

Geographical distribution and ecological diversification of South American octodontid rodents

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Abstract

Caviomorph rodents represent one of the most distinctive groups of mammals in southern South America drylands; they colonized South America from Africa via trans-oceanic dispersals in the Eocene (40–50 Ma) and underwent an extraordinary ecological radiation after their arrival, thus making this group of great interest for biogeographic and evolutionary studies. The aim of this article was to provide a working hypothesis regarding the biogeographical history and ecological diversification of one of its conspicuous families, the Octodontidae. We reconstruct the evolutionary theater where their ecological diversification took place, and potential events of dispersal, vicariance and extinctions. We analyzed the historical biogeography of the Octodontidae across the eight ecoregions where they occur, based on species phylogeny and divergence times. Four approaches were used to reconstruct ancestral area: (1) Statistical Dispersal–Vicariance Analysis (S-DIVA); (2) Bayesian binary Markov chain Monte Carlo (MCMC) analysis implemented in Reconstruct Ancestral State in Phylogenies (RASP); (3) Fitch optimization method; and (4) weighted ancestral area analysis (WAAA). Parsimony ancestral state reconstructions were implemented in order to explore the evolutionary history of an ecological character, mode of life. We propose the northern portion of the Monte desert ecoregion as the ancestral area in the evolution of the Octodontidae, with subsequent dispersal and enlargement of the family geographic range. The evolution of their ecological specialization (i.e. modes of life) suggests an ambiguous ancestral condition (saxicolous, generalist terrestrial, semifossorial) linked to species adaptation to arid environments, with fossoriality appearing later in octodontid evolution. The evolution of the Octodontidae is associated with contrasting environmental conditions (i.e. climate and vegetation) produced by the Andean Uplift between eastern and western sides.

Introduction

South America was an isolated continent during much of the Cenozoic. This isolation resulted in great variety of endemic mammal groups including marsupials, ungulates, xenarthrans, primates and rodents. South American drylands have played an especially important role in the evolution of mammalian biota (Reig, 1986; Mares, 1992; Ojeda, Blendinger & Brandl, 2000); globally, they have high biodiversity including high proportion of endemic genera and families (Mares, 1992). Caviomorph rodents represent one of the most distinctive groups of mammals in southern South America drylands; they appeared and diversified extensively during the Eocene (Antoine *et al.*, 2012). The history, origin and evolution of this group have been discussed by many authors (Lavocat, 1969; Patterson & Pascual, 1972; Reig, 1981; Woods, 1982; Poux *et al.*, 2006; Rowe *et al.*, 2010). The current prevailing hypoth-

esis suggests an early radiation that began in the Eocene when hystricognath rodents first arrived in South America from Africa via a trans-Atlantic dispersal event (40–50 Ma; Rowe *et al.*, 2010). Caviomorpha is composed of 13 families, which are grouped into four superfamilies: Cavoidea, Chinchilloidea, Erethizontoidea and Octodontoidea, the latter being the most diverse clade within the group (Huchon & Douzery, 2001; Upham & Patterson, 2012).

Within the Octodontoidea, Octodontidae is an endemic family of rodents distributed along southern South America (Reig, 1981; Mares & Ojeda, 1982). This family has a relatively narrow geographical range, which extends along both sides of the Andes in Argentina, Bolivia and Chile, between 15° and 40°S. Within this range, the family occurs in a wide range of habitats, including coastal areas in central Chile, pre-Andean and Andean regions, desert and semi-desert scrublands, rainforests and Mediterranean habitats (Gallardo *et al.*, 2007).

Living Octodontidae are a monophyletic group that includes two polytypic genera, *Aconaemys* (*A. fuscus*, *A. porteri* and *A. sagei*), and *Octodon* (*O. degus*, *O. bridgesi*, *O. lunatus* and *O. pacificus*), and six monotypic genera (*Spalacopus cyanus*, *Octodontomys gliroides*, *Octomys mimax*, *Tympanoctomys barrerae*, *Salinoctomys loschalchalersorum* and *Pipanaoctomys aureus*). The monophyly of the group is based on morphological and molecular characters such as: unique figure eight-shaped molars (Reig *et al.*, 1990), blood proteins (Woods, 1982), DNA reannealing (Gallardo & Kirsch, 2001), allozymes (Köhler *et al.*, 2000) and nucleotide sequences (Nedbal, Allard & Honeycutt, 1994; Honeycutt, Rowe & Gallardo, 2003). Although there is some ambiguity over the monophyly and branching relationships (low supported branches) among some genera of octodontoids which remain unresolved, for example the case of *Spalacopus* and *Aconaemys* (Honeycutt *et al.*, 2003; Upham & Patterson, 2012).

