

The history of South American octodontoid rodents and its contribution to evolutionary generalisations

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Introduction

The peculiar New World hystricomorph rodents comprise about half of the mammal species of South America (Upham and Patterson, 2012) and have been evolving in this continent for over 40 Ma (Antoine *et al.*, 2012). During this period, they developed an ecomorphological diversity much greater than that of other rodent clades, even when only the extant fauna is considered (Mares and Ojeda, 1982; Wilson and Sánchez-Villagra, 2010; Hautier *et al.*, 2012). This results especially from the evolution of particular morphologies in three of the four suprafamilial clades, Erethizontoidea (New World porcupines), Chinchilloidea (viscachas), and Caviioidea (maras and cavies), a pattern that begins to be apparent in the Oligocene fossil record (Wood and Patterson, 1959; Bertrand *et al.*, 2012). In contrast, the superfamily Octodontoidea has remained morphologically conservative for much longer, the rodents of this group being unique among South American hystricomorphs in retaining a rat-like appearance (e.g. Redford and Eisenberg, 1992: pl. 17; Eisenberg and Redford, 1999: pl. 13). Remarkably, when considered in combination with their apparently narrower range of morphological innovation, Octodontoidea is the most diverse clade of hystricomorph rodents. In particular, the families Echimyidae and Octodontidae (including the subfamily Ctenomyiinae, considered by neontologists as a family in their own right; see Verzi *et al.* 2014) comprise more than 60% of the extant species of South American hystricomorphs, and have the richest fossil record of the suborder (McKenna and Bell, 1997; Woods and Kilpatrick, 2005; Upham and Patterson, 2012).

The sister families Echimyidae and Octodontidae are two living clades with very different characteristics in terms of geographical distribution and diversity patterns. Echimyidae encompasses a high diversity (i.e. species richness) of small- to middle-sized rodents, with arboreal (spiny tree-rats, tree rats, bamboo rats), or terrestrial to fossorial (spiny rats) lifestyles, which occupy 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). It also

includes the semiaquatic coypu *Myocastor*, an exceptional large-sized representative widely distributed in southern South America. Unlike Echimyidae, Octodontidae is a moderately diversified clade, with the exception of the unusually polytypic tuco-tucos of the genus *Ctenomys* (Reig, 1989). Octodontids are mostly small-sized, 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), with some species possessing significant morpho-physiological adaptations to desert life (Ojeda *et al.*, 1999; Ojeda and Tabeni, 2009). [Fossorial and subterranean are used here as defined by Lessa *et al.* (2008). Fossorial species spend a substantial fraction of their lives outside their burrows, while subterranean ones perform most activities underground. *Ctenomys* (tuco-tucos) and *Spalacopus* (coruros) are the only living subterranean South American hystricomorphs.]

These evident adaptive differences and the associated clade-specific distributional patterns are interpreted as resulting from particular evolutionary pathways triggered by late Cenozoic palaeoclimatic changes (e.g. Pascual, 1967; Reig, 1986; Vucetich *et al.*, 1999). Since the global late Miocene cooling and drying pulse, octodontids acquired their identity in the increasingly diversified open biomes of the south of South America, whereas the distribution of echimyids became progressively restricted to northern tropical habitats (Pascual, 1967; Verzi *et al.*, 1994; Verzi, 2002).

It is unclear how these evolutionary pathways are reflected in the phylogeny and patterns of variation of the group. In this sense, the contribution of fossil evidence is still limited. Partly because of the fragmentary knowledge and frequent morphological resemblance of the oldest (late Oligocene–middle Miocene) remains, there is still no agreement on their meaning regarding the phylogenetic and chronological delimitation of lineages. Many of these early octodontoids have been assigned to Echimyidae, partly because the living species of this family retain lophate, low-crowned molars (Reig, 1986; Carvalho and Salles, 2004). In this palaeontological context, Octodontidae has been assumed either as a modern group (Reig, 1986; Vucetich *et al.*, 1999; Arnal and Pérez, 2013), or alternatively as an ancient clade, sister to Echimyidae (Patterson and Wood, 1982; Verzi *et al.*, 2014), as interpreted for living species (e.g. Honeycutt, 2009). Furthermore, so that palaeontology can make an operative contribution to the understanding of evolutionary patterns (whichever phylogenetic hypothesis is considered most robust), it is necessary to advance in the recognition of which stages of the evolution of a clade (i.e. origin or differentiation) are represented by fossil evidence. Likewise, given that anagenesis (used here to refer to evolutionary transformation, and not gradual directional evolutionary mode) is not necessarily associated to cladogenesis (Jablonski, 2009; Venditti *et al.*, 2011), attempts to understand adaptive pathways that involve morphological change should not be exclusively focused on the cladogenetic component. Instead, it is necessary to explore evolutionary modes and rates (Simpson, 1953).

Here we present an interpretation of the history of octodontoids based essentially on the evidence provided by the fossil record. We assess the proposal that the different responses of major clades to late Cenozoic palaeoenvironmental changes would result in

dissimilar phylogenetic structures and patterns of variation reflected in the taxonomic hierarchy of the recognised lineages (Verzi, 2002). In order to do this, we analyse phylogenetic relationships, timing of origin and differentiation of clades, and patterns of variation and disparity. Finally, we discuss the conceptual implications of our approach for more comprehensive evolutionary generalisations.

Materials and methods

Phylogenetic analysis

We performed a combined parsimony analysis of extinct and extant octodontoids (Figure 5.1), based on the dataset of 73 morphological characters in Verzi *et al.* (2014) and five marker sequences obtained from GenBank: two mitochondrial genes (Cytochrome b, 1140 bp; 12S rRNA, 932 bp) and three unlinked nuclear exons (GHR, Growth Hormone Receptor exon 10, 801 bp; vWF, von Willebrand Factor exon 28, 1149 bp; RAG1, part of the recombination activating gene, 1064 bp). Sequences of each of the five genes were aligned using CLUSTAL X (Thompson *et al.*, 1997) with the default values of gap opening and gap extension. The dataset of morphological traits was concatenated with the gene sequences, and extinct taxa were coded as missing for all molecular characters. This matrix contained a total of 63 taxa and 5159 characters; *Erethizon* (Erethizontoidea), *Cavia*, *Cuniculus*, *Dasyprocta*, *Dolichotis*, *Hydrochoerus*, *Microcavia* (Cavioidea), *Chinchilla* (Chinchilloidea), *Abrocoma*, *Cuscomys* and †*Spaniomys* (Octodontoidea, Abrocomidae) were included as outgroups. The parsimony analysis was conducted treating gaps as missing data in TNT 1.1 (Goloboff *et al.*, 2008a, b). The heuristic search consisted of 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 topologies of minimum length (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 modified Stratigraphic Manhattan Measure (MSM*, Pol and Norell, 2001) was used to integrate the temporal information of fossil record and the resulting phylogeny. Divergence date estimates were based on the first appearance (oldest fossil) confidently assigned to either of the two lineages arising from each branching point. Estimates thus obtained represent minimum constraints on the age of origin of clades (Benton and Donoghue, 2007), and are based on the most reliable date for the oldest levels bearing the indicative fossil. We calculated the MSM* both for the entire tree and for the two major octodontoid clades, with MSM* values for the latter being comparable owing to the similar number of taxa they contain (Pol *et al.*, 2004).

