligocene but are only recorded from the Late Miocene or Pliocene onwards. By contrast, our phylogenetic hypothesis for octodontids fits the stratigraphic record somewhat better (MSM*: 0.23). The MSM* scores for all trees are statistically significant ($P = 0.001$).

Estimated divergence times suggest Late Oligocene origins for the main octodontoid clades (Fig. 8; SOM 3). The potential antiquity of †*Eodelphomys* (Late Eocene?–Early Oligocene?) implies that some of these splits may have occurred even earlier; however, the age of this taxon is disputed (Frailey and Campbell 2004; Shockey et al. 2004) and hence was not taken into account here. Our results place the initial divergence of abrocomids (recorded since the Early Miocene), crown echimyids, and the main octodontid lineages in the Late Oligocene. By contrast, branching within modern (i.e., euhypsodont) octodontines and ctenomyines occurred at different times during the Late Miocene, with octodontines starting to diversify slightly earlier. The desert-adapted and mesic-adapted octodontines likely arose later during the Pliocene (Fig. 8). Finally, also during the Pliocene, the most recent branching event within ctenomyines gave rise to the extant genus *Ctenomys*.

Discussion

Phylogenetic relationships.—The clade defined by node A corresponds to extant Echimyidae (Galewski et al. 2005; Woods and Kilpatrick 2005), but excludes some of the Late Oligocene–Middle Miocene taxa referred to this family in previous studies (Fig. 1, Table 1). The relationships among echimyids are mostly, but not strictly, in agreement with previous morphological (Emmons 2005; Olivares et al. 2012; Candela and Rasia 2012) and molecular phylogenies

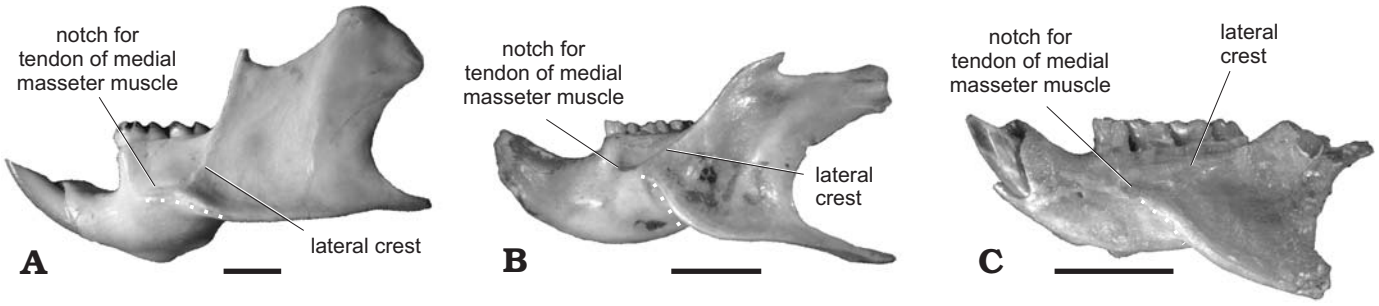

Fig. 4. Lateral view of the mandible of octodontoids. **A**. *Kannabateomys amblyonyx* (Wagner, 1845), Recent, MACN-Ma 15457. **B**. *Tympanoctomys barrerae* (Lawrence, 1941), Recent, MLP 2050. **C**. †*Protadelphomys* sp. from the Sarmiento Formation, Early Miocene, southern Argentina, CNP Pv 89-21a. Dotted line shows the anterior lower margin of the masseteric crest. Scale bars 5 mm.