In accordance with molecular data, the origin of crown Octodontidae dates back to the late Miocene; estimations vary from 7.79 (6.29, 9.29) Ma (Opazo, 2005), to 8 (5, 12) Ma (Rowe *et al.*, 2010) and 9 (6.7, 11.6) Ma (Upham & Patterson, 2012), with its major diversification occurring during the Plio-Pleistocene. This was concurrent with major changes in the landscape and habitat fragmentation in response to the Andean uplift and increasing aridity (Solbrig, 1976; Ortiz-Jaureguizar & Cladera, 2006). During its evolution, the family split it into two well-differentiated clades. The first one is represented by genera restricted to Argentina (*Octomys*, *Salinoctomys*, *Pipanaoctomys* and *Tympanoctomys*), and the second one is represented by three genera that primarily inhabit Chile (*Octodon*, *Spalacopus* and *Aconaemys*). The latter clade is the sister group of *Octodontomys*, which is distributed in the Andes region of northern Argentina, Chile and Bolivia. Although the family is not speciose, with only eight genera and 13 species, it is ecomorphologically diverse including species ranging from generalized terrestrial locomotion to semifossorial and fossorial forms (Mares & Ojeda, 1982; Contreras, Torres-Mura & Yáñez, 1987).

The octodontids are of great interest biogeographically and evolutionarily because of their broad ecological diversity, geographical ranges on both sides of the austral Andes, and time of origin and diversification. Different hypotheses, mostly related to major climate change during the Plio-Pleistocene, have been proposed to explain the distribution and ecological diversity of the family. These have varied from early adaptation to montane habitats and recent colonization of the Andean regions (Mares, 1975; Reig, 1986) to ancestral ground-dwelling forms living in forest and scrub habitat (Reig, 1986; Contreras *et al.*, 1987).

Our purpose here was to analyze and reexamine the biogeographical history that shaped the current distribution and the diverse ecological radiation of the Octodontidae.

Materials and methods

For our analyses, we follow the recent phylogeny of Upham & Patterson (2012) which included 11 octodontid species (excluding *O. pacificus* and the monotypic genus *S. loschal-*

chalersorum). This phylogeny includes the divergence time for members of the Octodontidae family using relaxed clock analyses of the combined 4-gene data set (12S rRNA + GHR + vWF + RAG1). Species distributional ranges were estimated from Nature Server Database (<http://www.natureserve.org/explorer/>), and updated following recent specialized literature (Saavedra & Simonetti, 2003; Gallardo *et al.*, 2007, 2009; Ojeda *et al.*, 2007; Ebensperger *et al.*, 2008; Opazo *et al.*, 2008; Sobrero *et al.*, 2010), and original data from the mammal collections (CMI) of the Instituto Argentino de Zonas Áridas (IADIZA), Centro Científico Tecnológico Mendoza (CCT), Argentina (Fig. 1a–c). Geographical regions were based on WWF Ecoregions (Olson *et al.*, 2001). The historical biogeography of the family was analyzed for eight main ecoregions: A (Dry Chaco), B (High Monte), C (Low Monte), D (Patagonian Steppe), E (Central Andean Puna), F (Central Andean Dry Puna), G (Valdivian Temperate Forest) and H (Chilean Scrublands).

Four different approaches were used to reconstruct the possible ancestral ranges of Octodontidae on the phylogenetic trees. For the first two approaches we used recently developed the Statistical Dispersal–Vicariance Analysis (S-DIVA) and the Bayesian binary MCMC [BBM; Markov chain Monte Carlo (MCMC)] analyses implemented in the Reconstruct Ancestral State in Phylogenies (RASP) (Yan, Harris & Xingjin, 2011). In these methods, the frequencies of an ancestral range at a node in ancestral reconstructions are averaged over all trees (Yan, Harris & Xingjin, 2010). The analysis is based on vicariance, minimized dispersal, and extinctions. The number of maximum areas allowed at the nodes was eight, corresponding to the ecoregions. The following options were used: maxareas = 8; hold = 32767; bound = 32767. The possible ancestral ranges at each node on a selected tree were obtained. BBM analysis was also conducted in a similar way. The MCMC chains were run simultaneously for 50000 generations. The state was sampled every 100 generations. Fixed Jukes–Cantor were used for BBM analysis with null root distribution. The maximum number of areas for this analysis was kept as 8. The third approach was the Fitch optimization method where the probability of each area was calculated as a part of the ancestral area (Ronquist, 1995). Fitch optimization was also calculated to graph the optimization, including the areas as a multistate character and run as unordered with tree analysis using new technology (TNT) (Goloboff, Farris & Nixon, 2003). The fourth approach was the weighted ancestral area analysis (WAAA) (Hausdorf, 1988). The number of weighted gain steps (GSW), weighted loss steps (LSW) and the PI (GSW/LSW) were calculated by hand. The PI of each area shows the probability of these areas as a part of the ancestral area. We used the results obtained by the fourth methodologies as well as the estimated divergence time in each node from Opazo (2005) and Upham & Patterson (2012), and compared them with the time of geologic and climatic events.

