Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Short Communication

Filling phylogenetic gaps and the biogeographic relationships of the Octodontidae (Mammalia: Hystricognathi)

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ABSTRACT

Endemic to South America, octodontid rodents are remarkable by being the only mammal taxa where allotetraploidy has been documented. The taxon's extensive morpho-physiological radiation associated to niche shifts has allowed testing phylogeographic hypotheses. Using maximum likelihood and Bayesian inference analyses, applied to all nominal species of octodontids, phylogenetic reconstructions based on sequences of 12S rRNA and growth hormone receptor gene are presented. Species boundaries were determined by coalescent analyses and divergence times among taxa were estimated based on mutation rates. Two main clades associated to the Andean orogenesis were recognized. The essentially western clade comprises genera *Aconaemys*, *Octodon*, *Spalacopus*, and *Octodontomys* whereas the eastern one included genera *Octomys*, *Pipanacoctomys*, *Salinoctomys*, and *Tympanoctomys*. Genetic relationships, coalescent analyses, and genetic distance supported the specific status given to *Octodon pacificus* and that given to *Pipanacoctomys aureus* as a species of *Tympanoctomys*. However, these analyses failed to recognize *Salinoctomys loschalchalerosorum* as a valid taxon considering its position within the diversity of *Tympanoctomys barrerae*. Although the origin of genome duplication remains contentious, the coincidence of the basal clade split with distinctive modes of karyotypic evolution across the Andes emphasizes the role of physiographic barriers and westerlies in shaping different edaphological conditions, selective grounds, and concomitantly distinct adaptations within the octodontids.

1. Introduction

The Octodontidae has evolved an extensive morpho-physiological radiation (Mares and Ojeda, 1982; Contreras et al., 1993; Olivares et al., 2004), karyotypic evolution (George and Weir, 1972; Gallardo, 1992) and extreme genome size variation (Gallardo et al., 1999, 2003). These contrasting features have resulted in the recognition of 14 nominal species distributed from coastal Central Chile to the eastern slopes of the Andes including Argentina and Bolivia, between 15°S and 43°S (Gallardo et al., 2007, 2009; Verzi et al., 2015a). The Octodondidae includes five monotypic genera (*Octodontomys*, *Octomys*, *Pipanacoctomys*, *Salinoctomys*, *Spalacopus*) and three polytypic ones (*Tympanoctomys*, *Aconaemys*, and *Octodon*; Gallardo et al., 2007; Teta et al., 2014), where desert specialists, above-surface dwellers, fossorial, and strictly subterranean forms can be found (Gallardo et al.,

2007). The octodontids exhibit intra- and interpopulational karyotypic stability, but extensive interspecific differences ranging from 2n = 38 (*Octodontomys gliroides*), to 2n = 102 (*Tympanoctomys barrerae*; Gallardo et al., 2007). Germinal and somatic DNA content estimates (Gallardo et al., 2003), gene copy number (Gallardo et al., 2004, 2006), and genome *in situ* hybridization (Suárez-Villota et al., 2012) support whole genome duplication in the red vizcacha rat *T. barrerae*.

The molecular phylogenetic relationships of caviomorph rodents have supported the Octodontidae's monophyly (Honeycutt et al., 2003; Upham and Patterson, 2012, 2015). Nevertheless, the relationships within some genera of octodontids have been so far hampered by the absence of genetic data for the insular *Octodon pacificus* (Hutterer, 1994) and probably by the analysis of only one specimen per species. Here, we included *O. pacificus*, the recently described *T. kirchnerorum* (Teta et al., 2014), and at least two individuals for most species. Thus, the complete phylogeny of the octodontid rodents using concatenated partial sequences of the mitochondrial 12S rRNA and the nuclear growth hormone

receptor (GHR) genes is presented. We aim to resolve the phylogenetic relationships within the Octodontidae and to determine the taxonomic status of all its nominal species, with special emphasis in *Octodon pacificus*, and *Salinoctomys loschalchalerosorum*, a desert dweller known only from its original description (Mares et al. (2000). By using specific mutation rates and a relaxed Bayesian method for multilocus data, we evaluated the trends and rhythms in the evolution of the octodontids and by using multilocus coalescent-based methods, we estimated its species boundaries. Finally, the adaptive radiation of the family and its correlation with the Andean orogenesis and Pleistocene climate shifts is further discussed.

