

Early evolutionary differentiation of morphological variation in the mandible of South American caviomorph rodents (Rodentia, Caviomorpha)

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Abstract

Caviomorphs are a clade of South American rodents recorded at least since the early Oligocene (> 31.5 Ma) that exhibit ample eco-morphological variation. It has been proposed that phylogenetic structure is more important than ecological factors for understanding mandibular shape variation in this clade. This was interpreted as a result of the long-standing evolutionary history of caviomorphs and the early divergence of major lineages. In this work, we test this hypothesis through the analysis of morphological variation in the mandible of living and extinct species and compare this information with that obtained through comparative phylogenetic analyses. Our results support the hypothesis of early origin of mandibular variation; moreover, they suggest the conservation of early differentiated morphologies, which could indicate the existence of constrained evolutionary diversification.

Introduction

The South American hystricomorphs ('caviomorphs') are the most ecologically diverse rodent clade and indeed one of the most varied groups of South American mammals (Mares & Ojeda, 1982; Nowak, 1991). Caviomorphs are considered monophyletic (Vilela *et al.*, 2009 and literature therein), and the consensus is that they probably came from Africa by rafting during the late Eocene (Vucetich *et al.*, 2010 and literature therein). Their fossil record in South America goes back to the early Oligocene (> 31.5 Ma; Flynn *et al.*, 2003; Ré *et al.*, 2010; Vucetich *et al.*, 2010) or even the late Eocene (Frailey & Campbell, 2004; although see Shockey *et al.*, 2004). At least since the late Oligocene Deseadan (24.5–29 Ma; Flynn & Swisher, 1995), the four superfamilies that make up the group – Erethizontoidea, Caviioidea, Chinchilloidea

and Octodontoidea – are recognized in the fossil record essentially on the basis of dental characters (Wood & Patterson, 1959; Patterson & Wood, 1982; Shockey *et al.*, 2009; Vucetich *et al.*, 2010).

In accordance with the wide ecological diversity of extant caviomorphs, great disparity has been detected in their morphology at craniomandibular, dental (Vassallo & Verzi, 2001; Olivares *et al.*, 2004; Vucetich *et al.*, 2005; Perez *et al.*, 2009; Alvarez *et al.*, 2011) and post-cranial (Morgan, 2009) levels. Although part of this disparity has been shown to be related to ecological factors at lower levels of phylogenetic divergence (Perez *et al.*, 2009), morphological variation has shown strong phylogenetic structure and weaker ecological signal at high taxonomic levels (Morgan, 2009; Alvarez *et al.*, 2011). In a recent analysis that encompassed a large number of caviomorph clades (Alvarez *et al.*, 2011), phylogenetic structure was found to be more important than ecological factors for understanding major differences in mandibular shape among major clades of caviomorphs. This was interpreted as a result of the long-standing evolutionary history of caviomorphs and the early divergence of superfamilial clades. In this context, the hypothesis was advanced that

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the major pathways of mandible specialization among major caviomorph clades were established early in the history of this rodent group, and this would explain the observed strong phylogenetic structure of the mandibular morphology, mainly at higher levels of phylogenetic divergence.

In this work, we examine this hypothesis through an analysis of the morphological variation of the mandible in living and extinct caviomorph rodents, and we compare these results to those obtained in a phylogenetic comparative context. A combination of comparative phylogenetic methods and the direct study of the fossil record of a clade is one of the most efficient approaches to test the hypotheses of morphological divergence between lineages (Gavrillets & Losos, 2009). Unlike the case of other phylogenetic groups, the palaeontological record of caviomorphs is unusually rich and provides abundant information on their morphological variation (Losos & Mahler, 2010; Pérez & Vucetich, 2011; Vucetich *et al.*, 2011). Fossil taxa provide direct information about the geological time at which the overall patterns of morphological diversity of the major evolutionary lineages could have been established. Given the early divergence of the major caviomorph lineages (Vucetich *et al.*, 1999) and the phylogenetic structure observed in the morphological variation of mandible in living representatives, the

morphology of fossils could be expected to show a pattern and degree of variation similar to that of their more closely related living species.