The ecological characters (i.e. modes of life) of octodontids were those macroniches dealing with substrate specializations (*sensu* Eisenberg, 1981). All the octodontids are 'herbivorous'. However, because of the incomplete and rather fragmentary characterization of their specific diets, we made no attempt

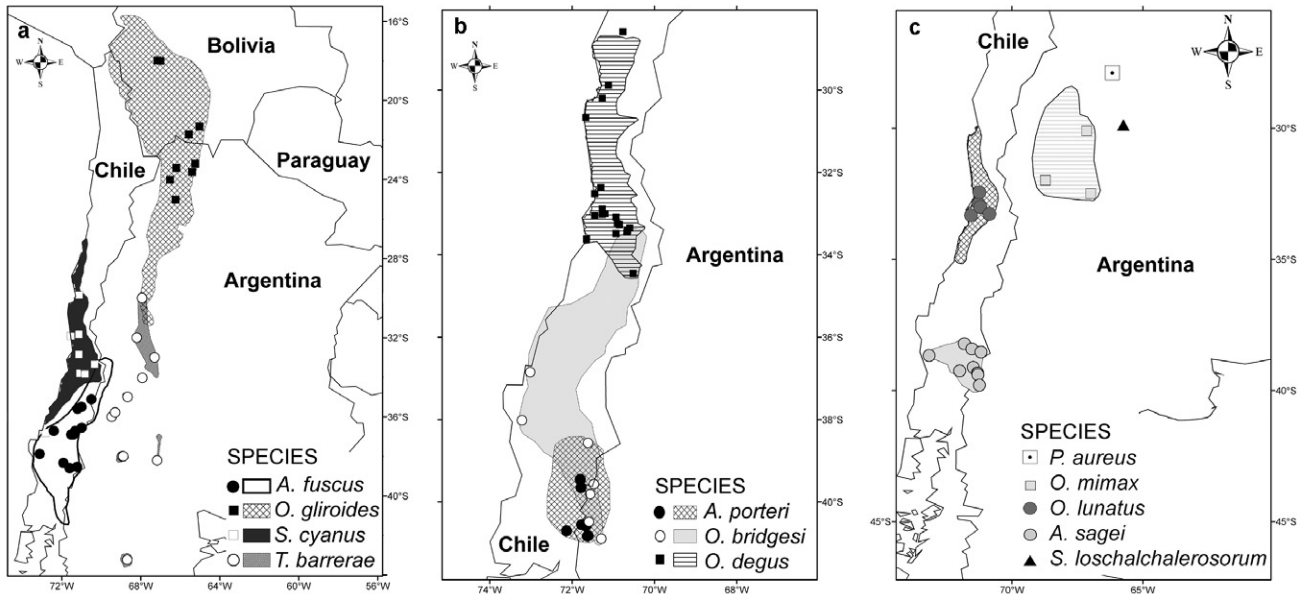


Figure 1 Geographical distribution range of 12 octodontid species. (a) *Tympanoctomys barrerae*, *Aconaemys fuscus*, *Octodontomys gliroides* and *Spalacopus cyanus*; (b) *Aconaemys porteri*, *Octodon bridgesi* and *Octodon degus*; (c) *Aconaemys sagei*, *Octodon lunatus*, *Octomys mimax*, *Pipanaoctomys aureus* and *Salinoctomys loschalchalersorum*.

in classifying them through their dietary specializations. The assignment of the different modes of life to each species follows the specialized literature on caviomorph rodents (Honeycutt *et al.*, 2003; Gallardo *et al.*, 2007), particularly some of the latest analyses regarding the evolution of digging and burrow complexity (Lessa *et al.*, 2008). We classified the following niches (i.e. substrate use) in terms of modal strategies or tendencies, and not the full spectrum that the species show in its annual cycle (Eisenberg, 1981): *Saxicolous*: The species shows morphological features and ability to move on rock surfaces and use crevices among rocks for shelter. Their occurrence is strongly associated to the presence of rock outcroppings (*Octomys*); *Generalist terrestrial*: The species shows mixed locomotion type as it forages on the surface but is also capable of climbing; it digs simple burrows from preexisting holes (*Octodontomys*, *Octodon*); *Semifossorial*: The species is able to dig complex burrows of several openings and these are typically used as a refuge. The animal shows ability to move on the surface (*Tympanoctomys*, *Pipanaoctomys* and *Aconaemys*); *Fossorial*: In this article we use the term fossorial as a synonym for subterranean of other authors. The species has specialized morphological features and conducts most of its activities underground, including foraging, resting and rearing young. However, it also goes to the surface for some foraging near the openings of complex burrows systems (*Spalacopus*). The ecological characters (i.e. modes of life) were mapped onto a phylogeny to explore their evolutionary history using the Parsimony Ancestral States module executed in Mesquite software version 2.75 (Maddison & Maddison, 2010). The character was coded as multi-state and unordered.