2. Material and methods

Sequences of 12S rRNA and GHR genes already reported were used to build the phylogenetic relationships within the Octodontidae (Table S1). To these data sets, new GHR and 12S rRNA sequences obtained from *O. pacificus*, *T. kirchnerorum*, *T. barrerae*, and *A. porteri* were included (Table S1, gray cells). By using conventional extraction procedures for ancient tissue (Paabo, 1989), whole genomic DNA was extracted from *O. pacificus* paratype (ZFMK 92.383; Hutterer, 1994). By conventional phenol-chloroform method (Sambrook et al., 1989), DNA was extracted from liver of nine *T. kirchnerorum*, 13 *T. barrerae,* and one *A. porteri,* from the Mammal Tissue Collection, Universidad Austral de Chile (see vouchers in Table S1). Fragments of 12S rRNA and GHR genes were amplified using the primers and PCR conditions described by Honeycutt et al. (2003). Nucleotide sequencing was conducted by Macrogen Inc. Sequences obtained were deposited in GenBank under accession numbers KX646495–KX646539.

Sequences were checked with Proseq v2.91 (Filatov, 2002), and multiple alignments were done with MAFFT v5.0 (Katoh et al., 2005) under the iterative model of global pairwise alignment (G-INSi). The evolutionary distance between pairs of sequences was estimated with MEGA v6.0.6 (Tamura et al., 2013), using Kimura 2-parameter model with rate variation among sites. The goodness of fit of this model to the concatenated data set was measured also in MEGA v6.0.6 by the Bayesian information criterion (BIC) and corrected by Akaike information criterion. By using each single gene sequence matrix and concatenated gene datasets, phylogenetic reconstructions using maximum likelihood (ML) and Bayesian inference (MCMC) were conducted. For best-fit partitioning schemes and models of nucleotide substitution employed in ML and MCMC analyses, BIC implemented in PartitionFinder v1.1.0 was used (Lanfear et al., 2012). Three ML analyses for topology convergence were performed with GARLI v2.1 (Bazinet et al., 2014) and their statistical nodal support was estimated by non-parametric bootstrap with 1000 pseudoreplicates (Felsenstein, 1985). We used MrBayes v3.2.6 for two MCMC analyses with independent runs on random trees and 10^7 generations sampled every 100 steps (Ronquist and Huelsenbeck, 2003). Through Tracer v1.6 (Rambaut and Drummond, 2009), the stationary phase was checked following Nylander et al. (2004). Sample points prior to the plateau were discarded as burn-in and the remaining trees were combined to find the maximum *a posteriori* probability estimated from the phylogeny. Branch support was estimated by Bayesian posterior probabilities.

Divergence times were estimated with BEAST v1.8.3 (Drummond and Rambaut, 2007), using the concatenated matrix of both gene sequences and nucleotide substitution models provided by PartitionFinder v1.1.1 (Lanfear et al., 2012). Mutation rates of 0.654% and 0.183% per million years for 12S rRNA and GHR genes, respectively, were used. These mutation rates were also estimated with BEAST, using (1) 12S rRNA and GHR sequences

used by Opazo (2005), (2) The GHR + I + G mutation model for 12S rRNA and the HKY + G for GHR; and (3) the caviomorph radiation at 41 Myr as the calibration point (Antoine et al., 2012). This calibration point was implemented as lognormal prior distributions with means of 0.01 and standard deviations of 0.6. We provided a minimum bound for each distribution such that the 5% quantile corresponds to the minimum age of the fossil while the 95% interval allows both for the uncertainty of the fossil age and for the incompleteness of the fossil record. To estimate both divergence times and mutation rates, uncorrelated lognormal relaxed-clock models were used to allow rate variation among branches (Drummond et al., 2006). Bayes factor analysis (Li and Drummond, 2012) indicated that this model received decisive support compared to an uncorrelated exponential or a strict-clock model. Markov chains in BEAST were initialized from the tree obtained from MCMC analyses to calculate posterior parameter distribution, including the tree topology and divergence times. BEAST analyses to estimate divergence times and mutation rates were run for 10^7 generations, sampling every 1000th generation. The first 10% of samples were discarded as burn-in. Convergence to the stationary distribution and acceptable mixing were investigated using Tracer v1.6 (Rambaut and Drummond, 2009).