Patterns of variation and disparity

We analysed the variation of the skull in lateral view, which allowed us to capture shape changes in the orbit, rostrum, auditory bulla and cranial vault. We used a

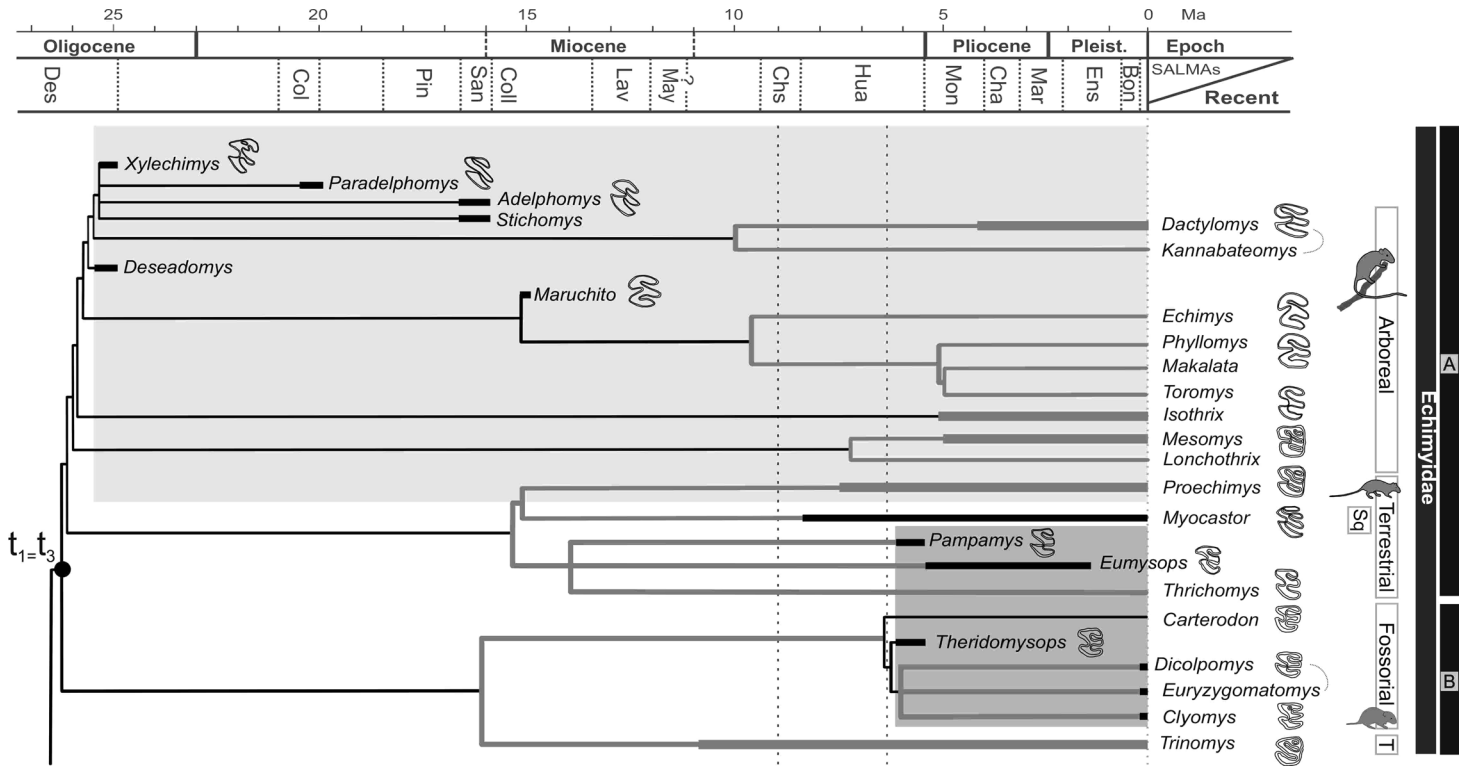


Figure 5.1 Most parsimonious tree showing the temporal range and divergence times of octodontoids mapped onto the tree. Black bars are biochrons and grey bars indicate molecular dating of diversification within living genera (after Upham and Patterson, 2012). Minimum ages of fossils (black lines) are shown when they are older than those from molecules (grey lines). Vertical dashed lines denote the origin of modern ctenomyines and (crown) octodontines for temporal comparisons with branching events within echimyids. Occlusal figures of the left m_1 or m_2 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 , t_3) and morphological differentiation (t_2 , modernisation) are indicated for the major clades; the latter stage is represented by the acquisition of euhyposodont molars (black occlusal figures). The light grey shaded background indicates clades of forest-dwellers; dark grey shaded backgrounds indicate clades from more open environments, which are first recorded during the late Miocene global cooling and drying event; dotted background indicates the desert-adapted octodontine subclade, which is first recorded during the late Pliocene–early Pleistocene

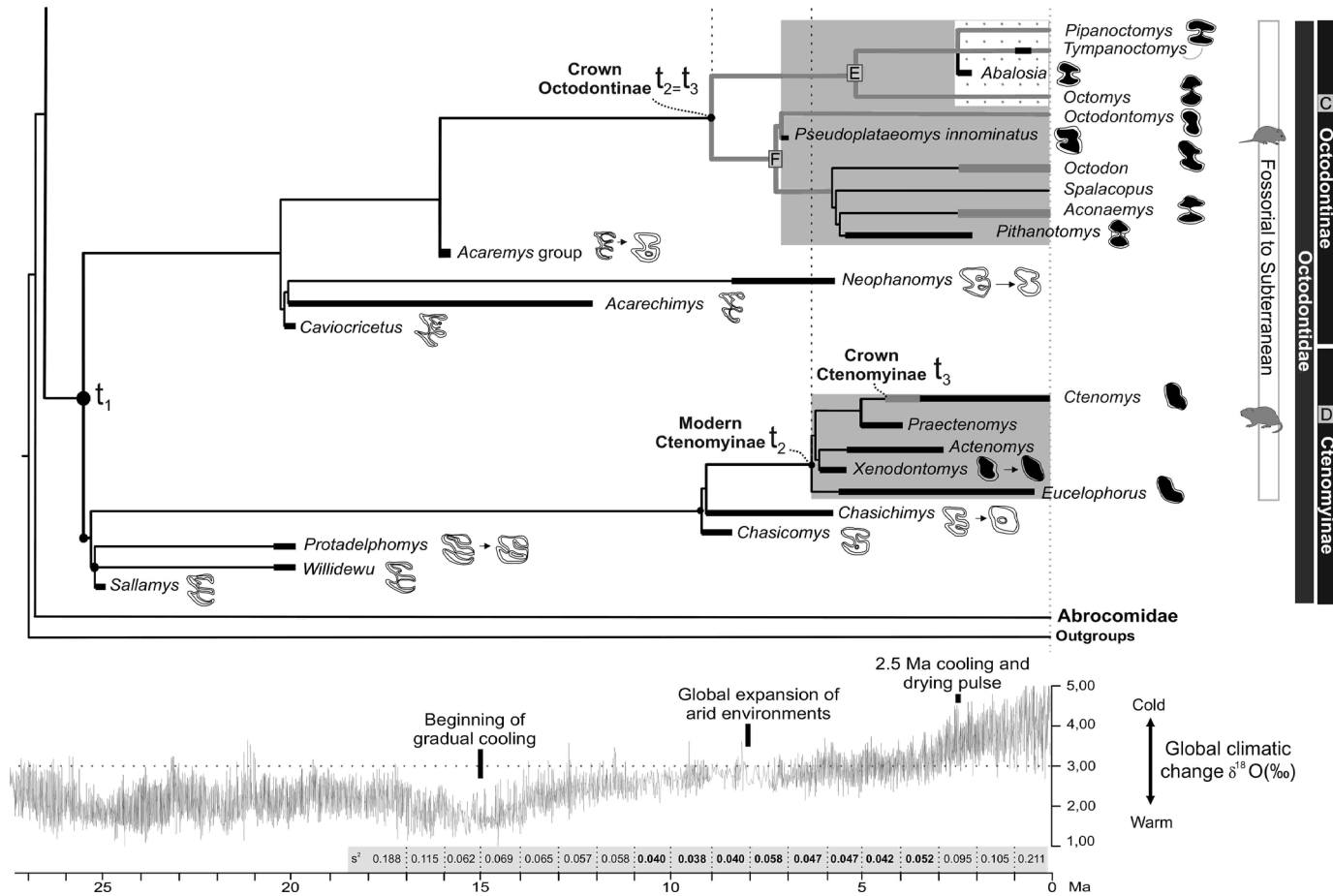


Figure 5.1 (cont.) (c. 2.5 Ma) global cooling and drying pulse. Timescale after Gradstein et al. (2008); isotopic curve after Zachos et al. (2008); variance values of oxygen isotope excursions below 0.60 are in bold); palaeoclimatic events after Vrba et al. (1995), Denton (1999), Verzi and Quintana (2005), Zachos et al. (2008) and Arakaki et al. (2011). Abbreviations: Bon, Bonaerian; Cha, Chapadmalalan; Chs, Chasicoan; Col, Colhuehuapian; Coll, Colloncuran; Des, Deseadan; Ens, Ensenadan; Hua, Huayquerian; Lav, Laventan; Mar, Marplatense; May, Mayoan; Mon, Montehermosan; Pin, Pinturan; SALMA, South American Land Mammal Age; San, Santacrucian; Sq, Semiaquatic; s₂, sample variance; T, terrestrial.