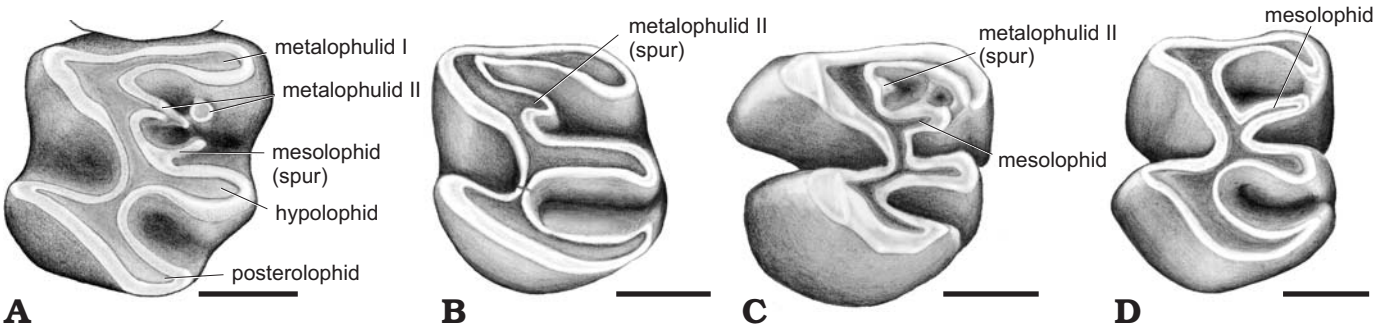

Fig. 5. Occlusal morphology of the left lower molars (right inverted in A–C) of octodontoids. **A**. m2 of †*Caviocricetus lucasi* Vucetich and Verzi, 1996 from the Sarmiento Formation, Early Miocene, southern Argentina, MPEF 5076. **B**. m1 of †*Willidewu esteparius* Vucetich and Verzi, 1991 from the Sarmiento Formation, Early Miocene, southern Argentina, MPEF 5034. **C**. m3 of †*Acaremys* group from the Santa Cruz Formation, late Early Miocene, southern Argentina, MLP 15-XII-13-151. **D**. m1 of †*Acaremys* group from the Santa Cruz Formation, late Early Miocene, southern Argentina, MLP 15-393. Scale bars 2.5 mm.

(Galewski et al. 2005; Upham and Patterson 2012; Fabre et al. 2013). In particular, our results resemble earlier studies in recovering a major subclade comprising fossorial echimyids (Fig. 1: node I) in addition to a further clade comprising terrestrial, semiaquatic, and arboreal forms (Fig. 1: node B, Fig. 8; see also Galewski et al. 2005: fig. 3; Upham and Patterson 2012: fig. 3; Fabre et al. 2013: fig. 1). Likewise, our results do not support the monophyly of most of the traditionally recognised subfamilies.

The clade comprising the fossorial echimyids, recognised by Emmons (2005) as the tribe Euryzygomatomyini, radiated in the Pampas of southern South America during the Late Miocene–Pliocene, alongside the terrestrial †*Pampamys* and †*Eumysops* (Fig. 8; Reig 1989; Olivares et al. 2012). Verzi et al. (1995) suggested all of these southern echimyids to form a clade, based on their shared possession of molars with a simplified occlusal morphology. However, this notion is contradicted by the present results (see also Olivares et al. 2012).

The position of *Myocastor* within Echimyidae agrees with the conclusions of several previous studies (Table 1; Emmons 2005; Galewski et al. 2005; Upham and Patterson 2012; Fabre et al. 2013). The precise relationships of this genus remain controversial (cf. Fig. 1; Candela and Rasia 2012; Upham and Patterson 2012), but it is worth noting that forcing *Myocastor* into a basal position as sister to all of the remaining echimyids (as in Candela and Rasia 2012) would require four extra steps.

The monophyly of the Late Oligocene–Early Miocene Patagonian subfamily †Adelphomyinae in its original sense (Patterson and Pascual 1968), is only partially supported by our results (Fig. 1: node G). In addition, the clade recovered here is not consistent with the more inclusive definition of the subfamily provided by Vucetich et al. (2010a: 215; Table 1). †*Maruchito*, previously included in the Adelphomyinae by these authors, is here grouped with extant echimyines, as proposed by Candela and Rasia (2012; see also Emmons and Vucetich 1998).