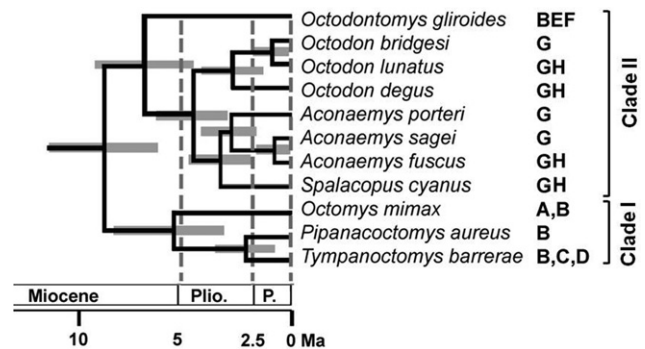


Figure 2 Phylogenetic relationships and divergence time estimates for members of the Octodontidae family. Modified from Upham & Patterson (2012). Currently occupied areas: A: Dry Chaco, B: High Monte, C: Low Monte, D: Patagonian steppe, E: Central Andean Puna, F: Central Andean Dry Puna, G: Valdivian Temperate Forest, H: Chilean Scrublands.

Results

The Octodontidae phylogeny shows two differentiated clades (Fig. 2). Clade I includes three species (*O. mimax*, *P. aureus* and *T. barrerae*) distributed along the eastern slope of the Andes, with ranges extending throughout the arid ecoregions of low and High Monte, Patagonian steppe, and marginally, the dry Chaco of Argentina. On the other hand, clade II consists of seven species (*O. degus*, *O. lunatus*, *O. bridgesi*, *S. cyanus*, *A. porteri*, *A. fuscus*, and *A. sagei*) primarily distributed throughout the Valdivian Temperate rainforest and

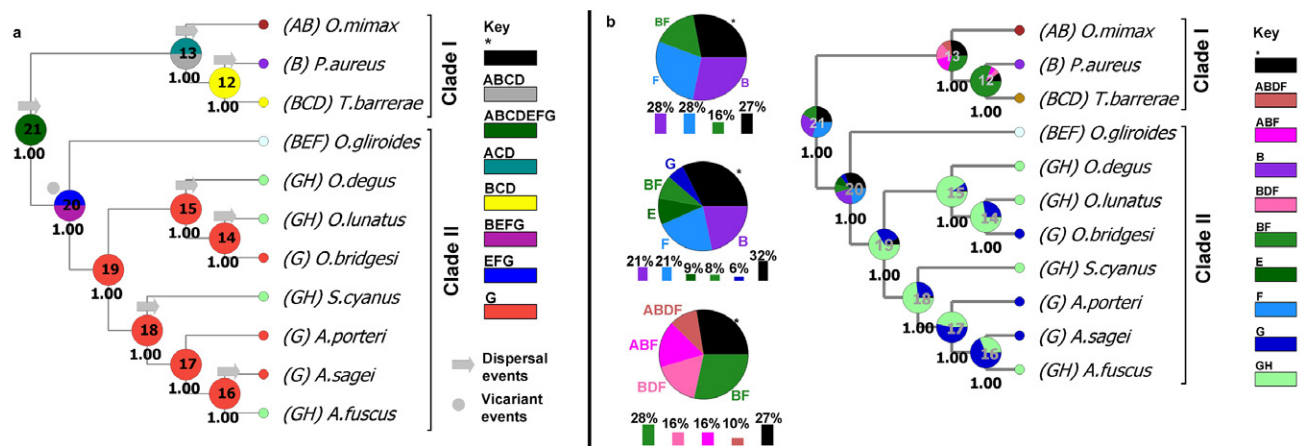


Figure 3 Ancestral areas reconstruction. (a) Graphical output results of ancestral distributions at each node of the Octodontidae phylogeny obtained by Statistical Dispersal-Vicariance Analysis (S-DIVA) Reconstruct Ancestral State in Phylogenies (RASP). (b) Graphical output results of ancestral distributions at each node of the Octodontidae phylogeny obtained by from Bayesian binary MCMC (BBM) analysis (exported from RASP). Alternative ancestral ranges of nodes 21, 20 and 13 (with frequency of occurrence) are shown in pie chart form. Color key represent possible ancestral ranges at different nodes; black with an asterisk represents other ancestral ranges. Areas: A: Dry Chaco, B: High Monte, C: Low Monte, D: Patagonian Steppe, E: Central Andean Puna, F: Central Andean Dry Puna, G: Valdivian Temperate Forest, H: Chilean Scrublands.