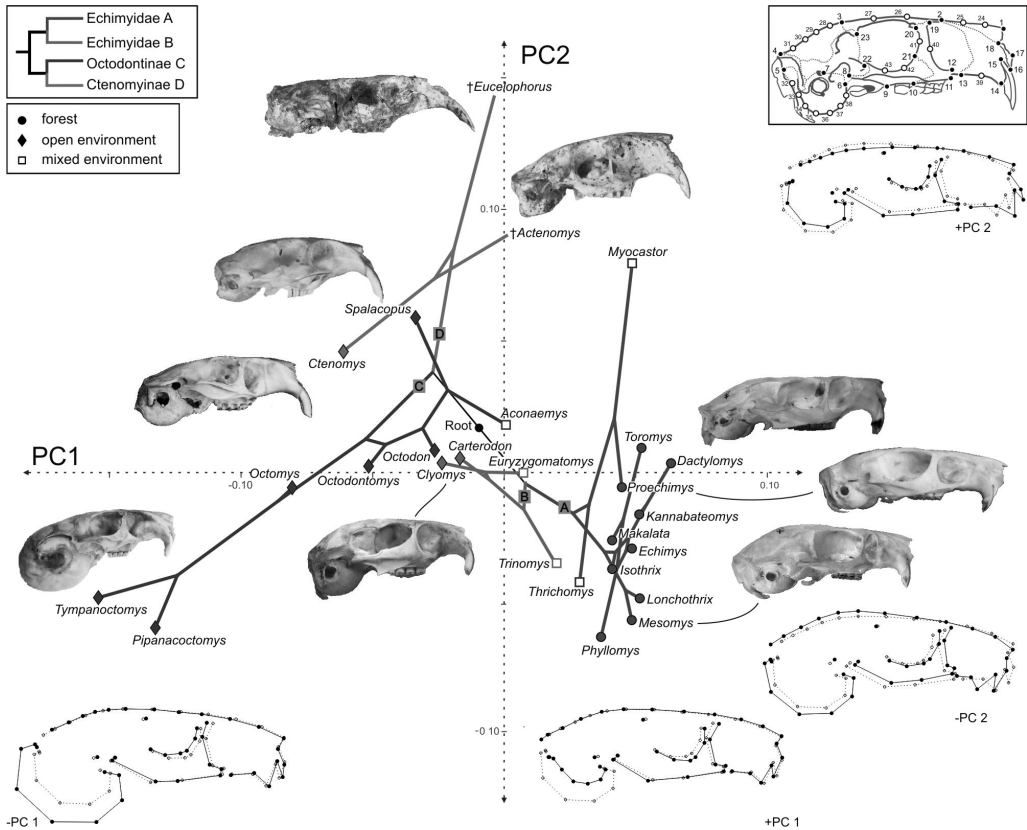


Figure 5.2 Phylogeny tree superimposed onto a plot of the first two principal components (PCs) among the genera analysed. The positions of internal nodes are reconstructed by squared-change parsimony using the tree topology obtained. At top right, schematic representation of lateral view of skull showing placement of landmarks (solid dots) and semi-landmarks (empty circles). Outline diagrams show shape change associated with each PC, from the consensus (dashed lines and empty circles) to positive or negative scores (black lines and solid dots). Scale factor indicates magnitude of shape change as Procrustes distance. Illustrated skulls not to scale. A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

sample of 167 specimens belonging to 38 species of 26 genera of the families Echimyidae and Octodontidae, the latter including Ctenomyiinae (Figure 5.2). Polytypic genera were represented by the following species: *Aconaemys porteri*, *Aconaemys sagei*, *Ctenomys leucodon*, *Ctenomys lewisi*, *Ctenomys magellanicus*, *Ctenomys mendocinus*, *Ctenomys talarum*, *Dactylomys dactylinus*, *Echimys chrysurus*, *Isothrix bistrata*, *Makalata didelphoides*, *Mesomys hispidus*, *Octodon degus*, *Octodon* sp., *Phyllomys blainvilli*, *Proechimys brevicauda*, *Proechimys poliopus*, *Proechimys* spp., *Trinomys albispinus*, *Trinomys dimidiatus*, *Trinomys eliasi*, *Trinomys setosus*, *Trinomys yonenagae*, *Thrichomys laurentius*. This dataset includes two sufficiently complete remains of the fossil modern ctenomyiines †*Eucelophorus chapalmalensis* and †*Actenomys 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 23 landmarks and 20 semi-landmarks (Figure 5.2; description available from the authors upon request) were chosen to capture skull morphology in detail. The x , y coordinates of landmarks and semi-landmarks were digitised using TPSDIG, version 2.12 (Rohlf, 2008). Semi-landmarks were slid using the minimum bending energy criterion (Bookstein, 1997) using TPSRelw 1.49 (Rohlf, 2010). The resulting aligned Procrustes coordinates were averaged by genus and the consensus configurations were analysed by Principal Components Analysis (PCA, also known as Relative Warps Analysis) in the software MorphoJ 1.05d (Klingenberg, 2011). Shape changes were visualized by means of transformation grids.

Disparity (i.e. morphological diversity; Foote, 1993) for each clade was calculated from the Procrustes coordinates averaged by species, using DisparityBox 7.14 of the Integrated Morphometrics Package (IMP7, Sheets, 2010–2012).

Phylogeny and timescale

Our analysis resulted in a single most parsimonious tree, 6821 steps long (CI = 0.42, RI = 0.35) whose topology is essentially (although not strictly) similar to that of previous morphological or molecular trees (Figure 5.1; Honeycutt *et al.*, 2003; Emmons, 2005; Galewski *et al.*, 2005; Verzi, 2008; Upham and Patterson, 2012; Fabre *et al.*, 2013; Verzi *et al.*, 2014). Octodontoidea is recovered as a monophyletic group, including Octodontidae and Echimyidae as sister clades.

The clade Echimyidae is consistent with the taxonomic definition of this family in the living fauna (Woods and Kilpatrick, 2005) but excludes some of the late Oligocene to middle Miocene genera referred to this taxon in previous studies (Verzi *et al.*, 2014: table 1). Monophyly of the traditionally recognised subfamilies is not supported except for Dactylomyinae. Similar to previous studies, two major subclades are recovered. One of them (here designated as subclade A; Figure 5.1) includes the arboreal representatives, i.e. spiny tree-rats *Mesomys–Lonchothrix*, brush-tailed rats *Isothrix*, tree rats *Echimyus–Phyllomys–Makalata–Toromys*, and bamboo rats *Dactylomys–Kannabateomys*, together with the late Oligocene to middle Miocene fossils †*Deseadomys*, †*Xylechimys*–†*Paradelphomys*–†*Adelphomys*–†*Stichomys* and †*Maruchito*. The terrestrial *Proechimys* and *Thrichomys* and the semiaquatic *Myocastor*, along with the late Miocene †*Pampamys* and the Pliocene †*Eumysops*, make up the sister-group of this arboreal clade. The second echimyid subclade (B) groups the extant fossorial spiny rats *Carterodon*, *Clyomys* and *Euryzygomatomys* with the Atlantic spiny rats *Trinomys* and the late Miocene †*Theridomysops* and late Pleistocene–Holocene †*Dicolpomys*.