The extant *Capromys* is currently included in a family of its own (Capromyidae), which represents an intra-Caribbean radiation (Woods and Kilpatrick 2005). However, consistent with our results, recent molecular analyses found *Capromys* to be nested within Echimyidae (Upham and Patterson 2012: fig. 4; Fabre et al. 2013). In addition, a sister relationship between *Capromys* and dactylomyines, as indicated in two of our three most parsimonious trees (SOM 1), was previously proposed by Reig (1986: 409). Nevertheless, wider sampling of the Caribbean radiation of octodontoids is necessary to settle the question of the phylogenetic affinities of capromyids (Table 1; Upham and Patterson 2012).

Rather than elevating Ctenomyinae and Octodontinae to family level, we prefer to retain the name Octodontidae for node J (Patterson and Wood 1982: 523; Verzi 2001, and literature therein) to avoid the creation of a new higher taxon. According to our results, Ctenomyinae (Fig. 1: node K) compris-

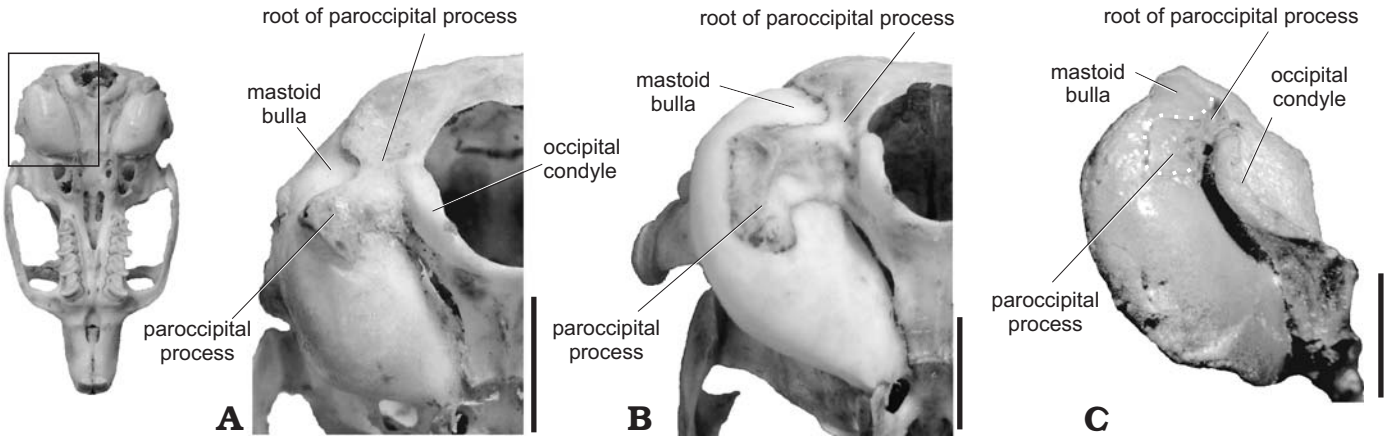

Fig. 6. Ventral view of the basicranial region of octodontids. **A**. *Octodon* sp., Recent, MLP 12.VII.88.2. **B**. *Ctenomys maulinus* Philippi, 1872, Recent, MLP 1.X.01.4. **C**. †*Protadelphomys latus* Ameghino, 1902 from the Sarmiento Formation, Early Miocene, southern Argentina, MPEF 5006. Scale bars 5 mm.

es both traditional (euhypsodont) ctenomyines and genera that were previously classified as Echimyidae or as Octodontoidea with uncertain affinities (Table 1). With the single exception of the Late Miocene †*Chasichimys* (Verzi 1999), these genera are here assigned to the ctenomyines for the first time. Although the novel, unorthodox position of †*Sallamys*, †*Protadelphomys*, and †*Willidewu* as basal ctenomyines is poorly supported (Fig. 1), forcing these genera into a more basal position, either as sister to echimyids + octodontids or as sister to echimyids only, would require 5 additional steps.

