



Evolutionary Patterns of Mandible Shape Diversification of Caviomorph Rodents

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Abstract

Caviomorphs are a mainly South American rodent clade with high taxonomic and ecomorphological diversity. In this study, we combine geometric morphometric, functional, ancestral reconstruction, and macroevolutionary analyses to quantify the magnitude, direction, and rates of shape diversification of the caviomorph mandible, and to explore the morpho-functional implications and potential ecological catalysts of the observed shape changes. The mandible shape was significantly related to habits and size, and had a better fit with an evolutionary model where the main clades occupy distinct adaptive peaks. The morphological evolution of octodontoids is characterized by pulses of rate acceleration, but without reaching high disparity. Such pulses are mainly linked to the acquisition of fossorial specializations, including short and robust mandibles, and the increasement of forces at incisors. Conversely, derived cavioids show slower but continuous shape changes that allowed them to reach the most divergent, grazing morphologies in which slender mandibles with more marked antero-posterior movements for grinding action are favored. Interestingly, the major morphological changes occurred mainly during the early Oligocene and lower late Miocene, two time periods that involved global climatic events and strong changes in the vegetational structure of South America. The evolution of octodontoid and cavioid mandibles seems to be related to the occupation of subterranean and epigeal niches, respectively, in the progressively expanded Cenozoic open landscapes of southern South America.

Keywords Evolutionary rates · Evolutionary models · Caviomorphs · Ancestral shape reconstruction · Functional morphology

Introduction

Environmental changes, geographic colonization, or key innovations can dramatically accelerate diversification by increasing ecological opportunities and availability of new ecological resources (Vrba 2005; Stroud and Losos 2016). In some cases, taxonomic and ecological diversity increase together, often rapidly, resulting in an adaptive radiation (Stroud

and Losos 2016, and citations therein). Some processes involving relatively low species richness could also lead to adaptive radiations, provided that adaptive disparity is present (Gavrillets and Losos 2009; Stroud and Losos 2016).

Caviomorphs are a highly diverse group of mainly South American rodents, whose fossil record can be tracked up to the middle Eocene (Antoine et al. 2012; Vucetich et al. 2015; Álvarez et al. 2017). Extant representatives present diverse morphologies and life habits, with body sizes ranging from 0.05 kg to 50 kg, subterranean to epigeal modes of life in widely diverse habitats, and varied dietary habits (Patton et al. 2015; Wilson et al. 2016). Previous contributions suggested that taxonomic and ecomorphological diversities of caviomorphs were reached in two or three major events that occurred mainly during the Eocene-Oligocene transition and middle-late Miocene in response to major climatic events (Fabre et al. 2012; Vucetich et al. 2015; Verzi et al. 2016; Álvarez et al. 2017). The inferences of evolutionary rates using time-calibrated phylogenies allow the analysis and quantification of the diversity and evolution of organisms in

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novel manners, assessing the tempo and mode of phenotypic evolution and the postulation of potential catalysts (Mahler et al. 2010; Rabosky et al. 2014; Stroud and Losos 2016).

The mandible is a highly plastic structure (e.g., Greaves 2012; Hautier et al. 2012; Casanovas-Vilar and van Dam 2013) and represents a very valuable element to study the morphological evolution of mammals given its wide range of variation associated with ecological, phylogenetic, and allometric factors. Major shape changes events that occurred during the evolution of the mandible of caviomorph rodents can be understood considering mainly their association with dietary and fossorial adaptations occurring during these events (e.g., Álvarez et al. 2011, 2020; Hautier et al. 2012). The previous studies that analyzed the evolutionary rates in caviomorphs focused on taxonomic and size diversity (Álvarez et al. 2017) or focused on a specific family of caviomorphs (i.e., Echimyidae; Tavares et al. 2016), but comprehensive analyses of evolutionary rates of shape are still lacking.

In this study we combine geometric morphometrics with macroevolutionary analyses to assess the rates and modes of shape diversification of caviomorph rodents and use a morpho-functional approach to evaluate the degree of coupling of the evolutionary patterns with potential ecological catalysts. The present study complements previous studies about size evolution rates, allometry, and mandibular modular integration of caviomorph rodents (Álvarez et al. 2017, 2020). We hypothesized that the large morphological diversity displayed by extant caviomorphs was attained through several disparification pulses, following a heterogeneous pattern, mostly linked to environmental changes that occurred during the Cenozoic.

Materials and Methods

We analyzed mandibles of 331 specimens of 133 extant caviomorph species and two species as outgroups (*Glis glis* and *Hystrix brachyurus*). All the studied specimens are from osteological museum collections (Online Resource 1). Except for *Mesocapromys*, all extant caviomorph genera are represented (Patton et al. 2015; Emmons and Fabre 2018).

Here we quantified and analyzed the mode and tempo of the shape evolution rates in caviomorph rodents. In this line, we performed a series of analyses (Online Resource 2) focusing in the assessment of the magnitude, direction, and rates of morphological changes on a time-calibrated phylogeny.

A two-dimensional geometric morphometrics analysis of the lateral view of the mandible was performed. The landmark design was the same used in Álvarez et al. (2020); it included 18 landmarks and 43 semilandmarks (Fig. 1; see Online Resource 3 for definitions). The landmarks and semilandmarks digitalization was executed using TPS

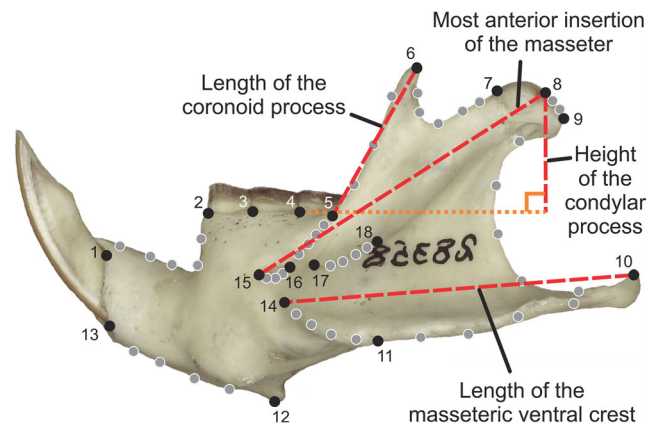


Fig. 1 Landmarks and semilandmarks design (black and gray circles, respectively) used to represent the mandibular shape (following Álvarez et al. 2020). Functional variables are illustrated (red dashed lines). The orange dotted line indicates the level from which the height of the condylar process was calculated

software (Rohlf 2015). Mean Procrustes coordinates for each species (i.e., terminals in phylogenetic tree) were obtained from MorphoJ software (Klingenberg 2011).