STEM multilocus coalescent-based method (Kubatko et al., 2009; Carstens and Dewey, 2010) and Bayesian approach (BPP; Yang and Rannala, 2010) were applied to species delimitation, following the recommendations of Harrington and Near (2012) and Yang (2015), respectively.

3. Results and discussion

After the amplification of 953 bp of the 12S rRNA and 888 bp of GHR totalizing 223 variable positions and 184 informative sites, the models selected for the phylogenetic analyses were GHR + I + G for 12S rRNA, and HKY + G, HKY + G, and K80 + G for each codon position, for GHR. The likelihood and Bayesian tree topologies obtained from independent and concatenated dataset were congruent among them and with previous phylogenetic studies (Figs. 1A and S1; Gallardo and Kirsch, 2001; Honeycutt et al., 2003). The monophyly of the Octodontidae was strongly supported (bootstrap: 97.6%, Bayesian posterior probabilities: 0.99). Two main lineages (with high bootstrap and posterior probability supports) associated to the Andean orogenesis were recognized (Fig. 1A). The essentially western lineage was composed by genera *Octodon*, *Spalacopus*, *Aconaemys*, and *Octodontomys* whereas the eastern one included desert specialist genera *Octomys*, *Tympanoctomys*, *Pipanacoctomys*, and *Salinoctomys* (Fig. 1A and B). This result is consistent with vicariant effects proposed in the eco-evolutionary hypothesis of Contreras et al. (1987) and with the model of karyotypic evolution that assumes a bidirectional trend from an ancestral 58-chromosome lineage (Gallardo, 1992; Gallardo et al., 2007). Indeed, the clade distributed essentially on the western slope of the Andes retained diploid numbers similar to, or lower than, the ancestral chromosomal form (Fig. 2). In the opposite direction of karyotypic evolution, genome duplication and the doubling