†*Chasichimys* has been suggested to have given rise to eumysopine echimyids (Table 1; Pascual 1967). Its position as sister to the euhypsodont ctenomyines in our phylogeny is poorly supported (Fig. 1), but placing it as the most basal octodontid or echimyid would require an additional 3 or 6 steps, respectively. The presumably related †*Chasicomys* was originally described as an octodontid (Pascual 1967) linked to modern octodontines (Reig 1989: 263). Given the low support for its inclusion in Ctenomyinae (Fig. 1: node L) and the fact that only one extra step is needed to move †*Chasicomys* to the base of Octodontidae, the position of this genus should thus be regarded as particularly tentative.

We consider the clade defined by node O to represent Octodontinae. Similar to ctenomyines, this clade groups traditional (euhypsodont) octodontines with genera here related to them for the first time (except for the †*Acaremys* group; Table 1). The interpretation of †*Caviocricetus* + †*Acarechimys*–†*Neophanomys* as stem Octodontinae is weakly supported (Fig. 1); however, forcing this clade into a basal position with respect to either Octodontidae + Echimyidae (as suggested by Vucetich et al. 2010a), or Echimyidae (as suggested by Patterson and Wood 1982), would each require 4 extra steps.

The topology of crown Octodontinae (node Q) is consistent with molecular phylogenies, except for the position of *Octodontomys,* which is usually placed closer to the mesic-adapted clade comprising *Octodon* + *Spalacopus* + *Aconaemys*–†*Pithanotomys* (Gallardo and Kirsch 2001; Honeycutt et al. 2003; Opazo 2005; Upham and Patterson 2012). Within the latter (Fig. 8), a close relationship between the extinct Pliocene †*Pithanotomys* and the extant *Aconaemys* was previously proposed by Reig (1986, 1989).

†*Spaniomys* has previously been interpreted as either a myocastorine or adelphomyine echimyid (Table 1) (Ameghino 1889; Scott 1905). Its relationship with abrocomids, as reported here, might represent the first evidence of the pre-Late Miocene history of this family.

Delimitation and dating of higher taxa.—Three successive stages can be recognised in the evolutionary history of any given clade, referred to as t_1, t_2, and t_3 by Hennig (1965: fig. 4): (i) its origin, i.e., divergence from its sister clade; (ii) acquisition of the apomorphies that characterise its extant members (modernisation); and (iii) the origin of the last common ancestor of the living representatives (Fig. 9). Recognition of these stages in the fossil record is essential in achieving an adequate understanding of the evolutionary history of a clade.

Octodontines, ctenomyines, and abrocomids have traditionally been recognised based on their hypsodont (especial-

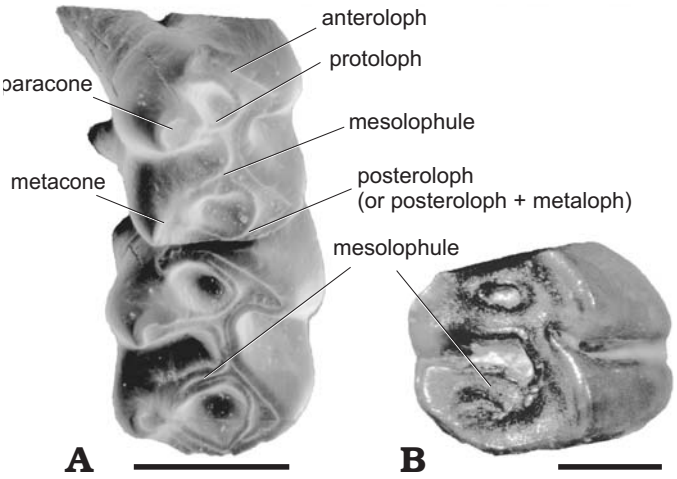

Fig. 7. Occlusal morphology of the right upper molars (left inverted in B) of octodontids. **A**. DP4-M1 of †*Caviocricetus lucasi* Vucetich and Verzi, 1996 from the Sarmiento Formation, Early Miocene, southern Argentina, MPEF 505. **B**. M1 of †*Acaremys* group from the Santa Cruz Formation, late Early Miocene, southern Argentina, MLP 15-197. Scale bars 1 mm.