Materials and methods

Two datasets were used in this work. The first one was a sample of 126 mandibles of 19 living species belonging to 17 genera and seven families, representing three of the four caviomorph superfamilies (Cavioidea, Chinchilloidea and Octodontoidea; Table 1). The second dataset included the fossil specimens corresponding to 19 hemimandibles representing 12 genera and six families of the three mentioned superfamilies (Table 1; Appendix 1). The systematics of living species follows Woods & Kilpatrick (2005) and Dunnum & Salazar-Bravo (2010). Assignment of the studied fossils to families and superfamilies follows Vucetich *et al.* (2011). In contrast to the latter revision, the genera †*Eocardia* and †*Schistomys* belonging to the stem group of Caviidae (Woods & Kilpatrick, 2005; Pérez & Vucetich, 2011) are here included in this family and not in the separate paraphyletic family 'Eocardiidae'. The taxonomic categories used in analyses are considered to be monophyletic and are supported by recent maximum likelihood and parsimony analyses on molecular data (Huchon & Douzery, 2001;

Table 1 Taxa studied, number of specimens examined (*N*) and habits assigned to each species. Systematics follows Woods & Kilpatrick (2005) and Dunnum & Salazar-Bravo (2010) for extant caviomorph and Vucetich *et al.* (2011) for extinct caviomorphs. Definition of habit categories follows Lessa *et al.* (2008).

Taxa	<i>N</i>	Habits	Taxa	<i>N</i>	Habits
Cavioidea			Octodontoidea		
Caviidae			Echimyidae		
<i>Cavia aperea</i>	8	Epigeant*	<i>Myocastor coypus</i>	10	Epigeant*
<i>Microcavia australis</i>	11	Fossorial*	<i>Proechimys guyannensis</i>	4	Epigeant‡
<i>Galea musteloides</i>	10	Epigeant*	† <i>Adelphomys</i>	1	?
<i>Dolichotis patagonum</i>	10	Epigeant*	† <i>Spaniomys</i>	3	?
<i>Pediolagus salinicola</i>	4	Epigeant*	Octodontidae		
<i>Hydrochoerus hydrochaeris</i>	4	Epigeant*	<i>Aconaemys porteri</i>	3	Fossorial‡
† <i>Eocardia</i>	2	?	<i>Aconaemys sagei</i>	1	Fossorial‡
† <i>Schistomys</i>	1	?	<i>Ctenomys australis</i>	9	Subterranean‡
Dasyproctidae			<i>Octodontomys gliroides</i>	7	Fossorial‡
<i>Dasyprocta</i> sp.	10	Epigeant*	<i>Octodon degus</i>	2	Fossorial‡
† <i>Neoreomys</i>	1	?	<i>Octodon bridgesi</i>	4	Fossorial‡
Chinchilloidea			<i>Spalacopus cyanus</i>	4	Subterranean‡
Chinchillidae			† <i>Caviocricetus</i>	1	?
<i>Chinchilla</i> sp.	5	Epigeant†	† <i>Prospaniomys</i>	1	?
<i>Lagidium viscacia</i>	10	Epigeant†	† <i>Protacaremys</i>	2	?
<i>Lagostomus maximus</i>	10	Fossorial*	† <i>Protadelphomys</i>	3	Fossorial?§
† <i>Prolagostomus</i>	1	?	† <i>Sciomyx</i>	1	?
Neoeplemidae					
† <i>Perimys</i>	2	?			

*Nowak (1991).

†Spotorno *et al.* (2004).

‡Lessa *et al.* (2008).

§Vucetich & Verzi (1991).

Blanga-Kanfi *et al.*, 2009; Honeycutt, 2009; Vilela *et al.*, 2009; Rowe *et al.*, 2010). Only adult specimens, defined by the presence of a functional third molar, were included. The absence of trabeculae on the bone surface was used as an additional indicator of adult condition (Montalvo, 2002). Fossils were selected based on both their age (no younger than the late–early Miocene Santacrucian, > 16 Ma; Flynn & Swisher, 1995; Appendix 2) and their preservation state allowing to analyse the alveolar region of mandible. Analysed materials are deposited in the mammalogical and palaeontological collections of Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; Museo de La Plata, Argentina; Museo Municipal de Ciencias Naturales de Mar del Plata ‘Lorenzo Scaglia’, Argentina; Museo Paleontológico ‘Egidio Feruglio’, Trelew, Argentina; and Yale Peabody Museum Princeton University, New Haven, USA.