of both diploid and fundamental numbers of arms characterizes the desert-adapted genera *Tympanoctomys* and *Pipanacoctomys* (Fig. 2; Gallardo et al., 2003, 2004). On the other hand, the well-supported inclusion of *Octodontomys gliroides* in the essentially western clade corroborates previous analyses (Gallardo and Kirsch, 2001; Honeycutt et al., 2003; Upham and Patterson, 2015; Verzi et al., 2016) and contradicts previous allegations based only on cranio- dental morphology (Verzi, 2001; Verzi et al., 2014; Candela, 2016). Having in mind that the phylogenetic position of *O. gliroides* remained uncertain in the two-gene analyses using one individual of this species (Upham and Patterson,
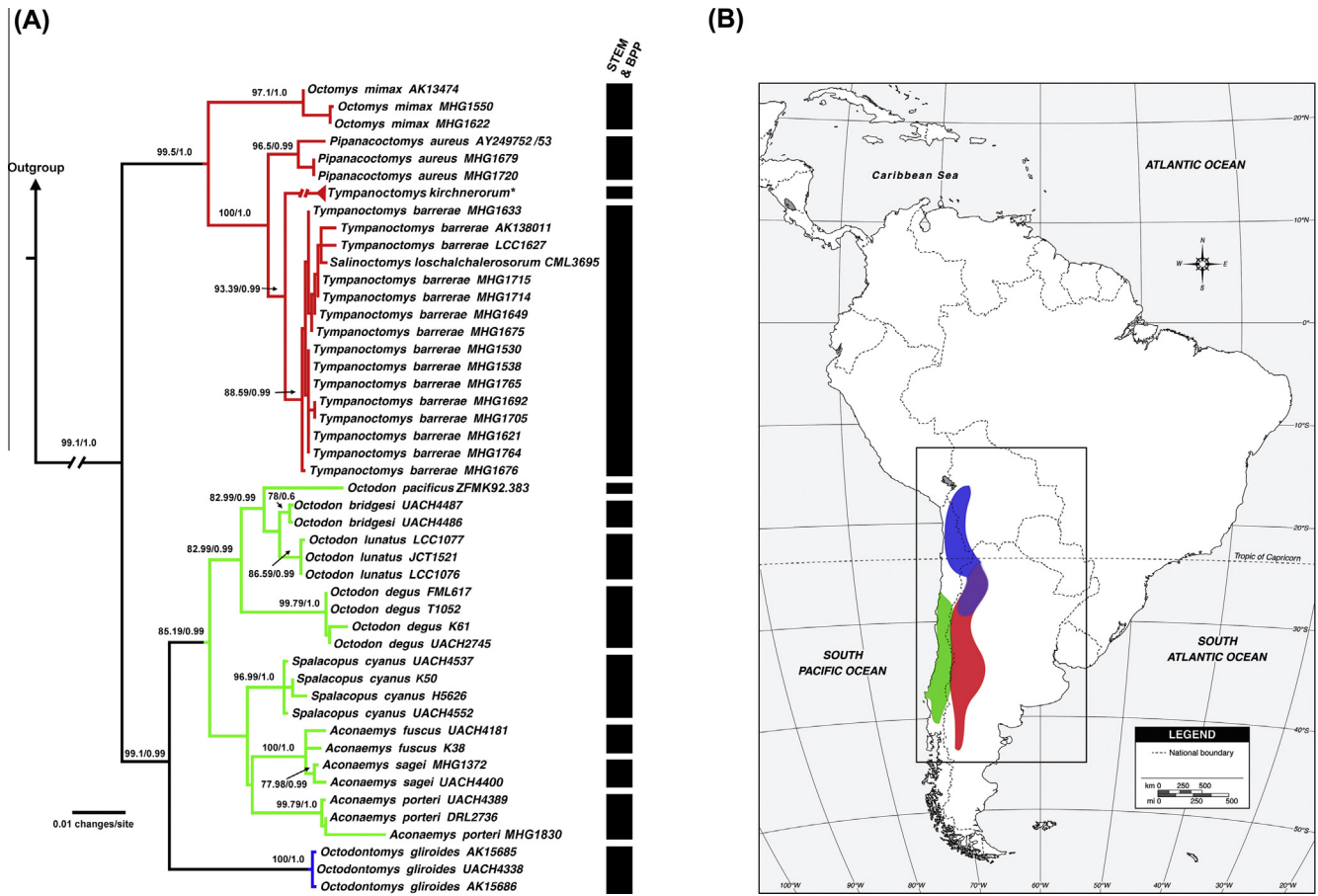
Fig. 1. Phylogenetic analyses and distribution of the Octodontidae. (A) Maximum likelihood tree reconstructed using concatenated 12S rRNA and growth hormone receptor genes. Numbers above the nodes represent ML bootstrap values/Bayesian posterior probabilities. Black bars (on the right) indicate species recognized by STEM and BPP analyses. (∗) The nine specimens of *T. kirchnerorum* were collapsed and their respective identification numbers are provided in Table S1. (B) Maps detailing the geographic distribution of the main clades of octodontids, the colors match those indicated in clades of ML tree. The violet color indicates shared geographic distribution between red and blue clades. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2012), our results highlight the importance of increasing sample size to prevent long branch attraction and conflicting phylogenetic trees (Hedtke et al., 2006; Gatesy et al., 2007). In fact, phylogenetic uncertainties associated to *O. gliroides* were solved when molecular or morphological characters were added (Upham and Patterson, 2015; Verzi et al., 2016).