Chilean scrublands (named here Chilean clade). One remaining species (*O. gliroides*) occurs in the High Monte ecoregion, including the Prepuna-Puna region of Argentina as well as the Puna of Bolivia and Chile.

Ancestral biogeographical reconstructions for the history of the Octodontidae show different scenarios depending on the method utilized. The optimal S-DIVA reconstruction for the history of the family required seven dispersal, one vicariant and zero extinction events. S-DIVA suggests one possible ancestral area for the family (node 21) which includes all ecoregions where octodontids currently occur, except the Chilean scrublands (area H) (Fig. 3a). This method also proposed two possible ancestral ranges for clade I (node 13): ABCD (Dry Chaco, High Monte, Low Monte, Patagonian Steppe) or ACD (Dry Chaco, Low Monte, Patagonian Steppe) with an occurrence of these ranges of 50% respectively. For clade II S-DIVA suggests two possible ancestral ranges (node 20): BEFG (High Monte, Central Andean Puna, Central Andean Dry Puna, Valdivian temperate Forest) or EFG (Central Andean Puna, Central Andean Dry Puna, Valdivian temperate Forest) with an occurrence of these ranges of 50% respectively. The directions of four of the seven dispersal events were from the Valdivian Temperate Forest (area G) to the Chilean Scrublands (area H). The other three involved dispersal from Dry Chaco, Low Monte and Patagonian steppe to the High Monte (area B) (Fig. 3a). BBM analysis suggests slightly different ancestral ranges at the basal node. The ancestral reconstruction at node 21 is ambiguous suggesting three possible ancestral ranges, B, F and BF. The occurrence of these ranges is: B (28.10 %); F (28.10 %); BF (16.9 %) (Fig. 3b). Ancestral reconstruction of clade I and II (node 13 and 20) is ambiguous, suggesting a different possible ancestral range. For clade I BE (28.57%); BDF (17%); ABF (17%),

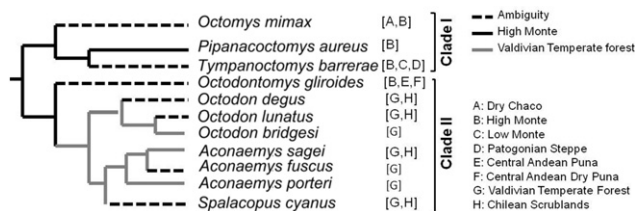


Figure 4 Reconstruction of ancestral areas using Fitch optimization method.

ABDF (11%) and for clade II B (21%) F (21%), BF (9%), E (8%), G (6.25%) (Fig. 3b).

We obtained different results using Fitch optimization method and WAAA analyses. Both approaches assigned a high probability to the High Monte ecoregion as the ancestral area of the family (Figs 4 & 5 Table 1). These results differ from S-DIVA and BBM analysis, as they assigned the High Monte ecoregion as the ancestral area for clade I (Figs 4 & 5), whereas S-DIVA and BBM analysis showed ambiguous results indicating other areas (A, B, C, D and F) as ancestral. With regard to clade II, areas B, E, F or G (High Monte, Central Andean Puna, Central Andean Dry Puna or Valdivian Temperate Forest) showed the same probability of being the ancestral areas (i.e. the four areas had the same value) (Table 2). All analyses were consistent in the fact that the Chilean Scrublands (area H) is not considered the ancestral area for the family neither for the clade II, but was later colonized via dispersions.

Parsimony ancestral reconstructions for the ecological character ‘mode of life’ reveal an ambiguous hypothetical ancestral state in which saxicolous, generalist terrestrial and

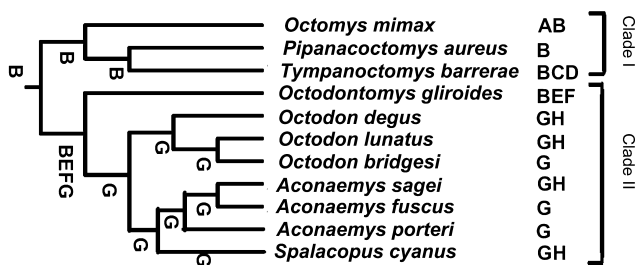


Figure 5 Reconstruction of ancestral areas using weighted ancestral area analysis. (WAAA). Areas: A: Dry Chaco, B: High Monte, C: Low Monte, D: Patagonian Steppe, E: Central Andean Puna, F: Central Andean Dry Puna, G: Valdivian Temperate Forest, H: Chilean Scrublands.