The clade Octodontidae of our phylogeny comprises two major subclades that include the traditionally recognised living and extinct Octodontinae and Ctenomyiinae, respectively. Neontologists currently consider these two groups as families (Woods and Kilpatrick, 2005; Honeycutt, 2009), but here we retain the name Octodontidae for the more encompassing clade, including both subclades and their more recent common

ancestor (see Verzi *et al.*, 2014). Subclade C includes the modern, late Miocene to Recent euhypsodont octodontines along with more ancient fossils with uncertain affinities (†*Caviocricetus*-†*Acarechimys*-†*Neophanomys*, and the †*Acaremys* group). Modern octodontines are clustered into two subclades, both encompassing open-environment species with diverse digging abilities: one of them includes mesic-adapted species plus the desert inhabitant *Octodontomys*, and the other, desert-adapted representatives (Figure 5.1). The sister subclade, D, includes traditional (modern) ctenomyines, i.e. the living subterranean tuco-tucos (*Ctenomys*), and the allied euhypsodont late Miocene–Pleistocene species and genera, together with late Oligocene to late Miocene fossils with more conservative, rooted molars, previously considered as echimyids or octodontoids with uncertain affinities (†*Protadelphomys*-†*Willidewu*-†*Sallamys*, †*Chasicomys* and †*Chasichimys*).

Age estimations made from the fossils in our phylogeny suggest a late Oligocene age for the divergence between echimyids and octodontids, and between the major lineages included within each of them. Branching within modern (i.e. euhypsodont) octodontines and ctenomyines would have occurred at different times during the late Miocene–Pliocene, with octodontines starting to diversify slightly earlier. A late Pliocene cladogenesis gave rise to the subclade of desert specialists †*Abalosia*-†*Tympanoctomys*-†*Pipanoctomys* (Figure 5.1). Also during the Pliocene, the most recent branching event within ctenomyines originated the extant genus *Ctenomys*.

The overall fit of our phylogenetic hypotheses with the stratigraphic record is low (MSM* score of 0.07) implying the existence of substantial ghost-lineages (i.e. lineages that are inferred to occur by the phylogenetic structure but for which there is no fossil record; Norell, 1992; Smith, 1994). We obtained a similarly low value for echimyids (MSM*: 0.13), most of whose 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*: 0.26). The MSM* scores for all trees are statistically significant ($P = 0.001$).

Phylogenetic structure and dating of evolutionary stages

Our fossil-based estimate is consistent with molecular datings in suggesting that the primary echimyid/octodontid split is at least late Oligocene in age. According to molecular estimates, the crown groups of Echimyidae and Octodontidae are younger than this split, suggesting the existence of stem groups not recognised in our analysis (Table 5.1). Even more informative than this inconsistency between fossils and genes, is that both this palaeontological estimate and the molecular ages for the origin of octodontids, octodontines and ctenomyines, exceed previous fossil-based datings (e.g. Reig, 1989; Vucetich *et al.*, 1999; Vucetich and Kramarz, 2003), largely as a result of differences in the definition of these higher taxa.

The early Oligocene to middle Miocene octodontoids possess recurrent dental morphologies, a fact that has contributed to maintain their systematic and phylogenetic

Table 5.1. Comparison of estimated ages for origin of total-groups (t_1) and crown-groups (t_3), and modernisation stage (morphological differentiation, t_2) of studied taxa. Values from this study are minimum age fossil-based estimates.

| | This study | Vucetich <i>et al.</i> (1999) ^a | Gallardo and Kirsch (2001) | Honeycutt <i>et al.</i> (2003) ^b | Opazo (2005) | Rowe <i>et al.</i> (2010) ^c | Upham and Patterson (2012) | Fabre <i>et al.</i> (2013) ^d |
|-----------------|------------|--|----------------------------|---|--------------------|--|----------------------------|---|
| Echimyidae | ~26.0 | >28.0? | | 27.4 | 17.5 | ~25.0 | 25.3 | 27.1 |
| t_1 (t_2) | (~26.0) | | | | | | | |
| Echimyidae | ~26.0 | | | | 8.6 ^(d) | 15.0 ^(d) | 18.8 | 20.5 |
| t_3 | | | | | | | | |
| Octodontidae | ~25.5 | >9.0 | | 27.4 | 17.5 | ~25.0 | 25.3 | 27.1 |
| t_1 | | | | | | | | |
| Octodontinae | ~25.5 | >9.0 | 25.5 | 19.6 | 15.0 | 22.0 | 19.1 | 22.6 |
| t_1 (t_2) | (~7.0) | | | | | | | |
| Octodontinae | ~7.0 | | 9.0 | 8.6 | 7.8 | 8.0 | 9.0 | |
| t_3 | | | | | | | | |
| Ctenomyinae | ~25.5 | >9.0 | 25.5 | 19.6 | 15.0 | 22.0 | 19.1 | 22.6 |
| t_1 (t_2) | (~6.0) | | | | | | | |
| Ctenomyinae | ~3.5 | | | | | | 4.3 | |
| t_3 | | | | | | | | |

^a Original chronology updated on the basis of current available information (Verzi *et al.*, 2014).

^b Data as averaged in Honeycutt (2009).

^c Calculated using 55 million years as maximum age for Caviomorpha.

^d Age estimation based on partial sampling. See references for calibration points and molecular data.

interpretations in a state of flux. As mentioned above, many of these early octodontoids with lophate, low-crowned molars have often been assigned to Echimyidae (Carvalho and Salles, 2004; Verzi *et al.*, 2014: table 1) because living species of the latter have conservative dental designs (Reig, 1986). Octodontids have been considered as an offshoot of an unnamed octodontoid stem (which includes echimyids; Reig, 1986; Vucetich and Kramarz, 2003; Arnal and Pérez, 2013), and defined through their hypsodont, especially euhypsodont, molars with simplified occlusal surfaces, which characterise their late Miocene–Recent representatives (Figure 5.1). In contrast, the present phylogenetic analysis (see also Verzi *et al.*, 2014) recovers Octodontidae and Echimyidae as ancient sister monophyletic groups.

Such different interpretations do not derive only from different tree topologies, but also from the implicit or explicit assumption of hypotheses assigning the fossils to particular evolutionary stages of the clades. In this regard, three successive stages can be recognised 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, i.e. divergence from its sister clade; t_2 , its modernisation, i.e. morphological differentiation by acquisition of the apomorphies that characterise its extant members; and t_3 , the origin of the last common ancestor of these living

representatives (Figure 5.1). Hennig (1965: 114) pointed out that stages t_1 and t_3 are two points in time of particular importance in the history of a clade, whereas the delimitation of the stage of modernisation, t_2 , depends on subjective criteria concerning the interpretation of the emergence of particular “types” or “Baupläne”. We believe that stages t_1 , t_2 and t_3 provide information regarding different processes. The times of origin of a clade (t_1) and of its crown group (t_3) represent cladogenesis and extinction; in our case, the period separating t_1 and t_3 in both octodontid subclades implies extinction of lineages. The stage t_2 is related to change within lineages, and although its delimitation may imply subjectivity (which is amenable to description), such differentiation stages can yield important evolutionary information when analysing environmentally driven changes in morphology.