The ancestral mandible shapes were reconstructed using the algorithm described in Goloboff and Catalano (2010; see also Catalano and Goloboff 2012), implemented in the software Tree Analysis using New Technology (TNT v.1.5; Goloboff et al. 2008; Goloboff and Catalano 2016). For this, the mentioned mean Procrustes coordinates obtained for terminals were optimized on a phylogenetic tree based on the calibrated molecular one obtained by Álvarez et al. (2017; see Online Resource 4). Terminal and ancestral reconstructions were exported as a second set of Procrustes coordinates, which were run through a Principal Component Analysis (PCA; see Online Resource 5).

To evaluate the magnitude of evolutionary shape changes, Euclidean distances on the whole morphospace (considering all the PCs) were computed. These Euclidean distances, instead of PC scores, were selected as a measure of morphological differences among taxa because they represent shape variation along the entire morphospace whereas the scores of a single PC (e.g., PC1) represent only a portion of the total variation. Euclidean distances to the ancestral shape of the node of the common ancestor of caviomorph rodents were measured for both internal nodes and terminals using PAST3 v.3.15 (Hammer et al. 2001). These Euclidean distances were plotted on the calibrated phylogeny illustrating the timing of shape diversification and magnitude of shape changes for each taxa and node.

To evaluate the speed of shape diversification, evolutionary rates of the abovementioned Euclidean distances were modeled using Bayesian Analysis of Macroevolutionary Mixtures (BAMM) v.2.5.0 software (Rabosky 2014). BAMM samples distinct evolutionary dynamics that best explain the whole diversification dynamics of the clade

(Rabosky 2014). The analysis involved a reversible jump MCMC run of 500,000,000 generations sampled every 50,000 steps and a burnin of 20%. The output of this analysis was analyzed using the BMMtools package v.2.1.6 (Rabosky et al. 2014) for R v.3.5.2 (R Development Core Team 2019). It allows the inference of evolutionary rates and their shifts along the phylogeny and plots them as ‘phylorate plots’, which represent the analyzed phylogeny with its branches colored to reflect the instantaneous trait rate. Additionally, we plotted the mandibular shape evolutionary rate through time to evaluate the timing of rate shifts.

In order to evaluate the functional meaning of particular shape changes, the following measures were calculated on landmark configurations (Fig. 1): height of the condylar process with respect to the molar series (perpendicular distance between landmarks 4 and 8); length of the anterior margin of the coronoid process (between landmarks 5 and 6); length of the ventral masseteric crest (between landmarks 10 and 14); anterior insertion of the m. masseter (between landmarks 8 and 15). The height of the condylar process is related to the magnitude of the lever arms of masticatory muscles (e.g., Maynard Smith and Savage 1959), and to the magnitude of the gape (Emerson and Radinsky 1980; Radinsky 1985; McIntosh and Cox 2016 and references therein). The length of the coronoid process and ventral masseteric crest are considered as proxies of the development of the m. temporalis and m. masseter, pars superficialis and lateralis, respectively (e.g., Woods 1972; Radinsky 1985). The most anterior insertion of the m. masseter can be associated with the largest in-lever arm of this muscle (see Becerra et al. 2014); this measure could be considered as standardized through scaling during the Procrustes alignment of landmarks configurations.

To evaluate evolutionary trends of these variables, they were plotted onto the phylogenetic tree using the function ‘plotBranchbyTrait’ of Phytools R package v.0.6–44 (Revell 2012).

In order to evaluate potential ecological driven factors, each extant species was classified into one of six categories that combine main feeding and fossorial habits (Online Resource 6), and four categories reflecting their preferred habitat (Online Resource 6). An extensive bibliographic search was performed for this and is enlisted in Online Resource 6. The classification design is a modification of previous proposal of Townsend and Croft (2008; see also Hautier et al. 2012).

We analyzed the relationship between shape and the multiple potential ecological and allometric factors considering the phylogenetic structure of the data. In this way, we performed five Phylogenetic Generalized Least Squares regression analyses (PGLS; Martins and Hansen 1997), analyzing each of the four functionally significant traits and the overall shape (considering the principal components of a PCA that included only terminals; see Online Resource 2) against the

three explanatory variables (i.e., feeding and fossorial habits, habitat, and size). For these analyses, we considered feeding and fossorial habits as a single categorical variable, habitat as a categorical and ordered variable, and size as a continuous variable (represented by the natural logarithm of centroid size). These analyses were performed with the Caper library v.1.0.1 for R (Orme et al. 2011).