The phylogenetic relationships of desert specialists using independent and concatenated data sets depict *P. aureus* external to *T. kirchnerorum*, *T. barrerae*, and *S. loschalchalerosorum* (Figs. S1 and 1A), concordant with previous analyses (Gallardo et al., 2013; Upham and Patterson, 2015). Taken together, the position of *S. loschalchalerosorum* within the *T. barrerae*'s clade (Fig. 1A) and the negligible genetic distance between them (0.3%; range: 0–0.64%) do not support *S. loschalchalerosorum* as a valid taxon. Species delimitation analysis further supports this conclusion (Fig. 1A). The phylogenetic relationships and taxonomic validity of *S. loschalchalerosorum* have been questioned since its original morphological description based on two specimens, considered as the sister taxon to *P. aureus* (Mares et al., 2000). Subsequent morphological and molecular analysis placed *Tympanoctomys-Salinoctomys* as sister taxa, with *Pipanacoctomys* external to them (Barquez et al., 2002; Upham and Patterson, 2015). Our molecular analyses of *T. barrerae*'s specimens encompassing five populations also support the close relationship proposed by Barquez et al. (2002) and Upham and Patterson (2015), but refuses the full recognition of *Salinoctomys* as a valid taxon (Fig. 1A). On the other hand,

genetic distance among desert specialist genera average only 1.79% (range: 2.30–0.54%), contrasting with the much higher value of the remaining genera (5.26%; range: 2.53–8.64%) and falling within the range of interspecific comparisons (mean: 2.38%, range: 0.65–4.13%). Following this criterium, genetic distance data suggests *Pipanacoctomys* and *Salinoctomys* to be included within *Tympanoctomys*, as suggests Verzi et al. (2015a). In short, our data analyses support the notion that *Salinoctomys* and *Pipanacotomys* are not distinct from *Tympanoctomys* although for Verzi et al. (2015a) *S. loschalchalerosorum* is considered a valid species.

Consistent with previous phylogenetic reconstructions (Gallardo and Kirsch, 2001; Honeycutt et al., 2003), *Octodon* was recovered as sister to the unresolved *Spalacopus/Aconaemys* clade (Fig. 1A). In fact, our data supports the monophyly of *Spalacopus* and *A. porteri* (bootstrap: >95, Bayesian posterior probabilities: 0.99) although the monophyly of other *Aconaemys* species remain unsupported (Fig. 1A) and *A. fuscus* appears paraphyletic (Fig. 1A). Nevertheless, interspecific recognition between *A. fuscus* and *A sagei* is supported by differences in diploid number (Fig. 2; Gallardo, 1992) and penial morphology (Contreras et al., 1993). Thus, additional sequences will be required to elucidate the phylogenetic relationships among the *Aconaemys* species.