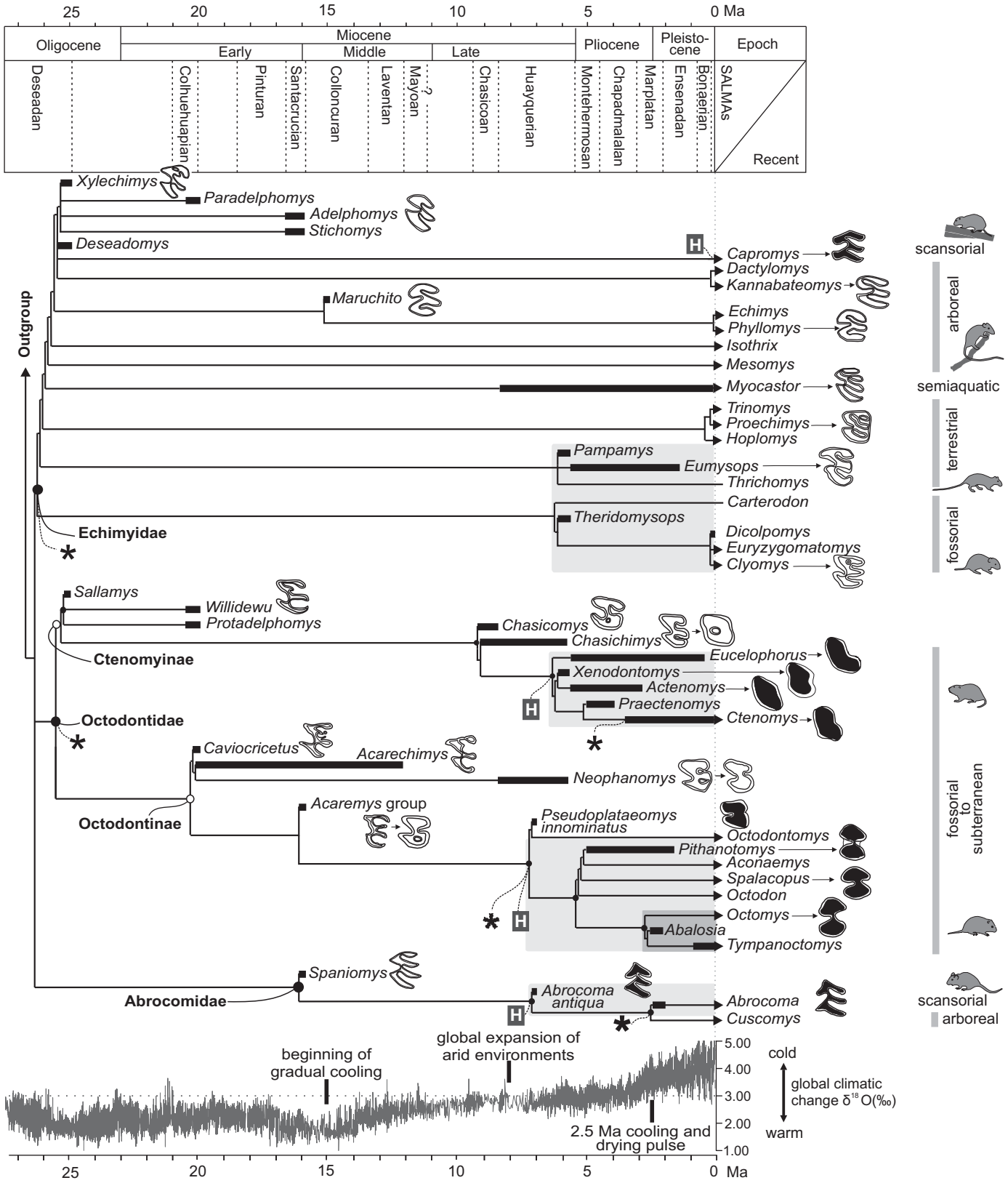

Fig. 8. Temporal ranges and divergence times of octodontoids mapped on to the strict consensus tree. Occlusal figures of the left m1 or m2 are illustrated next to the corresponding genus (when two figures are presented, the one to the right is ontogenetically more derived). Light gray background, clades adapted to xerophytic forest or open environments, first recorded during the Late Miocene global cooling and drying event; darker gray background, the desert-adapted octodontine clade first recorded during the Late Pliocene (ca. 2.5 Ma) global cooling and drying pulse; H, the modernisation stage represented by the acquisition of euhypsodont molars (black occlusal figures); asterisks, crown-groups. Timescale after Gradstein et al. (2008); isotopic curve after Zachos et al. (2008); palaeoclimatic events after Vrba et al. (1995), Verzi and Quintana (2005), Zachos et al. (2008), and Arakaki et al. (2011).

Table 2. Comparison of estimated ages of origin of total-groups (t_1) and crown-groups (t_3) with that of the modernisation stage (morphological differentiation, t_2) of the studied taxa (see Fig. 8). Values from this study are fossil-based estimates and represent minimum ages. Comments: 1, original chronology updated on the basis of current available information (SOM 3); 2, data as averaged in Honeycutt (2009); 3, age estimation based on partial sampling; 4, calculated using 55 million years as maximum age for Caviomorpha. See references for calibration points and molecular data.

	This study	Vucetich et al. (1999)[1]	Gallardo and Kirsch (2001)	Honeycutt et al. (2003)[2]	Opazo (2005)	Rowe et al. (2010)[4]	Upham and Patterson (2012)	Fabre et al. (2013)[3]
Echimyidae t_1 (t_2)	~26.0 (~26.0)	>28.0?		27.4	17.5	~25.0	25.3	27.1
Echimyidae t_3	~26.0				8.6[3]	15.0[3]	18.8	20.5
Octodontidae t_1	~25.5	>9.0		27.4	17.5	~25.0	25.3	27.1
Octodontinae t_1 (t_2)	~25.5 (~7.0)	>9.0	25.5	19.6	15.0	22.0	19.1	22.6
Octodontinae t_3	~7.0		9.0	8.6	7.8	8.0	9.0	
Ctenomyinae t_1 (t_2)	~25.5 (~6.0)	>9.0	25.5	19.6	15.0	22.0	19.1	22.6
Ctenomyinae t_3	~3.5						4.3	