Finally, in order to explore whether adaptation could explain the phylogenetic distribution of shape variation, or if the latter is, alternatively, the product of neutral processes represented by pure drift, an analysis of evolutionary models was performed. We assessed fit of several models to the shape data represented by scores of the first two PCs. A purely neutral model of evolution -Brownian Motion- (BM) and alternative, deterministic -Early Burst (EB) and Ornstein-Uhlenbeck (OU)- models explaining patterns of mandible shape were analyzed using the mvMORPH package v.1.1.0 for R (Clavel et al. 2015). OU processes with both a unique adaptive optimum (OU1) and with multiple optima were modeled (see Clavel et al. 2015). Multiple-optima OU models were constructed by assuming ecological factors (OU Habit and OU Habitat; see above) and phylogeny (OU Clades; each family is considered to occupy a separate adaptive peak) as responsible for the structuring of the adaptive landscape of caviomorph mandible (Butler and King 2004). For each hypothesis, the relative fit was assessed using the Akaike information criterion (AIC) and the sample size corrected AIC (AICc; Anderson et al. 1998).

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

Evolution of Mandibular Shape

Euclidean distances between terminals and reconstructed node shapes to the configuration of the common ancestor of caviomorphs revealed that caviids present the largest and earliest (late Oligocene) mandibular morphological (Fig. 2, right side). *Dinomys*, *Cuniculus*, *Myocastor*, some *Tympanoctomys* species, and some capromyines also present derived morphologies but less modified, and, except for *Dinomys*, more recently acquired (early and middle Miocene). Other taxa present morphologies that are moderately (e.g., ctenomyids and some abrocomids) to scarcely modified (e.g., many echimyids, octodontids, and erethizontids).

The pattern of evolutionary rates of shape was relatively simple. Nine distinct shift configurations explained 95% of data (Online Resource 7). The best sampled configuration was composed by one single shift (36% posterior probability; Fig. 2, left side) recorded in the common ancestor of

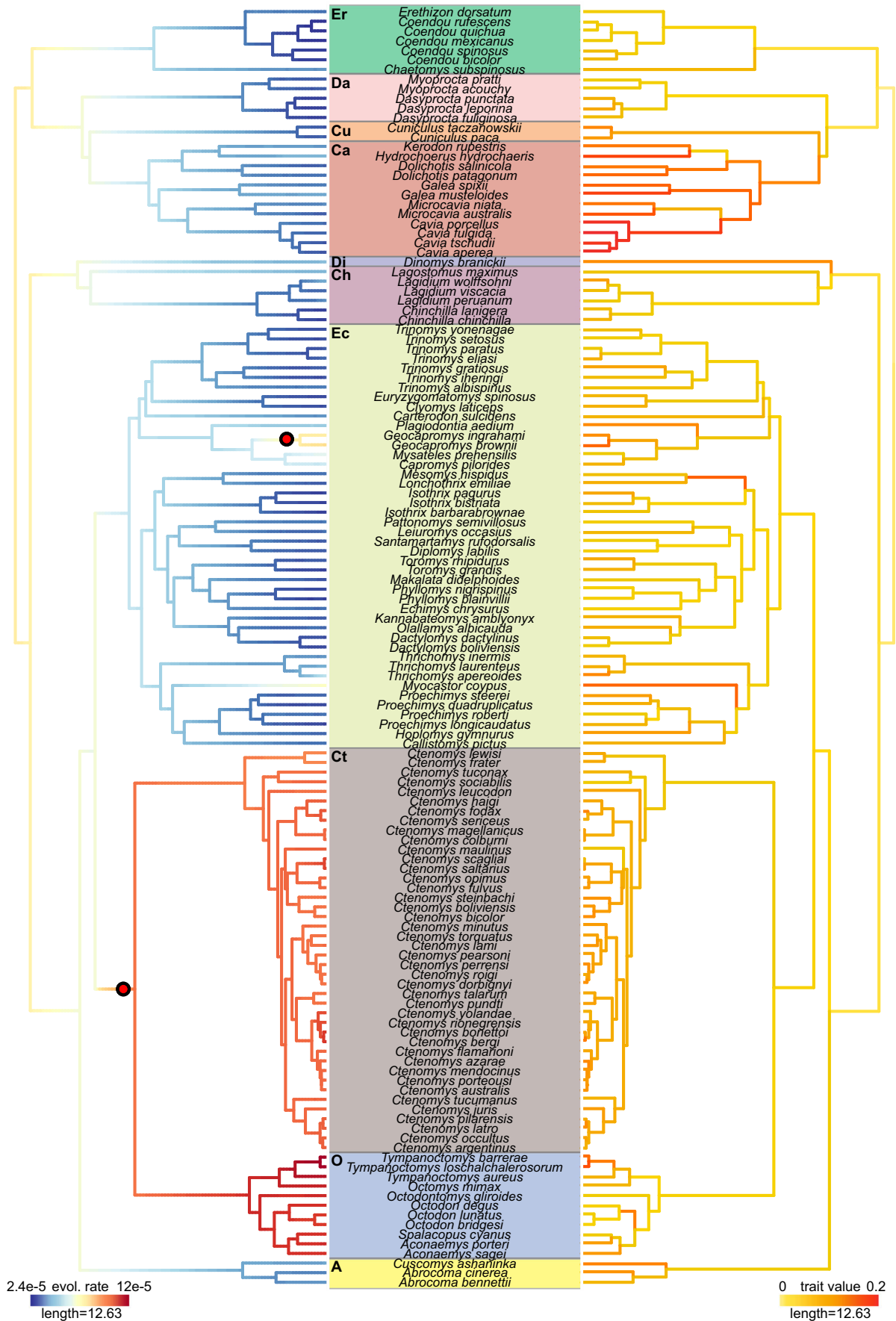


Fig. 2 Mean phylorate plot of evolutionary rates of the Euclidean distances (left) and optimization of the Euclidean distances raw values (right) calculated from the reconstructed ancestral and terminal mandibular shapes to the ancestral caviomorph shape, representing the magnitude of shape changes (see “Materials and Methods” section). For the phylorate plot, red circles indicate the most probable shifts recovered. Er = Erethizontidae, Da = Dasyproctidae, Cu = Cuniculidae, Ca = Caviidae, Di = Dinomyidae, Ch = Chinchillidae, Ec = Echimyidae, Ct = Ctenomyidae, O = Octodontidae, and A = Abrocomidae. Range of values for the Euclidean distances evolutionary rates (evol. rate, bottom left, in units of 1/Myr), the optimized Euclidean distances raw values trait (i.e., trait value, bottom right), and branch length scale in Myr are indicated