The interpretation of the first records of the derived morphologies of octodontids, octodontines and ctenomyines, as indicators of clade origin, yields ages younger than 10 Ma for each of these taxa (Table 5.1; Reig, 1989; Verzi, 1999; Vucetich *et al.*, 1999). Conversely, including stem representatives provides another way of defining and dating these clades. Although more unstable, because stem members are often poorly preserved and/or share few apomorphies with their corresponding crown groups (Briggs and Fortey, 2005), this definition has the advantage of taking into account the deep history of a lineage (Patterson, 1993a, b; Donoghue, 2005). Our definitions of Octodontidae, Octodontinae and Ctenomyiinae follow this last criterion (Figure 5.1), thus interpreting modern (i.e. euhypsodont) species as representing stages of differentiation characterised by the acquisition of the morphologies occurring in the extant species (t_2). These stages are decoupled from the splits that separated these families and subfamilies (t_1 ; Figure 5.1; Steiper and Young, 2008), and, at least in the case of ctenomyines, also from the origin of the crown group (t_3). In this latter case, the time of morphological differentiation can only be informed by fossils, highlighting the unique contribution of palaeontology to the appreciation of the true shape of trees (Helgen, 2011) and our understanding of macroevolutionary patterns.

It is noteworthy that, in our interpretation, neither a stage of modernisation (t_2), nor the origin of crown groups (t_3), are recognisable as stages distinct from the origin (t_1) in the case of echimyids and their two main subordinate clades. This major difference with respect to the octodontid pattern can potentially promote explanatory hypotheses.

Patterns of variation and disparity in modern representatives

Figure 5.2 shows the skull shape variation of living octodontoids and the extinct modern ctenomyines †*Actenomys* and †*Eucelophorus*. This variation is represented in the morphospace of the first two axes of a PCA of Procrustes coordinates. These first two principal components (PC) explained 63.3% of the total variation of our sample. Along PC1 (36.40% of total variance), forest-dwelling echimyids are clustered in a relatively restricted space within positive values, while octodontines, ctenomyines, and echimyids from open environments are more scattered in the shape space, most occupying negative values. The desert-specialist octodontines *Tympanoctomys* and *Pipanaoctomys*

have the most extreme negative scores. The main shape changes along this axis involve a larger auditory bulla toward negative values, and a larger orbit toward positive values. Hypertrophy of the auditory bullae, as represented in the negative PC₁ extreme, is a clear specialisation to desert environments (e.g. Lay, 1972; Ojeda *et al.*, 1999). Along PC₂ (26.9% of total variance), most echimyids and octodontines have negative or near-zero scores, while only the ctenomyines, the octodontine *Spalacopus* and the echimyid *Myocastor* show higher positive values. The skulls of the latter present higher zygomatic arches, a lower cranial vault, more retracted nasals, and longer procumbent premaxillae, all of these features being advantageous for digging (e.g. Stein, 2000); to a lesser extent, they also have somewhat smaller bullae.

As Figure 5.2 shows, the forest-dwelling echimyids present lower morphological diversity. The fossorial *Euryzygomatomys*, *Clyomys* and *Carterodon*, and to a lesser extent *Trinomys* and *Thrichomys*, which occupy intermediate to more open habitats, are at some distance from the forest dwellers. In particular, the fossorial *Carterodon* and *Clyomys*, which inhabit Chacoan environments, occupy positions closer to octodontids.

The position of *Myocastor*, separated from all other taxa in the morphospace, reflects its atypical features; as previously mentioned, unlike other members of the family this semiaquatic digger occurs widely in the Southern Cone and is the largest living echimyid. Nevertheless, in our analysis body size did not appear to have influence on shape changes; a multivariate regression of shape (all PCs) on size (as centroid size) was significant, but only 15.65% of the shape variation was predicted by size (10 000 permutations, $p = 0.0035$). Accordingly, the distribution of taxa in the morphospace was unrelated to their relative size.

The wide dispersion of octodontids in the morphospace reflects the considerable morphological variation between the desert inhabitants (*Octomys*, *Octodontomys*, *Pipanaoctomys* and *Tympanoctomys*) on one hand, and the strongly specialised subterranean representatives (*Spalacopus*, ctenomyines), on the other. *Spalacopus* shares the morphospace of modern ctenomyines, especially *Ctenomys*, which is not surprising considering their common subterranean specialisations. †*Eucllophorus*, the taxon with extreme positive values on PC₂, is the South American rodent with greatest cranio-dental specialisation for digging (Verzi and Olivares, 2006; Vieytes *et al.*, 2007).

As expected, the values of the disparity index (Foote's F) agree with the results of the exploratory PCA. As shown in Table 5.2, these disparity values are not related to the age or species richness of the clades. Concerning the latter, although our sampling is only partial in the case of highly polytypic genera, the species analysed are representative of the major subclades; this is especially true in the case of *Ctenomys* and *Trinomys*. The disparity of modern ctenomyines and octodontines was more than double that of the echimyid subclade A. The highest disparity values correspond to ctenomyines when the modern, extinct, species are included; their disparity is significantly lower when only the living *Ctenomys* is considered. The lowest disparity values correspond to forest-dwelling echimyids (as anticipated by their relatively more constrained dispersion in the PCA morphospace) which constitute the oldest and most species-rich subclade.

Table 5.2. Species richness, approximate age and disparity for the studied clades (see Figure 5.1). Species richness updated from Woods and Kilpatrick (2005); molecular datings after Upham and Patterson (2012: fig. 4, table 2).

| Clade | Species richness | Clade age fossils/ molecules (Ma) | Disparity (Foote's F) |
|---|------------------|--------------------------------------|-----------------------------|
| Echimyidae | | | |
| Subclade A (mainly forest environments) | 73 | 26.0 / 17.0 | 0.0039 |
| Subclade B (mainly open environments) | 14 | 26.0 / 16.0 | 0.0041 |
| Octodontidae | | | |
| Crown Octodontinae | 13 | 7.0 / 9.0 | 0.0084 |
| Modern Ctenomyiinae | 69 | 6.4 / – | 0.0120 |
| Crown Ctenomyiinae | 67 | 3.5 / 4.3 | 0.0043 |

When the species from forest environments, independent of their phylogeny, are compared to the non-forest-dwelling taxa, the disparity of the latter ($F = 0.0088$) is more than double that of forest species ($F = 0.0036$).

Even though formal analyses of rates of evolution, assessing the influence of phylogenetic structure in a taxonomically wider sample (e.g. Collar *et al.*, 2005; O'Meara *et al.*, 2006), are still needed, it is nonetheless clear that higher rates of morphological change occur in modern octodontids, irrespective of species richness. The fossil record of modern ctenomyiines is an example of how this could happen. Ctenomyiines became differentiated in the Pampasia. Fossil-bearing beds favourable from a taphonomic, geographic and temporal viewpoint, such as the late Miocene Cerro Azul Formation and the coastal Plio-Pleistocene deposits in central Argentina, show that the modernisation of ctenomyiines involved intense anagenesis (Figure 5.3). †*Actenomys priscus* and †*Eucelophorus chapalmalensis* are the results of directional evolution in lineages with no evidence of cladogenesis (phyletic evolution, in part, Simpson, 1953: 384–385; gradual directional change, Rasskin-Gutman and Esteve-Altava, 2008: fig. 1; see Verzi, 1999; 2008; Verzi *et al.*, 2004), and their contribution to the disparity of ctenomyiines is a product of the build-up of changes throughout a period equivalent to that of the cladogenesis of the highly polytypic *Ctenomys*.