Abrocomidae t_1 (t_2)	~25.5 (~7.0)	~7.0?			20.6	~26.0	~26.0	

ly euhypsodont) molars bearing simplified occlusal surfaces, which characterise their Late Miocene to Recent representatives (Fig. 8). The interpretation of the first record of these derived morphologies as an indicator of clade origin has yielded ages younger than 10 Ma for each of these taxa (e.g., Reig 1989; Verzi 1999; Vucetich et al. 1999). Including stem representatives provides an alternative way of defining and dating clades (Fig. 9). Although more unstable, as stem members are often poorly preserved and/or share few apomorphies with their corresponding crown-group (Briggs and Fortey 2005), this definition has the advantage of taking into account the deep history of a lineage, while at the same time avoiding paraphyletic taxa and the need for new names (Patterson 1993a, b; Donoghue 2005).

Following this line of reasoning, our reinterpretation of the phylogeny of octodontoids suggests that all of its major subclades are at least Late Oligocene in age (Fig. 8, Table 2), with the superfamily as a whole potentially being even older (Frailey and Campbell 2004; Vucetich et al. 2010b; Antoine et al. 2012). Both the times of origin of the major clades and the initial diversification of their respective crown groups are at least partially consistent with molecular age estimates (Table 2). In the case of Abrocomidae, Ctenomyinae and Octodontinae, our proposed dates exceed previous fossil-based estimates (e.g., Reig 1989; Vucetich et al. 1999; Cook et al. 2000; Vucetich and Kramarz 2003). This is largely a result of our different interpretation of the higher taxa, which regards modern (i.e., euhypsodont) abrocomids, ctenomyines and octodontines as stages of differentiation characterised by the acquisition of the morphology defining the extant species (t_2 of Hennig 1965: fig. 4; apomorphy-based clades sensu De Queiroz and Gauthier 1990, 1992; see also Sereno 2005). These stages are decoupled from the divergences that originally separated these families and subfamilies (Fig. 9; Steiper and Young 2008).