ctenomyids and octodontids, the latter family presenting the highest rate values. A configuration with two shifts had also a high posterior probability (29%). In this case, a second shift in the common ancestor of *Geocapromys* species is recovered (Fig. 2, left side). The mean diversification rate plot of the nine configurations indicated moderate background rate characterizing most of the remaining clades. The rates diminished toward derived branches, except for some caviids, *Dinomys*, *Lagostomus*, and some echimyids (e.g., capromyines, some *Thrichomys*, *Myocastor*), in which the rates maintain moderate values or reach relatively high values. The shape-through-time plot for caviomorphs (Fig. 3a) showed two inflexion points in the shape rate passing from deceleration to acceleration trends. The first change occurred during the early Oligocene, and the acceleration of rate lasted until the late Oligocene; the second one took place during the lower late Miocene, and the acceleration of the rate persists until present.

This pattern is explained by the rate curve of the octodontoid clade Echimyidae-Octodontidae-Ctenomyidae (Fig. 3b,c).

The regression analysis indicated that the mandible shape of caviomorphs was significantly related to the habits and size. Conversely, the habitat preference resulted non-significantly related to shape. The percentage of shape variation explained by the model was 28% (Table 1).

Among the explored evolutionary models, OU Clades with each caviomorph family occupying an adaptive peak of its own was the best-fitting hypothesis (Table 2). The OU Habit model showed the second highest AICc value (Table 2), in accordance with results of the phylogenetic regressions.

Patterns of Functional Variables

Condylar process height of optimized shapes- This measure reached minimal values mainly in extant caviids and secondarily cuniculids, retained since their early Oligocene common ancestor (Fig. 4; Online Resource 8); relatively low to moderate values were present in dasyproctids, partially reverting the cavioid acquisition, *Chinchilla*, and the ancestor of the octodontoids. High values were reached by erethizontids, *Dinomys*, and some octodontoids (Fig. 4).

Coronoid process length of optimized shapes- Estimations indicate that the common ancestors of both cavioids and chinchilloids early acquired a markedly reduced coronoid process, which was maintained or even exacerbated in extant representatives (especially *Cavia* and *Dinomys*). A reduced

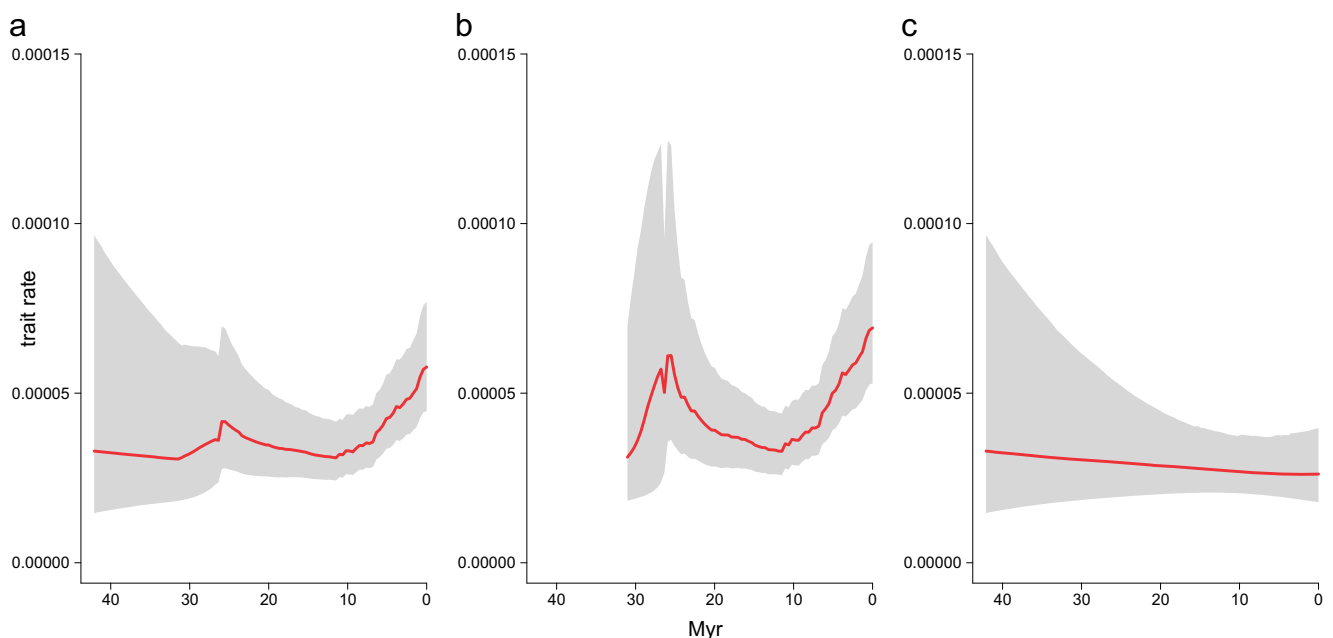


Fig. 3 Shape diversification rate-through-time plots. The estimated rates of the Euclidean distances to the ancestral caviomorph shape (i.e., trait rate on the vertical axes) are plotted through time for all caviomorph rodents (a), the selected clade octodontids + ctenomyids + echimyids

(b), and the background rate for remaining caviomorphs once the selected clade has been excluded (c). Lines indicate diversification rate curves. Shading around these lines represents 10% through 90% Bayesian credible regions on the distribution

Table 1 Phylogenetic regression analyses (PGLS) between shape variables (principal component analysis, most anterior insertion of masseter, length of coronoid process, length of ventral masseteric crest, and height of condylar process) and explanatory ones (habit, habitat, and size)