Variation in the mandibular morphology of living and extinct caviomorphs was analysed using geometric morphometric techniques. Two-dimensional coordinates were captured from digital images of the left hemimandible in lateral view; when this side was missing or damaged, the reflected image of the right side was used. Images were standardized for mandible and camera lens plane position and distance to camera lens (Zelditch *et al.*, 2004). The x , y coordinates of landmarks were digitized using *tpsDig* 2.12 software (Rohlf, 2008). From the set of 13 landmarks previously used by Alvarez *et al.* (2011), we selected a subset of seven landmarks that could be applied to the morphology preserved in fossil specimens (Fig. 1). This subset represents the configuration of the diastema and mandibular body (we consider the diastema as a region separate from the mandibular body, as it is a distinctive structure in rodents); the latter comprises the alveolar region of incisor and molars (Atchley & Hall, 1991). This is a well-defined module that contributes a large portion of the morphological variation of the mandible (Cheverud, 2004). To remove

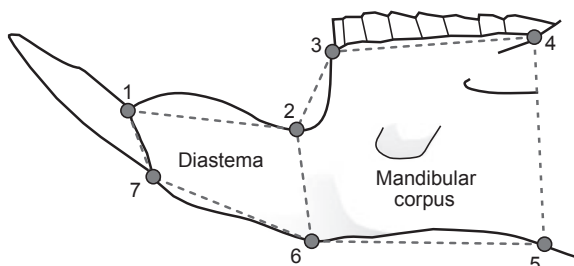


Fig. 1 Landmarks used in this study to represent the configuration of the mandibular alveolar region. (1) Antero-dorsal border of incisor alveolus, (2) extreme of diastema invagination, (3) anterior end of maxillary toothrow, (4) anterior end of base of coronoid process, (5) dorsalmost point on ventral border of mandibular corpus, (6) posterior extremity of mandibular symphysis and (7) antero-ventral border of incisor alveolus.

differences in location, orientation and scaling (i.e. nonshape variation) of the landmark coordinates, we performed Generalized Procrustes Analyses (Rohlf & Slice, 1990; Mitteroecker & Gunz, 2009). The resulting Procrustes shape coordinates were analysed through principal component analyses (PCA). Principal components [i.e. relative warps (RWs)] summarize and describe the major trends in mandible shape variation among genera and facilitate the visualization of shape ordination in a low-dimensional morphospace. Differences in shape between caviomorph genera were described by TPS deformation grids (Bookstein, 1991). Morphometric analyses were performed using *tpsRELW* 1.46 software (Rohlf, 2008).

To test our working hypothesis, we first assessed the phylogenetic signal present in the dataset of Procrustes shape coordinates of seven landmarks from living genera and the association between the detected shape changes and the habit of each genus. The phylogenetic signal contained in the shape dataset was evaluated by mapping the morphometric data onto a phylogenetic tree using squared-change parsimony and comparing the amount of change that occurred along the reference tree to the change implied by a random population of trees obtained by random taxon reshuffling (Laurin, 2004; Klingenberg & Gidaszewski, 2010). This test was performed on the Procrustes shape coordinates. At the same time, the K statistic proposed by Blomberg *et al.* (2003) was calculated on the first RW. Presence of strong phylogenetic signal (i.e. values greater than those expected from Brownian motion) could indicate the existence of association between morphological similarity and phylogenetic structure, as well as phylogenetic conservatism (Losos, 2008). Likewise, we measured the association between shape and habit using an ordinary regression model (OLS, Ordinary Least Squares) applied to the Procrustes shape coordinates and their independent contrasts. For this, we built two dummy variables to represent three habit categories (subterranean, fossorial and epigeal; Table 1) and used a composite phylogeny for the extant caviomorphs analysed in this study (Fig. 2) built from the data of Huchon & Douzery (2001), Rowe & Honeycutt (2002), Honeycutt *et al.* (2003) and Ledesma *et al.* (2009). The analyses of phylogenetic signal and regression were performed using the *Picante* package (Kembel *et al.*, 2010) for R (ver. 2.11.1, R Development Core Team., 2009) and *MORPHOJ* software (Klingenberg, 2010).