A stage of modernisation (t_2) distinct from the origin of the clade (t_1) is not recognisable within Echimyidae or any of the subordinate clades of this family with an early fossil record. Echimyids are morphologically conservative, especially with regards to their dental morphology (Fabre et al. 2013) and, with the exception of the Antillean capromyids (if these are indeed echimyids), never acquired euhypsodonty (Fig. 8). This likely led previous authors to include early fossil octodontoids with lophate, rooted molars within echimyids (see above and Table 1), even though this morphology may in fact represent the plesiomorphic condition for Octodontoidea as a whole.

Morphological differentiation and Cenozoic climatic changes.—The diverging evolutionary patterns of octodontids and abrocomids on the one hand and echimyids on the other may reflect different responses to Cenozoic climatic change. In the palaeoclimatic history of the Cenozoic, arid climates and open habitats are clearly derived, and arose more recently than environmental conditions similar to those of present-day tropical forests (e.g., Janis 1993; Partridge et al. 1995; Janis et al. 2000; Zachos et al. 2001). Echimyids responded to Cenozoic environmental changes (including diastrophic events) mostly by tracking their original habitats. Thus, their extant representatives primarily inhabit Amazonian and Atlantic forests (Fabre et al. 2013), with only a few species having colonised more open areas (Pascual 1967; Hoffstetter 1986; Verzi et al. 1994; Olivares et al. 2012; Upham and Patterson 2012).

The fossil record of echimyids from southern South America is an impoverished, marginal sample of the astonishing diversity achieved by this group in the tropical and subtropical areas of northern South America. Fossils linked to the extant arboreal species are present in Patagonia only until the Middle Miocene, coinciding with the persistence of forests with tropical elements at this latitude (Fig. 8; Palazzesi and Barreda 2007). By contrast, all of the known Late Miocene fossils are related to the few groups adapted to open areas (Fig. 8; Verzi et al. 1994; Olivares et al. 2012). Local studies illustrate the Late Miocene decline of echimyids in southern South America (Verzi et al. 2011), which led to their current absence in the area. It is to be expected that taxa which respond to environmental change by tracking their original habitats through local extinctions and distribution drift (Vrba 1992) will be morphologically more conservative than those that adapt to their new environment, irrespective of speciation rates (Verzi 2002). This might explain why the

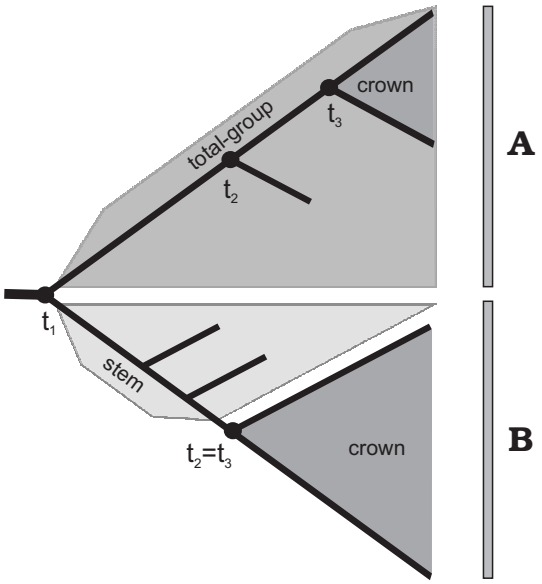

Fig. 9. Graphical representation of stem-, crown-, and total-groups, and related times of origin (t_1 and t_3) and morphological differentiation (t_2) (modified from Hennig 1965: fig. 4 and Sereno 2005: fig. 1). Note that in clade A (exemplified by Ctenomyinae and Abrocomidae), t_2 and t_3 are decoupled while in clade B (exemplified by Octodontinae) they are coincident.

origin and differentiation of echimyids are not recognisable as decoupled events, and furthermore may account for the morphological redundancy of some highly species-rich, unexpectedly ancient clades of living echimyids, such as *Proechimys–Trinomys* (Verzi 2002; see Lara et al. 1996: 410; Da Silva and Patton 1998; Fabre et al. 2013).