Table 1 Estimations of ancestral area for the family Octodontidae, using Fitch method and Weighted Ancestral Area Analysis

Area	Fitch (Ronquist, 1995)		WAAA (Hausdorf, 1988)		
	S	RP	GSW	LSW	PI
A	2	0.50	0.50	1.50	0.33
B	1	1.00	1.50	0.50	3.00
C	3	0.33	0.33	1.83	0.18
D	3	0.33	0.33	1.83	0.18
E	2	0.50	0.50	1.50	0.33
F	2	0.50	0.50	1.50	0.33
G	2	0.50	0.50	1.50	0.33
H	5	0.20	0.86	2.06	0.41

S, number of necessary steps if the area was the ancestral area; RP, S-values rescaled to a maximum value of 1 by inverting them and multiplying by the smallest S-value; GSW, number of weighted gain steps; LSW, number of weighted loss steps; PI, GSW/LSW, probability index for every area; WAAA, weighted ancestral area analysis.

Table 2 Estimations of ancestral area for clade II using Fitch method and Weighted Ancestral Area Analysis

Area	Fitch (Ronquist, 1995)		WAAA (Hausdorf, 1988)		
	S	RP	GSW	LSW	PI
B	1	1	1.00	1.00	1.00
E	1	1	1.00	1.00	1.00
F	1	1	1.00	1.00	1.00
G	1	1	1.00	1.00	1.00
H	4	0.25	0.88	1.75	0.50

S, number of necessary steps if the area was the ancestral area; RP, S-values rescaled to a maximum value of 1 by inverting them and multiplying by the smallest S-value; GSW, number of weighted gain steps; LSW, number of weighted loss steps; PI, GSW/LSW, probability index for every area; WAAA, weighted ancestral area analysis.

semifossorial forms are equally parsimonious as being as hypothetical ancestor (Fig. 6). The specialization to fossorial mode of life is the only ecological state which does not appear in the ancestor and emerges later in octodontid evolution, around 2 Ma, as represented by *S. cyanus* (Figs 2 & 6).

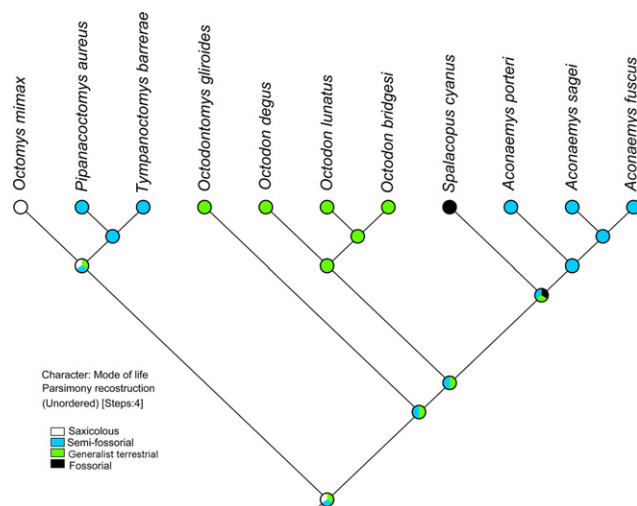


Figure 6 Parsimony ancestral reconstruction of the ecological characters 'modes of life' in the Octodontidae family.