Secondly, with the goal of comparing the pattern of variation in living and fossil genera, a principal component analysis of the consensus configurations for each genus included in the fossil and living taxa datasets was performed. In addition to this analysis, we performed a second PCA to analyse individual variation, particularly for the fossil taxa, within the space of variation of the consensus configurations (between-groups PCA; Mitteroecker & Bookstein, 2011). In this type of analysis, the

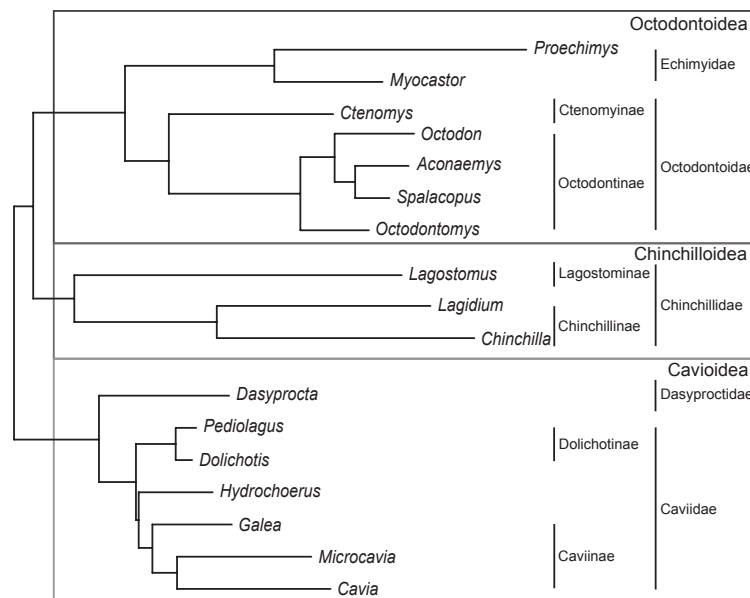


Fig. 2 Phylogenetic relationships of extant South American caviomorph rodents included in this study. Superfamilial to subfamilial clades are indicated. Branch lengths represent molecular substitutions. Topology follows several sources based on congruent phylogenetic (maximum likelihood) analyses (Huchon & Douzery, 2001; Rowe & Honeycutt, 2002; Honeycutt *et al.*, 2003; and Ledesma *et al.*, 2009).

shape data of individuals (in our case, two individuals per living genus plus the nineteen fossil specimens) are projected onto eigenvectors calculated from a covariance matrix of the means instead of a total covariance matrix as in a standard PCA.

Lastly, we evaluated the range of morphological variation in fossil and living taxa calculating the value of Foote's disparity measurement (D ; Foote, 1993; Neige, 2003). Disparity is estimated as the distance from the consensus of each genus (i.e. extant and extinct caviomorphs) to the consensus mean shape of all genera. Significance of the differences between disparity values was estimated calculating confidence intervals based on 900 bootstrap iterations. Disparity was calculated using the DisparityBox6f module of the *IMP* program series (Sheets, 2003).

Results

In the analysis of the alveolar region of the mandible for living genera, the first two principal component axes (i.e. RWs) explained about 75% of the variation (Fig. 3). The main shape differences were associated with the depth and length of this region and the depth of the diastema. Towards the negative values of RW1, the mandible becomes deeper and shorter and the diastema becomes deeper. The genera *Aconaemys* and *Ctenomys* were located on this end. The positive end was occupied by *Dolichotis* and *Pediolagus*, which showed longer and less-deep mandibles and a more slender diastema. Towards the

positive values of RW2, the diastema becomes elongated and the mandibular body is shortened, as shown by *Proechimys* and *Octodontomys*. This analysis showed phylogenetic structure in the distribution pattern of the genera. The cavioid taxa were mostly concentrated towards the positive values of RW1 and negative values of RW2, whereas the chinchilloids had positive values on both RW1 and RW2. The octodontoids presented negative values on RW1 and near-zero values on RW2, with the exception of *Octodontomys* and *Proechimys* that were more separated, located towards the positive values of the second axis.

The phylogenetic signal for the living species dataset was statistically significant (tree length = 0.117, $P < 0.0001$). The K statistic indicated clear phylogenetic signal for RW1 ($K = 1.055$, $P < 0.001$). The regression analysis of the independent contrasts of alveolar region shape onto habit variables explained a low percentage of shape variation, and the relationship was not statistically significant (9.89% of explained variance, $P = 0.687$). An ordinary regression analysis of the original shape variables onto habit showed that the latter explained a greater but still nonsignificant percentage of the shape variation (23.78% of explained variance, $P = 0.068$).