Variables	PCA		Most anterior insertion of masseter		Length of coronoid process		Length of ventral masseteric crest		Height of condylar process						
	t	p value	t	p value	t	p value	t	p value	t	p value					
Habit	A	4.14	0.0001*	19.39	<0.0001*	6.64	<0.0001*	6.49	<0.0001*	1.62	0.1078				
	B	4.32	<0.0001*	19.30	<0.0001*	6.57	<0.0001*	6.28	<0.0001*	1.55	0.1233				
	C	4.55	<0.0001*	19.63	<0.0001*	6.36	<0.0001*	6.07	<0.0001*	1.58	0.1176				
	D	4.26	<0.0001*	19.21	<0.0001*	6.25	<0.0001*	6.23	<0.0001*	1.94	0.0546				
	E	5.49	<0.0001*	19.44	<0.0001*	6.27	<0.0001*	6.00	<0.0001*	1.72	0.0880				
	F	5.36	<0.0001*	18.09	<0.0001*	5.92	<0.0001*	5.27	<0.0001*	1.16	0.2483				
Habitat	-1.74	0.0850	-0.58	0.5662	0.18	0.8553	0.93	0.3559	1.53	0.1280					
Size	-4.41	<0.0001*	-3.65	0.0004*	-3.64	0.0004*	2.17	0.0320*	0.88	0.3814					
	R ²	F	p value	R ²	F	p value	R ²	F	p value	R ²	F	p value			
Model	0.28	6.82	<0.0001*	0.16	3.37	0.0025*	0.13	2.66	0.0136*	0.09	1.78	0.0978	0.08	1.58	0.1461

Statistics for each explanatory factor (t and p values) and the global model (R², F, and p values) are summarized. * = significant relationships at alpha = 0.05, A = fossorial, B = fruit-seed feeder, C = fruit-leaf feeder, D = stem-leaf feeder, E = generalist grass feeder, and F = specialist grass feeder

coronoid process also occurred in some echimyids, especially in *Myocastor* (Fig. 4; Online Resource 8). Conversely, the common ancestor at family level and extant representatives of erethizontids, octodontids+ctenomyids (principally *Tympanoctomys* and *Ctenomys*), and the echimyid clade *Carterodon* + *Euryzygomatomys* + *Clyomys* + *Trinomys* acquired a long coronoid process mainly during the Oligocene/Miocene boundary (Fig. 4; Online Resource 8).

Ventral masseteric crest length of optimized shapes- This structure is relatively short and scarcely variant for most of clades, but some echimyids (e.g., *Makalata*, *Myocastor*, *Thrichomys*, *Toromys*, capromyines) and *Dinomys* stand out by the presence of a relatively long ventral crest (Fig. 5; Online Resource 8).

Most anterior insertion of m. masseter of optimized shapes- Estimates of the distance between the most anterior masseteric scars and the condyle indicated that the range of variation of this distance is small and maintained relatively constant along the evolutionary history of major clades (Fig. 5; Online

Resource 8). The common ancestor at the family level and most of the extant representatives of echimyids, octodontids, and abrocomids present larger values than ctenomyids and cuniculids+caviids, which present the lowest values; dasyproctids and erethizontids typically present intermediate values.

The regression analyses indicated that the length of the coronoid process and the most anterior insertion of the m. masseter were significantly related to habits and size, but explaining a small portion of the total variation (Table 1). Conversely, the height of the condylar process and length of ventral masseteric crest were not significantly related to the explanatory factors according to the statistical model (Table 1).

Discussion

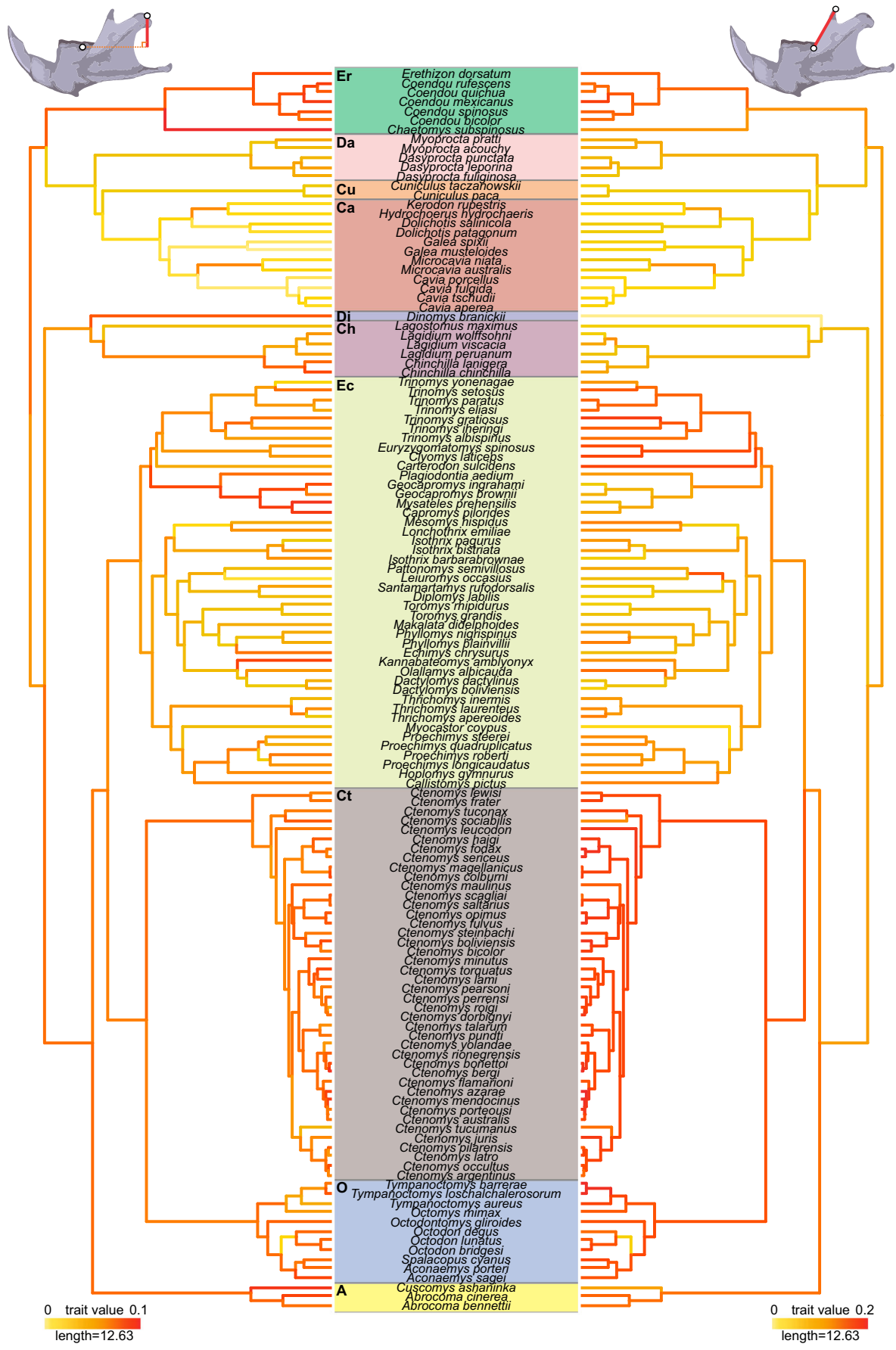
Two main mandible shapes have been traditionally recognized for caviomorphs: the “octodontoid” and “cavioid” types (Vassallo and Verzi 2001; Verzi 2002; Hautier et al. 2011, 2012). The integrative analysis of tempo, magnitude, and direction of the shape changes suggests a complex