The early divergence of *O. degus*, followed by *O. pacificus* characterizes the *Octodon* clade in which *O. lunatus*, and *O. bridgesi* form a derived sister group (Fig. 1A). These species, recognized as valid by the delimitation analysis (Fig. 1A), share pairwise distances (K2P)
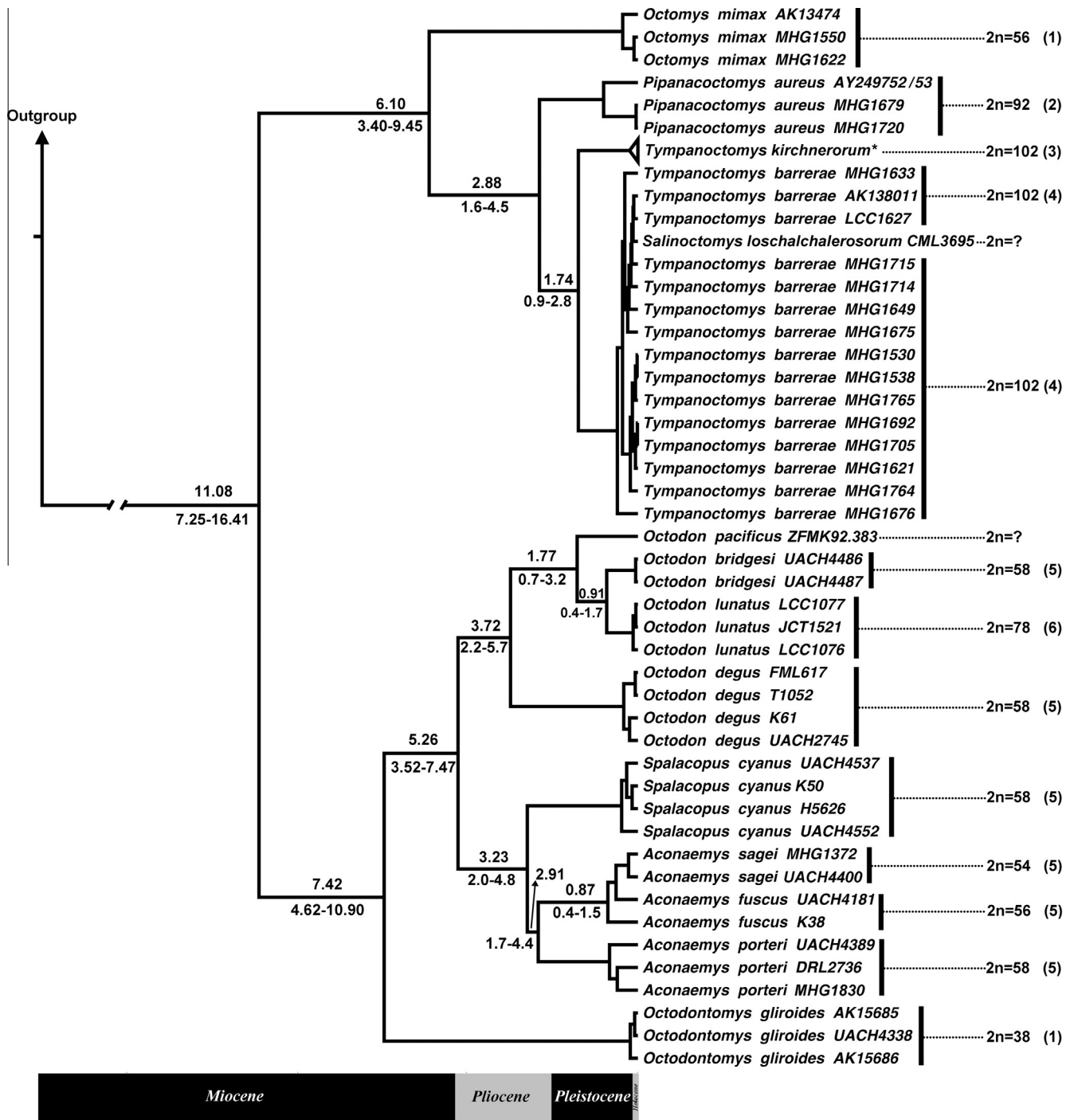
Fig. 2. Divergence time estimates for the Octodontidae using a relaxed molecular clock. Values represent the divergence time in millions of years (above the branches) and 95% credible intervals (below the branches). Geological times are reported according to Walker et al. (2013). Diploid numbers indicate on the right of the tree were taken from (1) Contreras et al. (1994), (2) Gallardo et al. (2004), (3) Gallardo et al. (2009), (4) Gallardo et al. (2006), (5) Gallardo (1992), and (6) Spotorno et al. (1995). (∗) The nine specimens of *T. kirchnerorum* were collapsed and their respective identification numbers are provided in Table S1.

ranging from 0.6% to 2.7%. *O. pacificus* was captured in 1959 and described as a new species based on morphological data (Hutterer, 1994) but no further records have been documented ever since (Pefaur and Yañez, 1980; Saavedra et al., 2003). The high genetic distance of *O. pacificus* relative to the remaining congenerics (2.3%) indicate its distinctiveness. Hence, the phylogenetic relationships, species delimitation analyses, and pairwise distances support the distinctive taxonomic status of *O. pacificus*, in spite of its morphological similarity with *O. bridgesi* (Saavedra et al., 2003).