In the joint analysis with living and fossil taxa, the first two components accounted for 49% and 17% of the total variation, respectively (Fig. 4). The ordination was similar to the one observed for living genera only. The main changes were associated with the depth of the mandible and the dorsoventral and anteroposterior development of

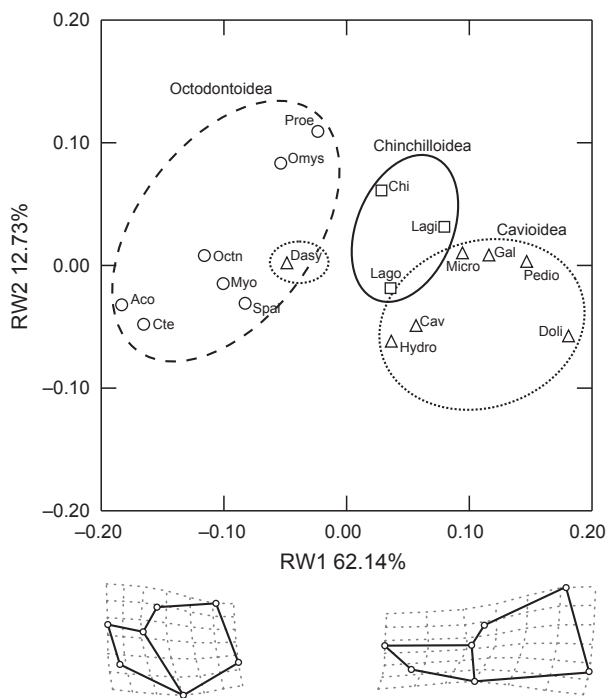


Fig. 3 Ordination of 17 extant caviomorph genera in the morphospace defined by the first two relative warps (RWs). Symbols represent caviomorph families: triangles, caviids; stars, dasyproctids; circles, octodontids; diamonds, echimyids; squares, chinchillids; and crosses, neopiblemids. Superfamilies are indicated by line type: dashed (Octodontoidea), dotted (Caviioidea) and full (Chinchilloidea). Mandible shape changes along the first relative warp (RW1), from negative (–) to positive (+) values, are shown as deformation grids. Abbreviations: Aco, *Aconaemys*; Cav, *Cavia aperea*; Chi, *Chinchilla*; Cte, *Ctenomys australis*; Dol, *Dolichotis patagonum*; Gal, *Galea*; Hydro, *Hydrochoerus hydrochaeris*; Lagi, *Lagidium viscacia*; Lago, *Lagostomus maximus*; Micro, *Microcavia australis*; Myo, *Myocastor coypus*; Oct, *Octodon*; Omys, *Octodontomys gliroides*; Pedio, *Pediolagus salinicola*; Proe, *Proechimys guyannensis*; and Spal, *Spalacopus cyanus*.

the diastema. A between-groups PCA resulted in a similar arrangement to the one obtained from the common PCA (Fig. S1), although with less data dispersion. The fossil genera were distributed close to the living representatives of their corresponding superfamilies, although overlapping was only partial. The fossil chinchilloids (*†Perimys* and *†Prolagostomus*) were closer to the octodontoids, whereas the living representatives of the superfamily were closer to the cavioids. The cavioid genera *†Neoreomys* and *Dasyprocta* (Dasyproctidae) were located among the octodontoids, because of their deeper mandibles and diastemas and more marked mentonian processes compared with the representatives of the other cavioid family included in this analysis (Caviidae). The only fossil octodontoids that were located near the living representatives of this superfamily were *†Sciomyss* and *†Protadelphomys*, and only the living genus *Proechimys* fell near the fossils. The main morphological difference (occurring