Table 2 Results of the multivariate model-fitting analyses

Model	P	AIC	AICc
OU Clades	26	-1184.651	-1178.677
OU Habit	18	-1123.836	-1121.022
OU1	8	-1108.744	-1108.184
OU Habitat	14	-1108.907	-1107.206
BM	5	-1101.295	-1101.065
EB	6	-1099.37	-1099.046

Abbreviations: P, parameters; AIC, Akaike information criterion; AICc, sample size corrected AIC

Fig. 4 Optimization of the height of the condylar process (left) and length of the coronoid process (right) values calculated from the optimized ancestral and terminal mandibular shapes (see “Materials and Methods” section). Er = Erethizontidae, Da = Dasyproctidae, Cu = Cuniculidae, Ca = Caviidae, Di = Dinomyidae, Ch = Chinchillidae, Ec = Echimyidae, Ct = Ctenomyidae, O = Octodontidae, and A = Abrocomidae. Range of values for each trait (i.e., height of the condylar process and length of the coronoid) and branch length scale in Myr are indicated



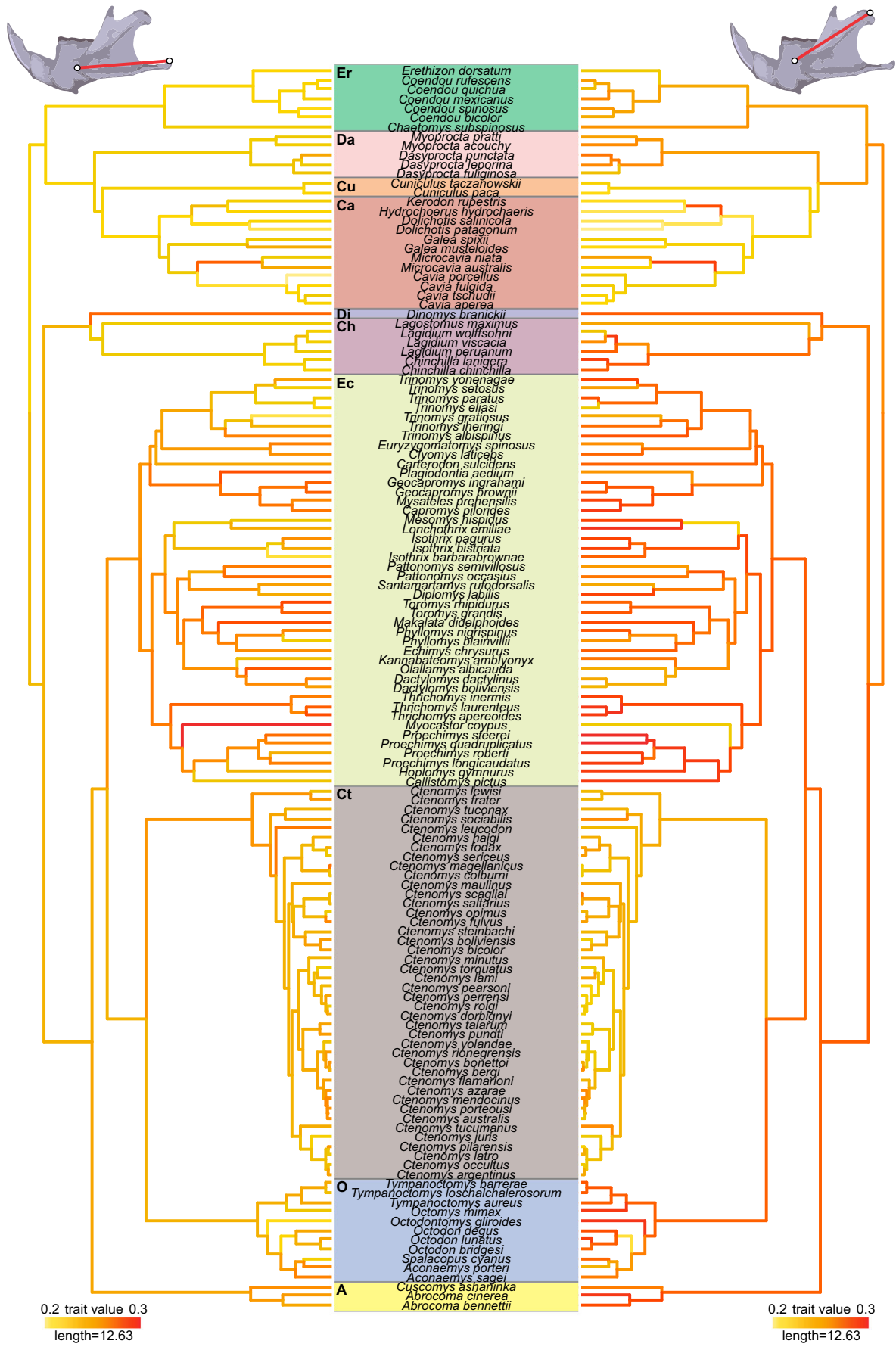
macroevolutionary pattern in caviomorphs, with particular features for the diverse octodontoids and cavioids. Fast morphological diversification of Octodontoidea, and particularly octodontids and ctenomyids, occurred mainly during the late Oligocene, and through a second pulse of acceleration during the lower late Miocene (see also Upham and Patterson 2015; Verzi et al. 2016; Gomes Rodrigues et al. 2016). Although the evolutionary rates of these octodontoid clades stand out, their mandibular morphology is not as disparate as that of other caviomorph clades. Most of the evolutionary changes, especially for ctenomyids, and some octodontid and echimyid clades, were linked to specific shape and size changes related to adaptations to fossorial habits; interestingly, they occur in lineages that include both tooth-diggers (e.g., *Spalacopus*) and scratch-diggers (e.g., most of other fossorial octodontids). Specializations imposed by life underground involve the restriction to relatively small sizes and, for the case of tooth-diggers, the need for increasing biting forces achieved through the robustness and shortness of the mandible and the lengthening of the coronoid process (Vassallo and Verzi 2001; Olivares et al. 2004; Lessa et al. 2008; Druzinsky 2010a; Becerra et al. 2014; Gomes Rodrigues et al. 2016; Morgan et al. 2017; McIntosh and Cox 2019). Although differences in mandibular shape are expected to occur between tooth-digger and non-tooth-digger rodents (McIntosh and Cox 2019), morphological specializations were recorded to be similar, in some degree, between scratch- and tooth-digger species (Becerra et al. 2014; Gomes Rodrigues et al. 2016). Different factors could explain this pattern, including the involvement of the masticatory apparatus when digging through harder substrates, hard-food items consumption, or the retention of features of tooth-digger ancestors (Gomes Rodrigues et al. 2016; McIntosh and Cox 2019; Álvarez et al. 2020).

A markedly anterior insertion of the masseteric musculature and a short snout in front of this insertion are expected traits for fossorial mammals, because these features allow greater incisive forces by increasing the mechanical advantage of those muscles (e.g., Becerra et al. 2014; Gomes Rodrigues et al. 2016). Conversely, some authors indicated that long instead of short snouts are present in fossorial, in particular tooth-digger, rodents with very procumbent incisors; but in such cases, the rostral length is measured as the distance from incisors tips to cheek teeth instead to the mentioned