The different patterns of variation here described for modern octodontoids were already reflected in their contrasting taxonomic histories. The supraspecific octodontid taxa recognised on the basis of their morphology have remained stable. The relationship between the two major clades has been recognised through morphology, fossils and molecules (Simpson, 1945; Honeycutt *et al.*, 2003; Verzi *et al.*, 2014), although without agreement regarding the taxonomic rank assigned to both lineages (familial hierarchy, Octodontidae and Ctenomyiidae, is currently accepted in neontology). In contrast to this stability, molecular studies of echimyids (Lara *et al.*, 1996; Leite and Patton, 2002; Galewski *et al.*, 2005; Fabre *et al.*, 2013) have not been able to recover the subfamilies previously

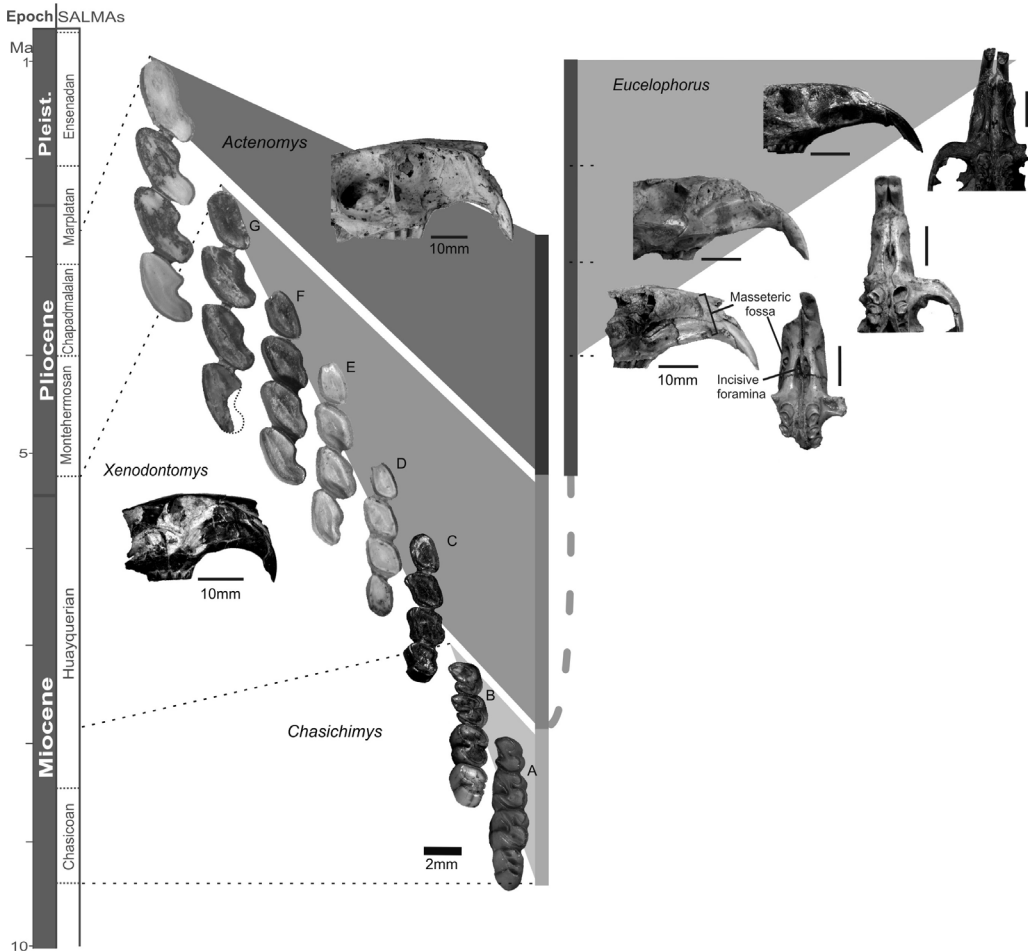


Figure 5.3 Directional gradual evolution in †*Chasichimys*–†*Xenodontomys*–†*Actenomys priscus* (Chasicocoan–Marplatan) and †*Eucelophorus chapalmalensis* (Montehermosan–Ensenadan) lineages. In the first lineage (left), note the simplification of the occlusal surface (coupled with increased hypsodonty) and subsequent elongation of the occlusal outline, and overall size increase; in †*Eucelophorus* (right), the rostrum becoming longer, lower and more procumbent, the masseteric fossa deepening, and the incisive foramina becoming reduced. Occlusal figures correspond to left dp4–m3. A,B: †*Chasichimys scagliai*; C,D: †*Xenodontomys simpsoni*; E,F: †*Xenodontomys ellipticus*; G: †*Xenodontomys elongatus* (see Verzi *et al.*, 2004).

recognised through the morphological approach of alpha systematics (Woods and Kilpatrick, 2005) as monophyletic groups. In addition, echimyid systematics at the genus level are still in a state of flux (see Emmons, 2005; Lack-Ximenes *et al.*, 2005). The case of *Trinomys* and *Proechimys* is particularly illustrative; molecular phylogenies show that the divergence between these two genera is deep, close to the base of the Echimyidae cladogenesis (Lara *et al.*, 1996; Leite and Patton, 2002; Galewski *et al.*, 2005; Fabre *et al.*, 2013); however, before these results, their strongly conservative morphology (Lara *et al.*, 1996) led to their being considered as congeneric (e.g. Moojen, 1948; Pessôa and dos Reis, 2002).

Cenozoic climatic changes, and geographical and temporal hierarchies of the fossil record

Rainforests occurred in South America up to high latitudes at least since 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), 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 corresponding to the Quechua phase of Andean orogeny, gave rise to the development of diverse, more open biomes from the late Miocene (Pascual and Ortiz Jaureguizar, 1990; Palazzesi and Barreda, 2007; Le Roux, 2012).

Differences in the evolutionary patterns of echimyids and octodontids reflect different responses to these Cenozoic environmental changes (Pascual, 1967; Verzi, 2002; Verzi *et al.*, 2014). Echimyids responded to environmental changes by tracking their original habitats, with their extant representatives primarily occurring in the Amazonian, Andean and Atlantic forests (Fabre *et al.*, 2013), and only a few species having colonised more open areas (Hoffstetter, 1986; Verzi *et al.*, 1994; Olivares *et al.*, 2012; Upham and Patterson, 2012). Octodontids, in contrast, evolved diverse adaptations to the new emerging environments.

Because of the biased distribution of fossil beds in South America (Pascual *et al.*, 1985), octodontoids have an essentially southern fossil record. Our phylogenetic results (including the low MSM* values) suggest that fossil echimyids were less numerous in these deposits than previously thought (in contrast to octodontids), supporting the idea that the presence of this group in southern South America has always represented an impoverished, marginal sample of its astonishing diversity in the northern tropical areas. Early echimyids from the Oligocene to middle Miocene are related to living arboreal tree rats and bamboo rats from the tropical forests (Figure 5.4; Emmons and Feer, 1999). In contrast, since the late Miocene the record is restricted to species related to living fossorial and terrestrial spiny rats (Figure 5.1; Vucetich *et al.*, 1997; Olivares *et al.*, 2012) occurring mostly in more open, essentially Chacoan areas (Caatinga, Cerrado and Pantanal), and grasslands (Bonvicino *et al.*, 2008; Catzefflis *et al.*, 2008). The progressive decline of these echimyids in this period, heralding their current absence from southern South America, took place along with a marked turnover in the octodontid record in the area. This turnover comprises radiation of hypsodont species and extinction of lineages with primitive molars (Figure 5.1; Verzi, 2008; Verzi *et al.*, 2011: fig. 8), marking the beginning of the stage of modernisation of octodontines and ctenomyines. The first appearance of marked desert specialisations among euhypsodont octodontines occurred later, coinciding with the profound global late Pliocene cooling and drying event around 2.5 Ma (Figure 5.1; Verzi, 2001; Verzi and Quintana, 2005 and references therein).