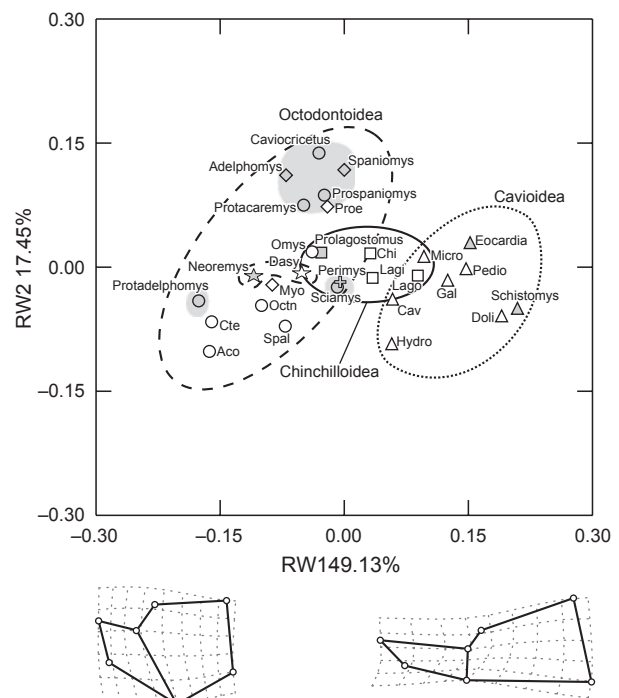


Fig. 4 Ordination of extant and extinct caviomorph genera in the morphospace defined by the first two relative warps (RWs). Symbols represent caviomorph families: triangles, caviids; stars, dasyproctids; circles, octodontids; diamonds, echimyids; squares, chinchillids; and crosses, neopiblemids. Superfamilies are indicated by line type: dashed (Octodontoidea), dotted (Caviioidea) and full (Chinchilloidea). Mandible shape changes along the first relative warp (RW1), from negative (–) to positive (+) values, are shown as deformation grids. Abbreviations for extant caviomorphs as mentioned in Fig. 3. Shaded areas indicate the position of extinct octodontoids.

along RW2) between extinct and living octodontoids is the position of the base of the coronoid process, which in living taxa is more anterior with respect to the landmark that represents the beginning of the angular process (Fig. S2). The case of the genus *†Protadelphomys* is noteworthy; it occupies an extreme position, because of its morphology similar to that of the genera *Aconaemys* and *Ctenomys* although with more marked features, such as the deeper and shorter anterior portion of the alveolar region.

The analyses of disparity showed similar levels of variation between living and fossil datasets, suggesting that, at least since the late early Miocene Santacrucian, the extinct taxa had already reached ranges of variation similar to those of the living representatives [extinct caviomorphs, $D = 0.025$ (0.013–0.033) and extant caviomorphs, $D = 0.019$ (0.013–0.023)].

Discussion

In general, hypotheses about the origin of morphological variation in diverse clades have been approached

primarily through comparative methods applied to information taken from living species (e.g. Perez *et al.*, 2009; Rabosky, 2009; Mahler *et al.*, 2010). This work is one of the first analyses of the morphological evolution of a clade that incorporates evidence from fossils to that supplied by comparative phylogenetic analyses; although several previous works have discussed the contribution of fossils to the calculation of extinction rates, origin and age of lineages, these have not focused on a morphometric approach (Brochu, 2004; Finarelli & Flynn, 2006; Marjanovic & Laurin, 2007, 2008; Mayhew, 2007; Quental & Marshall, 2009, 2010).

In a previous work, Alvarez *et al.* (2011), using comparative phylogenetic methods, observed a clear relationship between the morphological variation of the mandible and the phylogenetic relationships of living caviomorph rodent species. This study again found significant phylogenetic signal, but on this occasion, for a set of landmark coordinates restricted to the alveolar region of the mandible. The ordination obtained for this mandibular region was similar to the one obtained with the data extracted from the whole mandible. The present results show that at a large scale of phylogenetic divergence there is little relationship between ecology and morphological changes, in contrast to previous analyses made at smaller scales (Perez *et al.*, 2009). However, regarding our original hypothesis, the phylogenetic signal obtained for the mandibular shape data does not conclusively support the hypothesis of phylogenetic conservatism (K values close to 1, as in the case of this work, are as expected for a character evolving under a Brownian movement model of evolution; Losos, 2008).

Our results show that the fossil and living genera were distributed according to the corresponding major clades (i.e. superfamilies and families) in a manner similar to the pattern observed in the analysis that involved only living species. Although overlap between living and fossil taxa was only partial, both showed similar ranges of variation. An equivalent position in the shape space was evident among the cavioids of the family Caviidae. This suggests that the Santacrucian Caviidae analysed had already acquired the gracile alveolar region of the mandible that characterizes the modern representatives of the family; from a functional viewpoint, this represents a restriction for tooth digging (Vassallo & Verzi, 2001; Alvarez *et al.*, 2011). At the other extreme of the variation range, only the Colhuehuapian †*Protadelphomys* showed a morphology similar to that of the fossorial to subterranean living octodontids *Aconaemys* and *Ctenomys* (Vucetich & Verzi, 1991).