muscular scars (McIntosh and Cox 2016). Although our analyses support the existence of a significant association between the anterior position of the m. masseter and the habits in caviomorphs, moderate, instead of high, values of this anterior insertion are found in ctenomyids and some other fossorial octodontoids. The shortening of the diastema in these rodents would increase the bite forces at the incisors, not by increasing the mechanical advantage but because of the vertical rather than anteriorly inclined resultant vector of m. masseter pars medialis infraorbitalis. This results in the fact

Fig. 5 Optimization of the length of the ventral masseteric crest (left) and the most anterior insertion of the masseter (right) values calculated from the optimized ancestral and terminal mandibular shapes (see “Materials and Methods” section). Er = Erethizontidae, Da = Dasyproctidae, Cu = Cuniculidae, Ca = Caviidae, Di = Dinomyidae, Ch = Chinchillidae, Ec = Echimyidae, Ct = Ctenomyidae, O = Octodontidae, and A = Abrocomidae. Range of values for each trait (i.e., length of the ventral masseteric crest and most anterior insertion of the masseter) and branch length scale in Myr are indicated

that a large component of the resultant force acts in the same direction as the incisive bite. Becerra et al. (2014) found no significant differences in the estimated mechanical advantage of three species of caviomorphs with divergent cranial morphology; this is attributed to the fact that a shortening of the jaw affects both the out-lever arm and the in-lever arm of the adductor muscles. But this model does not consider the abovementioned change in the direction of the muscle fibers. A probable reason for the absence of a marked advance in the position of the anterior masseteric scars could be the presence of structural restrictions imposed by the hystricomorphous condition of caviomorphs. The position and direction of the insertion fibers of the m. masseter pars medialis infraorbitalis (the most anterior masseteric bundle) are restricted by the position of the infraorbital foramen (through which this muscle runs from its rostral origin), which in turn is bounded by the snout anteriorly and the orbit posteriorly. In consequence, in hystricomorph rodents, the line of action of the muscle is always posterior to the rostrum and the ventral anterior root of the zygomatic arch. Conversely, in non-hystricomorph fossorial rodents the anterior portions of the m. masseter are mainly (myomorphous) or totally (sciurumorphous and protrogomorphous) not linked to an infraorbital passage, and would not present the same structural limitations (Druzinsky 2010a, b; Cox et al. 2012; Casanovas-Vilar and van Dam 2013), and in consequence would present a more forward insertion of the anterior position of the m. masseter. It is important to note that the anteriormost position of the masseter scar as analyzed here is a limited estimate of the mechanical advantage of this muscle (see “Materials and Methods” section). On the other hand, other features typical for fossorial rodents are convergently shared by most of the fossorial caviomorphs. This is the case of the presence of a well-developed coronoid process, which gives a large attachment site for the m. temporalis and increases its in-lever arm (Radinsky 1985). These modifications allow this muscle to play a major role in incisive biting without the restrictions described for the masseteric muscle (Olivares et al. 2004; Becerra et al. 2014).