Divergence time calibrations using mutation rates are slightly older than previous ones (Opazo, 2005; Gallardo et al., 2013) and congruent in general terms with Gallardo and Kirsch (2001), Honeycutt et al. (2003), Upham and Patterson (2012, 2015), and Verzi et al. (2016) (Fig. 2, Table S2). Concordance between our calibration and those of Upham and Patterson (2015) and Verzi et al. (2016) rests on the use of a more ancient caviomorph fossil, as the one recently found in Yahuarango Formation (Antoine et al., 2012). The octodontid' split into an eastern and western clade is esti-

mated at 11.08 (7.25–16.41) Myr, coinciding with the vicariant effect that triggered new ecological settings for the evolution of caviomorph rodents, as derived by the uplift of the Andes (Pascual et al., 1996; Pascual, 2006; Upham and Patterson, 2012, 2015). By affecting water vapor transportation along western South America, the dramatic effects of plate tectonics resulted in different climatic regimes across and along the mountain chain (Hartley, 2003; Hoorn et al., 2010). This basal split could be the result of the contrasting environmental conditions and barriers across the eastern and western slopes of the Andes, as suggested previously (Contreras et al., 1987; Ojeda et al., 2013) The divergence between the *Octodontomys* lineage and the essentially western species is estimated at 7.42 (4.62–10.9) Myr, whereas the differentiation process within this western clade started at 5.26 (3.52–7.47) Myr (Fig. 2). These estimations are consistent with the intensification of the tectonic processes initiated during the upper Miocene and Pliocene (Hinojosa and Villagrán, 1997). The uplift of the Andes changed the physiographic context that generated new, more open biomes (Pascual and Jaureguizar, 1990; Le Roux, 2012). It has been suggested that diverse morphological adaptations of octodontids to the new emerging environments, reflect responses to these Cenozoic environmental changes (Verzi et al., 2015b, 2016).

The origin of the polyptypic genera *Aconaemys* and *Octodon* is estimated at 2.91 (1.7–4.4) and 3.72 (2.2–5.7) Myr, respectively whereas the split between *O. pacificus* and *O. bridgesi/O. lunatus* is around 1.77 (0.7–3.2) Myr (Fig. 2). The oldest deposit of Mocha island are dated from the Eocene and Miocene (Tavera and Veyl, 1958) whereas extensive terraces from Pliocene and Pleistocene characterize more recent settings (Melnick et al., 2003). Although the arrival of *O. pacificus* to the island remains unknown, these large terraces might have been a suitable habitat for its settlement and for its differentiation from the three continental *Octodon* species (Fig. 1). The ancestral stock of the desert dwellers dates back to 6.10 (3.4–9.4) Myr, coinciding with the origination and subsequent division of salt flats in northwestern of Argentina (Mares et al., 2000). The divergence between *Tympanoctomys* and *Pipanacoctomys* is estimated at 2.88 (1.6–4.5) Myr. Currently, these taxa are distributed in extreme saline habitats on piedmonts, salt flats and basins, from the Pipanaco salt flat (27° S) to Patagonia (43° S) (Gallardo et al., 2007, 2009; Ojeda et al., 2013). Considering this estimate and the present distribution of the desert dwellers, its ancestor could have been affected by periodic latitudinal and altitudinal shifts of the glacial ice sheets during the Pleistocene (Dynesius and Jansson, 2000; Patterson, 2010). Thus, suitable Pleistocene habitats probably contracted from south to north during periods of glacial advance, whereas distributional ranges shifted westward and southward again, during glacial retreats and warming (Verzi et al., 2002; Gallardo et al., 2013). Accordingly, glacial advances during the ice ages probably fragmented and isolated populations. With the retreat of ice during interglacial periods, divergent lineages may have re-established contact in suture zones (Schönswetter et al., 2005). Such an scenario probably accounts for the hybrid origin of *T. barrerae* (Suárez-Villota et al., 2012; Gallardo et al., 2013), the structured genetic pattern of several mammals including octodontids (Himes et al., 2008; González-Ittig et al., 2010; Mapelli et al., 2012), and for the origin of the isolated species, *T. kirchnerorum* (Gallardo et al., 2013; Teta et al., 2014).

This study stress the importance of having a complete phylogeny of this endemic, peculiar group to fill in this fuzzy picture of octodontid relationships and to get a better understanding of genome duplication for future genomic studies (Gallardo et al., 1999; Suárez-Villota et al., 2012). It will also provides new insights into the evolution of octodontids and its temporal speciation processes dynamics associated to environmental changes derived from the Andes uplift and patterns of Pleistocene glaciations.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2016.08.015.

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