Discussion

Based on our results we proposed the northern portion of the Monte desert (i.e. High Monte; 'protopuna' of Reig, 1981) as the most likely ancestral area for the family. This was supported by Fitch, WAAA methods and BBM analyses. While the BBM analyses show an ambiguous ancestral area, the High Monte or Central Andean Dry Puna have the same high probability of being part of the ancestral area. The geographical reconstruction of this ancestral area is consistent with paleoenvironmental reconstructions for the Neogene (Barreda *et al.*, 2007); at that time was already present xeric-shrub plant communities that characterize the High Monte. On the other hand, the S-DIVA analyses proposed all regions as a possible ancestral range with a 100% marginal probability, with the exception of Chilean Scrublands ecoregion (Fig. 3a; node 21). The assignment of all these areas as ancestral, can be seen as a methodological artifact of DIVA analysis, since it maximizes the vicariance (cost of zero) over dispersal events (cost of one) and assigns most of the areas as ancestral, thus creating an ancestral cosmopolitan distribution (Domínguez & Roig-Juñent, 2011). S-DIVA suggests a unique vicariant event (node 20) that results in the split of *O. gliroides* from the rest of the component species (Chilean clade). This early split of *O. gliroides* that dates from the Late Miocene (6.07 ± 1.34 Ma) (Opazo, 2005), is also supported by studies on crani-odontal anatomy, which shows similarities with late Miocene representatives suggesting that *O. gliroides* belongs to an early offshoot and consequently is the most primitive living octodontid (Verzi, 2001). While *O. gliroides* extends its distribution along the High desert Puna and High Monte Prepuna of Argentina, Chile and Bolivia, the remaining species of clade II are mostly restricted to scrublands and Valdivian Temperate Forest in Chile. However, by the Late Miocene, the Andes cordillera was already largely uplifted (14–10 Ma) (Ortiz-Jaureguizar & Cladera, 2006), and this basal split could be the

result of the contrasting environmental conditions and putative barriers between eastern and western sides of southern South America created as the Andes uplifted. Thus, for example, the uplift of the Sierras Pampeanas (<5 Ma) led to a rain shadow effect, which intensified the aridity and xeric conditions on the east side of the Andes (i.e. Monte desert ecoregion) while the western side remained more mesic (Ortiz-Jaureguizar & Cladera, 2006; Veblen, Young & Orne, 2007).

For clade I, Fitch and WAAA methods indicated the high Monte as the ancestral area. On the other hand, S-DIVA and BBM analyses showed ambiguous results indicating most areas (A, B, C, D and F) as possible ancestral areas. In the case of clade II, the High Monte, Central Andean Puna, Central Andean Dry Puna, Valdivian Temperate forest or all these areas together, showed the same probability of being the ancestral areas under the different methods with later dispersals to area H (Chilean scrublands). Our analyses provides evidence for diversification, dispersal and colonization events during the mid-Pliocene to mid-Pleistocene, previously reported by Opazo, 2005, for the octodontid species occurring in Chile, and this is congruent with the geologic history of the Andes. During the Pliocene–Pleistocene, the Andes was already a barrier up to the 37° south latitude, blocking dispersal from the east (i.e. from Argentina). The dispersal process of the ‘Chilean clade’ matches the paleoclimatic fluctuations of global cooling and warming periods, and associated vegetation changes during the Pleistocene in the southern temperate ecosystem (Markgraf, McGlone & Hope, 1995).

The ecomorphological diversity of the Octodontidae appears associated with a geographic subdivision within the family, with fossorial and semifossorial forms (*Spalacopus* and *Aconaemys*), and the terrestrial generalist (*Octodon*) adapted to Mediterranean sclerophyllous woodlands and forests and semiarid open scrublands in central Chile, and saxicolous (*Octomys*) and semifossorial xeric adapted species (*Tympanoctomys*, *Pipanaoctomys*) inhabiting lowland aridlands in Argentina, and *Octodontomys* inhabiting pre-Andean Prepuna and Puna habitats in northern Argentina, southern Bolivia and north-eastern Chile (Contreras *et al.*, 1987). This diversity of environmental conditions is accompanied by variation at physiological (Díaz & Ojeda, 1999), genetic (Gallardo, 1992), and behavioral (Giannoni, Borghi & Ojeda, 2000; Torres *et al.*, 2003) levels. Different hypotheses regarding the role of major climate change during Plio-Pleistocene have been proposed to explain the distribution and ecological diversity of the family (Mares, 1975; Reig, 1986; Contreras *et al.*, 1987; Honeycutt *et al.*, 2003). They range from early adaptation to montane habitats (Miocene–Pliocene) with recent colonization of Andean regions (mid-Pliocene) (Mares, 1975; Reig, 1986) to ancestral ground-dwelling forms living in forest and scrub habitat (Reig, 1986; Contreras *et al.*, 1987). Honeycutt *et al.* (2003) analyzed several ecological traits and concluded that the adaptation for arid environments occurred early in the Octodontidae. We propose an hypothetical ancestral proto-octodontid, adapted to desert environments, during the early evolution of the Octodontidae in the Late Miocene–Pliocene, as was earlier proposed by Honeycutt *et al.* (2003) and Mares (1975). This proto-octodontid could have been a