Contrary to the K results obtained for living genera dataset in the present work, the results of the analysis of living and fossil taxa support the hypothesis of an early origin of mandibular variation in caviomorphs that had been previously suggested on the basis of the observed mandibular variation in extant species (Alvarez *et al.*, 2011). At least as early as the Santacrucian (> 16 Ma),

the alveolar region of the mandible of caviomorphs was already differentiated into the morphological groups that characterize each of the superfamilial clades. In contrast to the pattern of spreading in the morphospace that would be expected when a clade diversifies (Foote, 1993; Erwin, 2007), in this study, we detected certain stability from the early differentiated morphologies to extant species, suggesting the existence of constrained evolutionary diversification (Losos, 2008). In agreement with this pattern observed in shape space, the values of disparity obtained were similar for both living and fossil caviomorphs. Nevertheless, it should be taken into account that this relative morphological stability at major clade level is restricted to the alveolar region of the mandible, as allowed by the preservation of materials.

Our results suggest that new advances in the understanding of the process of morphological diversification in caviomorphs depend to a great extent on the finding and study of older fossils with good preservation, which would allow the analysis of larger samples of specimens and traits and the assessment of morphological disparity in a more remote past.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Ordination of specimens representing 17 extant and 12 extinct caviomorph genera in the morphospace defined by the first two relative warps (RWs).

Figure S2 Lateral view of alveolar portion of the mandible of representative extant and extinct genera analyzed in this study.

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Appendix 1

Detailed list of specimens included in the present study

Abbreviations: Mastozoological collections, MLP, Museo de La Plata, Buenos Aires, Argentina; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Ciudad de Buenos Aires, Argentina; MMPMa, Museo Municipal de Ciencias Naturales ‘Lorenzo Scaglia’, Mar del Plata, Buenos Aires, Argentina. Palaeontological collections, MLP, Museo de La Plata, Paleontología

de Vertebrados, Buenos Aires, Argentina; MACN A, Ameghino collection of Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Ciudad de Buenos Aires, Argentina; YPM-PU, Yale Peabody Museum at Princeton University, New Haven, Estados Unidos; MPEF-PV, Museo Paleontológico 'Egidio Feruglio' Paleontología de Vertebrados, Trelew, Chubut, Argentina; and MMP, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia', Mar del Plata, Buenos Aires, Argentina.

Cavioidea. Caviidae

†*Eocardia montana* MACN A 2015; †*Eocardia* MACN A 10210; †*Schistomys erro* YPM-PU 15648; *Cavia aperea* MLP 151, 523, 542.M15, 573.3, 1801, 1803, 5.VI.00.8, 30.V.02.8; *Galea musteloides* complex: *G. leucoblephara* MLP 676, 738.4, 738.6, 738.7, 6.XII.35.2, 15.X.98.5, MACN 34.193, 15324, *Galea* sp. MACN 31.30, 36.419; *Microcavia australis* MLP 683a, 683b, 683.9, 683.12, 683.13, 683.15, 683.16, 683.18, 683.24, 683.25, 26.VIII.01.22; *Dolichotis patagonum* MACN 9.17, 26.65, 28.183, 28.190, 29.894, 49.59, 52.16, 13755, 14532, 15533; *Pediolagus salinicola* MACN 28.188, 41.216, 41.218, 17366; and *Hydrochoerus hydrochaeris* MACN 4343, 5266, 14038, 49303.

Dasyproctidae

†*Neoreomys australis* MACN A 20; *Dasyprocta* sp. MACN 3175, 14213, 31163, 34678, 47140, 47345, 49348, 50298, 50572.

Chinchilloidea. Chinchillidae.

†*Prolagostomus* MACN A 4425; *Chinchilla* sp. MLP 1767, 1768, 11.VIII.99.41, MACN 13037, 20632; *Lagidium viscacia* MACN 14.16, 34.218, 34.228, 34.244, 34.264, 39.500, 41.54, 16330, 16474, 18829; and *Lagostomus maximus* MLP 1593, 1594, 1601, 1649, 1651, 1654, 5.II.49.1, 2.VI.60.6, 2.VI.60.10, 19.V.98.3.