In contrast to octodontids and ctenomyids, the mandibular changes of derived Caviioidea did not show remarkably high rates or significant rate shifts; however, the morphologies of their extant representatives are the most distinctive and intensively modified with respect to the ancestral caviomorph



shape. The derived cavioids showed slower but relatively continuous morphological mandibular changes toward gracile morphotypes (specialized to grazing habits), which began probably during the early Oligocene (Álvarez et al. 2020) and reached their highest degree in the late Miocene radiation of *Cavia* species. The shape changes related to this specialization imply a strong reduction of the coronoid process and caudal positioning of the anterior masseteric scars, which were significantly related to dietary habits. Additionally, other shape changes were noted for this clade in previous contributions, including the enlargement of the diastema and posterior position of the ventral masseteric crest (Vassallo and Verzi 2001; Hautier et al. 2012; Álvarez and Pérez 2019; Álvarez et al. 2020). This complex of features enhances the postero-anterior direction of the movements generated by the superficial layers of the m. masseter and pterygoideus in relation to a more effective grinding action (Vassallo and Verzi 2001; Hautier et al. 2012; Maestri et al. 2016; Marivaux and Boivin 2019). It seems that the almost propalinal grinding acquired by these rodents, in opposition to the typically latero-medial grinding of other mammalian grazers (e.g., Radinsky 1985), is a main factor related to the significant association between dietary habits and the posterior displacement of the ventral masseteric crest (resulting in more suitable configuration for postero-anterior movements of the most external m. masseter) (Table 1). Different to other mammalian clades (e.g., Radinsky 1985), the condylar process height was not recovered as significantly related to dietary habits in the global regression of caviomorphs. Nevertheless, the markedly low position of the condyle in cavioids has been understood as related to the complex of morphofunctional features related to the masticatory mode and dietary specialization of these rodents (e.g., Hautier et al. 2012). Another functional implication of low condylar process is the enhancing of the maximum gapes by diminishing the stretching of masticatory muscles (Turnbull 1970; Emerson and Radinsky 1980; Radinsky 1985; McIntosh and Cox 2016), as this can be seen in a comparison between *Cavia* and *Coendou* (see Herring and Herring 1974: Table 1). Nevertheless, large gapes seem not to be as relevant as the changes in masticatory modes for this strictly herbivore clade (Herring and Herring 1974: 570). Given that this modification only occurred in cavioids, and is not an excluding feature for grazing species (absent in the grass-feeder chinchillids), this would explain the lack of a globally significant association between shape and habits. In parallel with this, one characteristic of cavioid evolution (as well as in chinchillids), is the presence of many shifts in the evolutionary rate of size change as body size increases (Vucetich et al. 2015; Álvarez et al. 2017). The increase of body size in grazing mammals is a common pattern also recorded in ungulates, in relation to the physiological requirements of the consumption of

low-quality foods, with high content of cellulose fibers, such as grasses (Raia et al. 2010; Cassini et al. 2012). This is especially valid for the case of strictly epigeal taxa, in which the fastest rates of increase of body size were detected, such as hydrochoerine and dolichotine cavioids (Álvarez et al. 2017).

It is worth noting that the major or fastest morphological and size changes described for both cavioid and octodontoid caviomorph types occurred mainly during the early Oligocene and lower late Miocene (Vucetich et al. 2015; Álvarez et al. 2017; this study), two time periods that involved major global climatic events and strong changes in the vegetational structure of South America (Barreda and Palazzesi 2007; Strömberg 2011). The shape evolution leading to the octodontoid and cavioid mandibular morphotypes (mainly represented by ctenomyids + octodontids and cavioids) seems to be related to the occupation of subterranean and epigeal niches, respectively, in the open landscapes of southern South America, which progressively expanded through the Cenozoic. This seems to be a completely different eco-evolutionary pathway to that of echimyids, which adapted essentially to forested environments of Central and northern South America (Fabre et al. 2017; Fergnani and Ruggiero 2017).

This morphological evolution of the caviomorph mandible would have resulted from selective processes determining multiple optima occupied by distinct clade-specific phenotypes. As mentioned, timing of differentiation of such morphologies was variable through the phylogeny of the group; this explains the low support obtained for the Early Burst model of adaptive radiation, where evolution is expected to be initially rapid in the whole clade giving rise to multiple morphotypes and then slows through time (Harmon et al. 2010). Thus, both these results as those obtained by Álvarez et al. (2017) reject an adaptive radiation process underlying the evolutionary pattern of extant caviomorphs. Nevertheless, studies including historical information from the available rich fossil record are required to test the tempo and mode of evolution of these rodents.

Conclusions

The patterns of morphological diversification of the mandible of caviomorph rodents were conditioned by a complex set of factors, promoted by major Cenozoic climatic changes, but at the same time restricted by structural limitations and phylogenetic inertia. The effect of these factors was different along clades, in relation to the ecological niches occupied by each one of them. Octodontids, and especially ctenomyids, showed a fast evolution towards morphotypes specialized to fossorial modes of life. However, their resultant morphological diversity is relatively low and related to small sizes needed for life

underground. Derived cavioids had a progressive morphological specialization to abrasive diets (including grass-feeding), being a taxonomically less rich clade, but more diverse in its morphologies and sizes.

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