saxicolous, generalist terrestrial or semifossorial because those modes of substrate utilization appear as hypothetical ancestral state. This is unsurprising, as those modes of substrate utilization characterize the octodontid species inhabiting xeric environments (i.e. *Octodontomys* in the central arid Andes; *Octomys*, *Tympanoctomys* and *Pipanaoctomys* in Monte and Patagonian desert areas). The ecological diversification of species in clade I is associated with the last uplift of the Andes (Diaguita phase) during the Pliocene (4.28 ± 1.08 Ma). The uplift of the central Andes and Pampean Mountains had marked ecological consequences enhancing the xeric conditions of the northern Monte Desert through a rain shadow effect (Ortiz-Jaureguizar & Cladera, 2006; Veblen *et al.*, 2007). Thus, divergence at the generic level has been accompanied by specialization for desert existence of the member species of clade I through marked changes in morphology, diet, physiology and behavior (Ojeda *et al.*, 1996, 1999; Mares *et al.*, 1997; Díaz & Ojeda, 1999; Giannoni *et al.*, 2000; Berman, 2003; Ebensperger *et al.*, 2008). Whereas *Octomys* developed saxicolous life habits, with narrow geographic distribution and specialization for life and burrowing in rock formations of the Monte desert (Ebensperger *et al.*, 2008; Sobrero *et al.*, 2010), its sister genera (i.e. *Pipanaoctomys* and *Tympanoctomys*) are semifossorial and strongly associated to salt basin habitats. Furthermore, whereas *Pipanaoctomys* is restricted to one particular salt pan locality in the Monte desert, ‘Salina de Pipanaco’, its sister species, *T. barrerae* ranges into the cold Patagonian steppe, with naturally patchy distribution and genetically distinct populations (Gallardo *et al.*, 2009; Ojeda, 2010). The colonization success and expanded range of *Tympanoctomys*, in contrast to *Octomys*, *Pipanaoctomys*, and *Salinoctomys* (the latter not treated here), has been suggested to be the result of a set of behavioral, ecomorphological and physiological features that allows better utilization of salt basin, open xeric habitats and hypersaline food resources (Mares *et al.*, 1997; Ojeda *et al.*, 1999; Gallardo *et al.*, 2007), enabling the species to occupy a new adaptive zone (Simpson, 1944).

The ecological diversification among species in clade II into semi-fossorial and fossorial forms occurred later in octodontid evolution. Previous studies have shown that the fossorial *Spalacopus* evolved to fully subterranean life and acquired numerous morphological traits for a fossorial mode at about 2.2 million years ago (Lessa *et al.*, 2008). Semifossorial species in the genus *Aconaemys* are sister to the fossorial species, *Spalacopus cyanus*, with *Aconaemys* being paraphyletic relative to *Spalacopus* (Honeycutt *et al.*, 2003). The ambiguity of this relationship could suggest that fossorial habits of *Spalacopus* may have arisen within this group. Although the evolutionary origin of fossorial habits in mammals has been associated with the expansion of an open country biota since the Miocene (Nevo, 1979), subterranean mammals inhabit a great range of environmental and climatic conditions. In the case of *Aconaemys* and *Spalacopus*, the evolution toward semi-fossorial and fossorial habits could be associated with the appearance of novel habitats (i.e. Chilean Scrublands), which emerged after the Andean uplift. Subsequently, the Pleistocene paleoclimate cycled between global cool and warm

phases, and was accompanied by vegetational changes in the southern temperate ecosystems (Markgraf *et al.*, 1995), promoting the development of new habitats.

In modern-day habitats, the adaptive radiation of caviomorph rodents in South America has resulted in 13 families and 246 species (Upham & Patterson, 2012). One of these lineages, the Octodontidae, reflects a dynamic scenario on both sides of the Andes, where the interplay between the history of the area and that of the lineage resulted in their diversification in eight living genera across arid and semiarid landscapes, and a wide range of ecological, morphological, behavioral, physiological and ecological attributes. Our results draw attention to the ancestral scenario of octodontids evolution in the High Monte ('protopuna' of Reig, 1981), and bring to light the ecological diversification of their species, ranging from a more generalized terrestrial mode of life to fossoriality. Thus, the evolution of octodontid rodents reflects a dynamic scenario linked to the Andes uplift and associated environmental changes on both sides of the high Andean Cordillera.

In conclusion, future investigations on biogeographical and ecological diversification should look for a closer integration among phylogeny, distribution and ecological understanding (Losos, 1996; Wiens & Donoghue, 2004). Despite of the gaps in the current knowledge of caviomorph rodent species, our findings suggest that the phylogenetic matrix offers a sound background for further research and hypothesis testing on the geographical distribution, diversification, and evolution of ecological attributes (e.g. macroniches), as well as an important integral component to explore into the ultimate causes of ecological radiation along the niche axis of habitat and diet and species coexistence at the community level.

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