By contrast, abrocomids, octodontines, and ctenomyines show stages of differentiation that are distinctly decoupled from their respective origins (Fig. 9, Table 2), with the hierarchy of these stages following that of concurrent palaeoenvironmental changes. A derived, hypsodont dental morphology appeared in all of these groups by the Late Miocene, likely in response to increased aridity (Vucetich and Verzi 1999; Verzi 1999; Verzi et al. 2004) and the subsequent rise of extensive open biomes in southern South America (Fig. 8; Pascual and Ortiz Jaureguizar 1990; Rabassa et al. 2005; Palazzesi and Barreda 2007; Le Roux 2012). Available data show the global nature of this Late Miocene cooling and drying, resulting in the expansion of open environments worldwide (e.g., Janis 1993; Vrba et al. 1995; Zachos et al. 2001, 2008; Arakaki et al. 2011). The radiation of hypsodont species and the extinction of lineages with primitive molars (Verzi et al. 2011: fig. 8) marked the beginning of the stage of modernisation of these clades. The subsequent appearance of desert specialists among hypsodont octodontines coincided with a profound global Late Pliocene cooling and drying event (Fig. 8; Verzi 2001; Verzi and Quintana 2005 and references therein). Together, these observations suggest that the extratropics may have acted as a cradle of evolutionary novelties through fixation of new adaptations to newly emerging open habitats (Verzi 2002).

The importance of recognising morphological differentiation in the fossil record.—Hennig (1965: 114) noted that the delimitation of the stage of morphological differentiation in the history of a clade (t_2) depends on subjective criteria concerning the interpretation of the emergence of particular "types" or "Baupläne". Indeed, whereas the origin of a clade (t_1) and of its crown-group (t_3) can be determined using both molecular and palaeontological evidence, the time of morphological differentiation (i.e., modernisation, t_2) can only be informed by fossils, and is constrained by biases affecting the minimum ages provided by the fossil record (Benton and Donoghue 2007). Nevertheless, as demonstrated here, such differentiation stages can yield important evolutionary information regarding environmentally driven changes in morphology that occurred before the emergence of the crown group. This highlights the unique contribution of fossils to the appreciation of the true shape of trees (Helgen 2011) and our understanding of macroevolutionary patterns.

Acknowledgements

We thank Federico Anaya (Universidad Autónoma Tomás Frías, Potosí, Peru), Eileen Lacey, James Patton (both Museum of Vertebrate Zoology, Berkeley, USA), João de Oliveira (Museu Nacional, Universidade Federal do Rio de Janeiro, Argentina), and Guiomar Vucetich (Museo de La Plata, Argentina) for actively facilitating access to materials; Diego Pol and María Pérez (both Museo Paleontológico Egidio Feruglio, Trelew, Argentina) for their valuable assistance with methodological aspects of the cladistic analysis; Diego Pol for providing the TNT script for MSM*, and for his valuable comments on an earlier version of this manuscript; James Zachos (Earth and Planetary Sciences Department, University of California Santa Cruz, USA) for allowing use of his original isotope dataset; and Fernando Ballejo (Universidad Nacional de La Plata, Argentina) for drawing the illustrations in Fig. 5. We are especially grateful to Philip Cox (Hull York Medical School, University of York, UK) and Laurent Marivaux (Laboratoire de Paléontologie, Institut des Sciences de l´Évolution de Montpellier, Université Montpellier 2, France) for their critical reviews and Felix Marx (National Museum of Nature and Science, Tsukuba, Japan) for his thorough editorial work, all of which helped to improve this paper. Access to the software TNT was available thanks to the sponsorship of the Willi Hennig Society. This paper is a contribution to projects ANPCyT PICT 2007-01744 and CONICET PIP 0270.

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