Neopiblemidae

†*Perimys* MMP 111-M, 936-M.

Octodontoidea. Echimyidae.

†*Adelphomys* MMP 242-M; †*Spaniomys* MMP 243-M; †*Spaniomys modestus* MLP 15-37; †*Spaniomys riparius* MLP 15-80; *Myocastor coypus* MLP 1172, 20.XII.89.8, 20.XII.89.10, 30.XII.02.72, MACN 16272, 16273, 16323, 19367, 19375, 19379; and *Proechimys guyannensis* MACN 50.342, 50.343, 50.362, 50.414.

Octodontidae

†*Caviocricetus* MPEF-PV 5064; †*Protacaremys* MPEF-PV 5471, 7561; †*Protadelphomys* MPEF-PV 8162, 9163, 8164; †*Sciamys* MLP 63-XII-19-137; †*Prospaniomys* MPEF-PV 5039; *Aconaemys porteri* MLP 17.II.92.4, 17.II.92.6, 17.II.92.11; *Aconaemys sagei* MLP 17.II.92.9; *Ctenomys australis* MMPMa I1047, I1048, I1051, I1052, I1061, I1072, I1088, I1089, I1803; *Octodon bridgesi* MLP 12.VII.88.1, 12.VII.88.3, 12.VII.88.4, 12.VII.88.9; *Octodon degus* MLP 30.XI.93.2, 12.XI.02.15; *Octodontomys gliroides* MACN 27.92, 27.95, 30.52, 17832, 17834, 17835, 19199; and *Spalacopus cyanus* MLP 10.XI.95.5, MMPMa 3585, 3590, 3807.

Appendix 2

Stratigraphic provenance of the fossil materials analysed in this study

Cavioidea

Caviidae

†*Eocardia montana* MACN A 2015. Santacrucean (late early Miocene).

†*Eocardia* MACN A 10210. Corriguen Kaik, Santa Cruz province; Santacrucean (late early Miocene).

†*Schistomys erro* YPM-PU 15648. Killik Aike, Santa Cruz province; Santacrucean (late early Miocene).

Dasyproctidae

†*Neoreomys australis* MACN A 20. Santacrucean (late early Miocene).

Chinchilloidea

Chinchillidae

†*Prolagostomus* MACN A 4425. Monte Observación, Santa Cruz province; Santacrucean (late early Miocene).

Neopiblemidae

†*Perimys* MMP 111-M. Barranca Sur Lago Colhue-Huapi, Chubut province; Colhuehuapian (early Miocene).

†*Perimys* MMP 936-M. Barranca Sur Lago Colhue-Huapi, Chubut province; Colhuehuapian (early Miocene).

Octodontoidea

Octodontidae

†*Caviocricetus* MPEF-PV 5064. Bryn Gwyn, Chubut province; Colhuehuapian (early Miocene).

†*Prospaniomys* MPEF-PV 5039. Bryn Gwyn, Chubut province; Colhuehuapian (early Miocene).

†*Protacaremys* MPEF-PV 7561. Gran Barranca, Chubut province; Colhuehuapian (early Miocene).

†*Protacaremys* MPEF-PV 5471. Gran Barranca, Chubut; Colhuehuapian (early Miocene).

†*Protadelphomys* MPEF-PV 8162. Bryn Gwyn, Chubut province; Colhuehuapian (early Miocene).

†*Protadelphomys* MPEF-PV 8163. Bryn Gwyn, Chubut province; Colhuehuapian (early Miocene).

†*Protadelphomys* MPEF-PV 8164. Bryn Gwyn, Chubut province; Colhuehuapian (early Miocene).

†*Sciamys* MLP 63-XII-19-137. Barrancas of Santa Cruz River, Santa Cruz province; Santacrucean (late early Miocene).

Echimyidae

†*Spaniomys* MMP 243-M. Monte Observación, Santa Cruz province; Santacrucean (late early Miocene).

†*Spaniomys modestus* MLP 15-37. Barrancas of Santa Cruz River, Santa Cruz province; Santacrucean (late early Miocene).

†*Spaniomys riparius* MLP 15-80. Santa Cruz province; Santacrucean (late early Miocene).

†*Adelphomys* MMP 242-M. Monte Observación, Santa Cruz province; Santacrucean (late early Miocene).

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