The hierarchy of these clade stages, which follows that of concurrent palaeoenvironmental changes, resulted in the current geographical pattern of octodontoids, in which

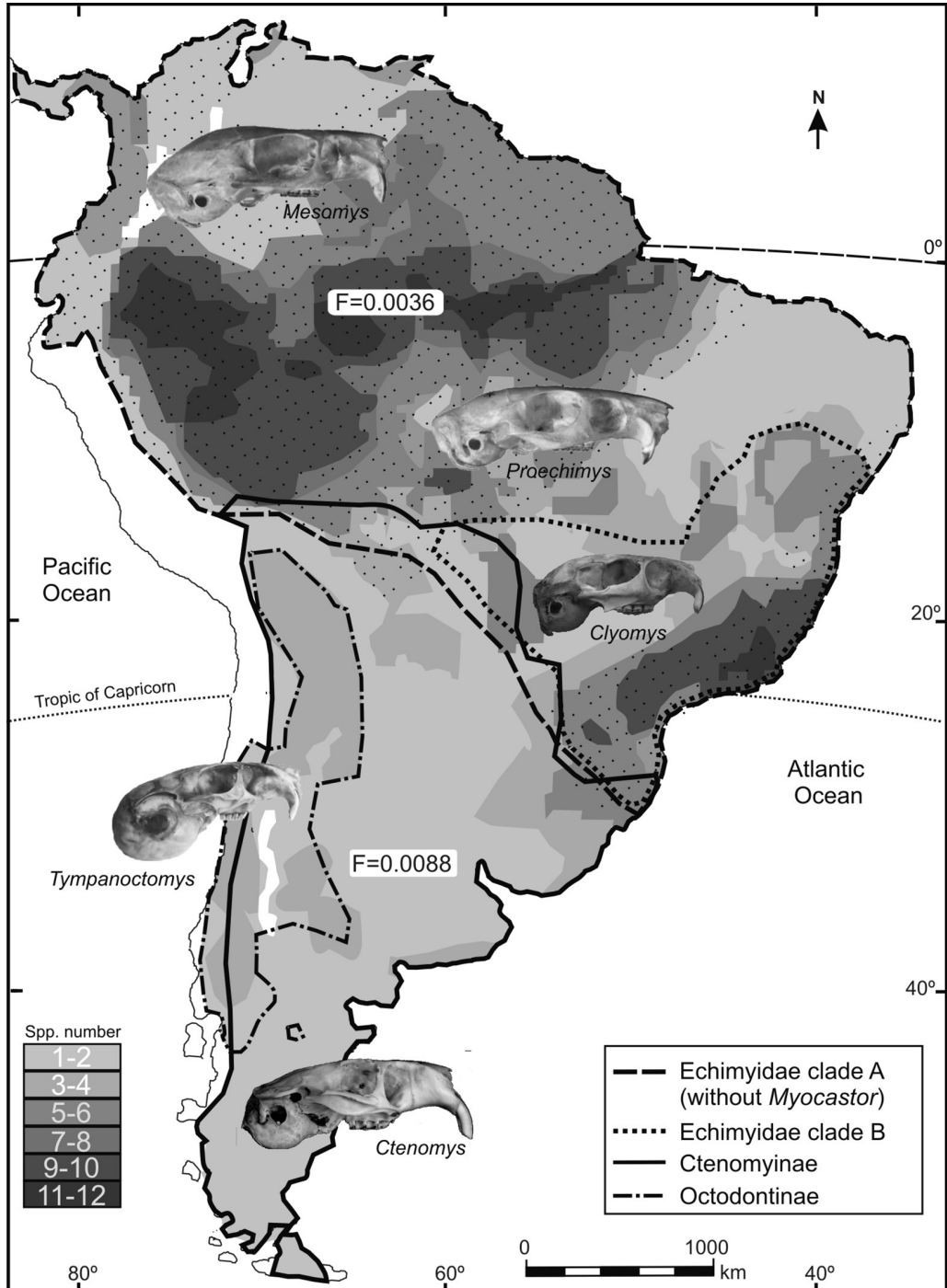


Figure 5.4 Distribution of major clades of echimyids and octodontids showing species density (based on species occurrences in 0.5 by 0.5° grid cells; modified from Upham and Patterson, 2012: fig. 1), and values of the disparity index (Foote's F) for forest- vs. non-forest-dwelling representatives (see text). Dotted areas indicate distribution of tropical and subtropical moist forests (after Olson *et al.*, 2001). Illustrated skulls not to scale.

species adjusted to (in this context) “primitive” northern tropical forests (most of the echimyid subclade A) coexist with those occupying more derived habitats, including Chacoan (most of the echimyid subclade B) and southern mesic scrublands and grasslands (most of the mesic-adapted octodontine subclade F), and the more recently arisen desert environments (desert-adapted octodontine subclade E).

Such a pattern is not exclusive to octodontoids. In this respect, Janis (2001: III) points out that: “Differences between early Tertiary and present-day mammals are largely the result of a change from equable, globally tropical conditions to a cooler, drier, and more climatically zoned world. Eocene-like mammals remain in the restricted equatorial forests (. . .) while some extreme specialists have evolved adaptations to environmental conditions unique to the past few million years . . .”. As is clear from this statement, the temporal and spatial dimensions of this pattern are associated with the vector that represents morphology.

Structure of disparity. The importance of the anagenetic perspective for evolutionary generalisations

Evolutionary generalisations about the origin and dynamics of biological diversity are among the most revisited, especially with the aim of understanding the processes that generate and maintain high species richness in the tropics (Chown and Gaston, 2000; Wiens and Donoghue, 2004; Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007; Weir and Schluter, 2007; Arita and Vázquez-Domínguez, 2008; Buckley *et al.*, 2010; Hoorn *et al.*, 2010; Davies *et al.*, 2011; Rull, 2011). The evolutionary dynamics of other components of diversity, such as morphology (i.e. disparity, Roy and Foote, 1997; e.g. Shepherd, 1998), or function (Safi *et al.*, 2011), remain less well known, partly because species richness is not an adequate metric to explain them (Jablonski, 2009: 479). In this regard, whether the high tropical diversity is explained by a higher pure speciation or net (relative to extinction) diversification rate, or by a greater time for diversification (see review in Mittelbach *et al.*, 2007), the morphological similarity generally associated with this diversity is a counterintuitive product of these processes, at least in terrestrial faunas. Eldredge (1996: 52–53) explained this paradox of the punctuated equilibria model, which assumes that morphological change is linked to speciation, by proposing that successful speciation in the tropics requires less adaptive change. Likewise, Safi *et al.* (2011) showed that the high levels of speciation in the tropics seem to produce many species with “conserved niches”, resulting in a higher degree of functional redundancy.

It is possible to analyse patterns such as those mentioned from the perspective of the change involved (anagenesis) rather than on the basis of cladogenetic events, as a non-exclusive alternative. Weir and Schluter (2007) detected that a longer lag time between population splitting and species designation (i.e. longer speciation process) in birds and mammals occurs in the tropics and, as a consequence, sister-species pairs from those regions are older. Octodontoids fit this pattern, with most of the tropical forest-dwelling extant species of echimyids being older than those of temperate-areas octodontines and ctenomyines (Upham and Patterson, 2012: fig. 4). But this generalisation can be extended

by assessing levels of differentiation that resulted from time-equivalent splits (nodes of similar height): initial splits within genera or small clades of octodontoids in the tropics of South America are of similar age (although not strictly contemporaneous) to those that led to the differentiation of higher taxa in the south. In particular, the beginning of diversification of species within the morphologically similar echimyids *Trinomys*, *Proechimys*, *Mesomys*–*Lonchothrix* or *Dactylomys*–*Kannabateomys*, is close in time to the differentiation of octodontines and ctenomyines, considered as two families in the taxonomy of living mammals (Figure 5.1).

In this generalisation we assume that, beyond ecological circumstances, anagenesis is not restricted to speciation. As stated by Szalay (1999: 52) “. . . rate-varying anagenesis occurs with or without incipient or populational cladogenesis or full or complete cladogenesis, i.e. speciation”. The anagenesis that underlies the adaptation of a population, whether it entails the formation of a new species or a long-term gradual directional change giving rise to a new grade (Simpson, 1953), requires cohesion of the evolving lineage (Futuyma, 1987) rather than the contingent perturbation of such cohesion that underlies splitting events. Indeed, diverse interpretations of the formation of species are focused on explaining the processes that lead to cohesion, and not on describing the innumerable contingent circumstances that are able to disturb it (Templeton, 1989; Hausdorf, 2011). Thus, the rates of species diversification and morphological change should not be expected to be necessarily coupled (see Kozak *et al.*, 2006; Adams *et al.*, 2009; Jablonski, 2009; Venditti *et al.*, 2011).

When environmental change occurs, species respond by tracking their preferred habitats, adapting or going extinct (Meloro *et al.*, 2013). It is to be expected that taxa which respond by tracking “original” habitats will be morphologically more conservative (Raia *et al.*, 2012) than those that respond by adapting to their new environment, independently of their speciation rates (Table 5.2). This might explain why the origin and differentiation of echimyids are not perceptible as decoupled events, and may furthermore account for the morphological similarity shown by their anciently diverged lineages (Lara *et al.*, 1996: 410; Da Silva and Patton, 1998; Fabre *et al.*, 2013). In octodontines and ctenomyines, the adaptation to new emerging environmental conditions shows stages of southern differentiation that are distinctly decoupled from their respective origins. As in the case of the geographical and temporal dimensions, the hierarchy of these morphological stages follows that of concurrent palaeoenvironmental changes.

Most records of long-term gradual directional change resulting in deep morphological change in octodontoids date from the late Miocene–Pliocene (Verzi *et al.*, 2011), when the already-established cooling and drying trend shows largely narrower oscillations (as represented by the variance of oxygen isotope excursions) than those observed for the succession of ice ages that began in the latest Pliocene (Figure 5.1). Although this remark is here merely exploratory, this is consistent with the model proposed by Sheldon (1996), which predicts that long-term phyletic change requires climatic trends with small-amplitude oscillations. According to this model, such conditions in tropical environments should also favour gradual directional change; possibly, given that the magnitude of environmental change is lower (Colinvaux and De Oliveira, 2001),

a lower change rate is also to be expected, beyond its assumed greater constancy (as shown by the results of Weir and Schluter, 2007).

Croizat's (1962) dictum "earth and life evolved together" possesses an anagenetic dimension that has been scarcely attended in comparison with a vicariant, or in a broader sense cladogenetic, perspective. This is despite the fact that the former probably necessitates less systematisation of contingent factors to provide explanations. As Jablonski (2009: 478) pointed out, '...one of the most striking facts of the fossil record (...) [is] that evolutionary novelties do not arise randomly in time and space'. Derived environments trigger morphological adaptation, independently of the frequency of cladogenetic events. In the context of the evolutionary history of octodontoids, and even of terrestrial mammals (Janis, 2001), derived environments are represented in the extratropics; thus, regardless of how the latitudinal diversity gradients occur, the extratropics play an important role as a cradle of evolutionary novelties.

In the complex dynamics of the organic world, the immanent (unchangeable, and therefore predictable) properties of matter become manifest through configurational, i.e. historical, circumstances, which are essentially unrepeatable or putatively recurring (Simpson, 1963). In the face of the difficulty of providing laws, the central aim of historical sciences is the search for increasingly wider explanatory generalisations. We believe that mutually dependent cohesion and change (anagenesis) are core concepts to explain the dynamics of life (Templeton, 1989; Maynard Smith and Szathmáry, 1997: 6–9), which should be more often considered when exploring configurational events in search of patterns.

Summary

South American Octodontoidea is the most species-rich clade among both extinct and extant hystricomorph rodents. The evolutionary histories of its two major groups, Octodontidae and Echimyidae, are differentially linked to the main Cenozoic palaeoenvironmental changes. According to a combined parsimony analysis of morphological and molecular data, they represent sister families, which were already separated in the late Oligocene, as well as the two major subclades comprised by each one. Whereas the octodontid subclades Octodontinae and Ctenomyiinae show progressive stages of differentiation (modernisation) since the late Miocene, similar phases uncoupled from their respective origins are not recognisable in the echimyid subclades. The greater spread of modern octodontids in the morphospace of skull variation, and their greater relative disparity, independent of age and species richness, result from the abovementioned stages of differentiation and imply specialisation to open environments. Thus, the history of octodontoids suggests that the acquisition of evolutionary novelties is linked to the progressive emergence of new environments, and this link is manifested through different hierarchies, i.e. geographic, temporal and anagenetic (amount of change, irrespective of cladogenetic events). For these rodents, as well as for other terrestrial mammals, derived environments occur out of the tropics, thus highlighting the importance of the extratropics as a cradle of evolutionary novelties.

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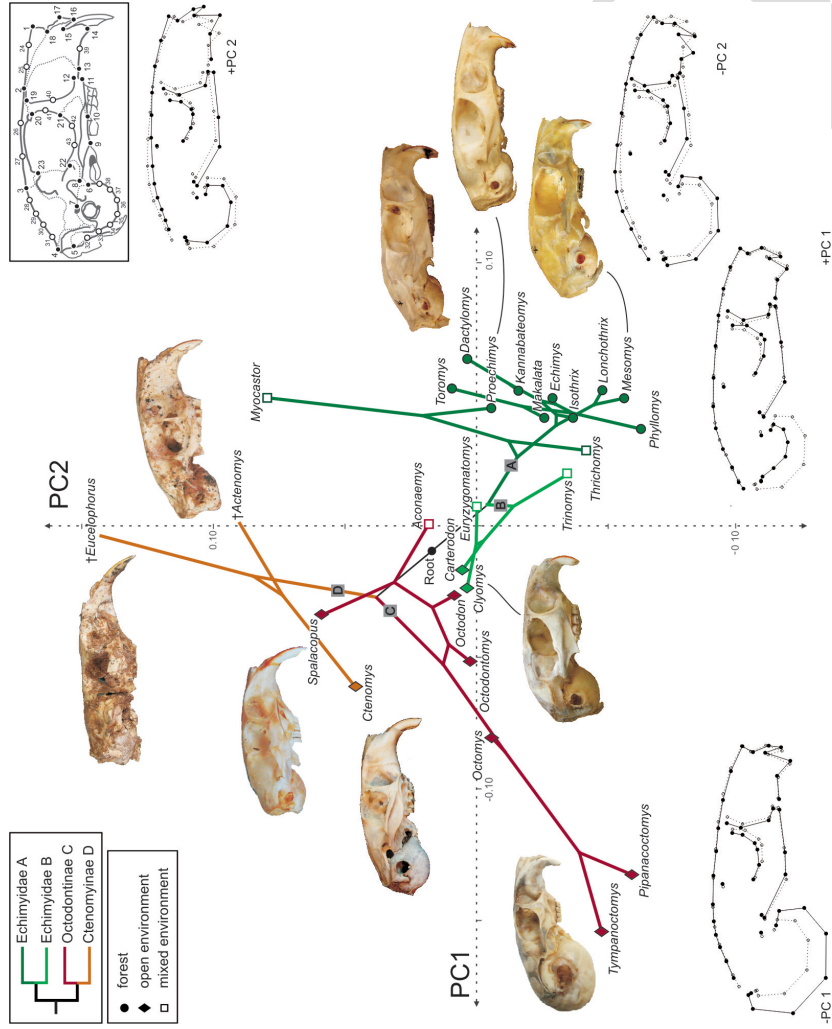


Figure 5.2 Phylogeny tree superimposed onto a plot of the first two principal components (PCs) among the genera analysed. The positions of internal nodes are reconstructed by squared-change parsimony using the tree topology obtained. At top right, schematic representation of lateral view of skull showing placement of landmarks (solid dots) and semilandmarks (empty circles). Outline diagrams show shape change associated with each PC, from the consensus (dashed lines and empty circles) to positive or negative scores (black lines and solid dots). Scale factor indicates magnitude of shape change as Procrustes distance. Illustrated skulls not to scale. A black and white version of this figure will appear in some formats.