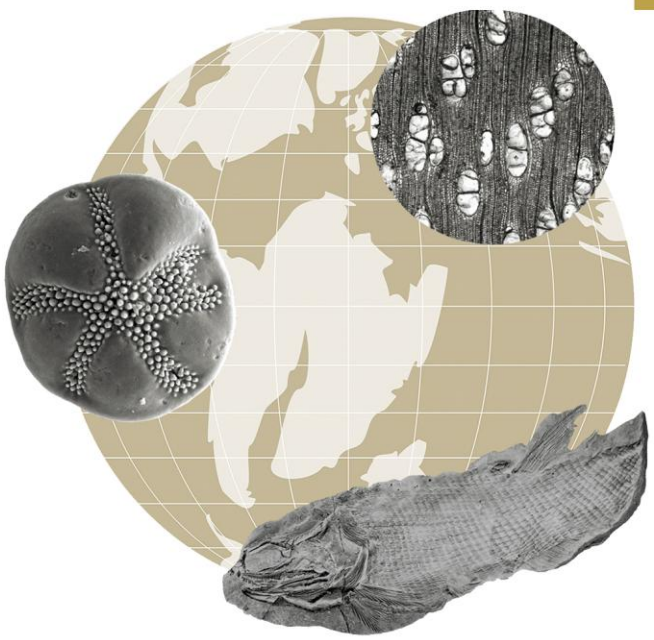
AMEGHINIANA
A GONDWANAN PALEONTOLOGICAL JOURNAL



This file is an uncorrected accepted manuscript (i.e., postprint). Please be aware that this version will change during the production process. This postprint will be removed once the paper is officially published. All legal disclaimers that apply to the journal pertain.

Submitted: 05 January 2026 - **Accepted**: 26 October 2026 - **Posted online**: 27 October 2026

To link and cite this article:

doi: 10.5710/AMGH.26.10.2026.3685

PLEASE SCROLL DOWN FOR ARTICLE

Masticatory muscle reconstruction of extinct caviomorph rodents and its paleobiological implications

Alicia Álvarez[1,2,3], Marcos D. Ercoli[1,2,3], and Guillermo H. Cassini[1,4,5]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Godoy Cruz 2290, C1425FQB Ciudad Autónoma de Buenos Aires, Argentina

[2]Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy (UNJu-CONICET), Av. Bolivia 1239, Y4600GNE San Salvador de Jujuy, Jujuy, Argentina

[3]Laboratorio de Paleontología de Vertebrados, Instituto de Geología y Minería, UNJu, Av. Bolivia 1661, Y4600GNE San Salvador de Jujuy, Jujuy, Argentina.
aalvarez@idgym.unju.edu.ar; mercoli@idgym.unju.edu.ar

[4]División Mastozoología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN-BR), Av. Ángel Gallardo 470, C1405DJR Ciudad Autónoma de Buenos Aires, Argentina

[5]Departamento de Ciencias Básicas, Universidad Nacional de Luján (UNLu), Ruta 5 and Av. Constitución s/n, 6700 Luján, Buenos Aires, Argentina. gcassini@macn.gov.ar

38 pp. (text + references); 3 figs.; 3 tables; 4 Supplementary Online Information

Running Header: Álvarez et al.: Masticatory muscle reconstruction in extinct caviomorphs

Short description: Masticatory muscle proportions and sizes are reconstructed for several extinct caviomorphs and comparisons with extant taxa and paleobiological inferences are presented.

Corresponding author: Alicia Álvarez, Instituto de Geología y Minería, UNJu, Av. Bolivia 1661, Y4600GNE San Salvador de Jujuy, Jujuy, Argentina,
aalvarez@idgym.unju.edu.ar

Abstract. The masticatory apparatus of caviomorphs has functionally relevant myological variants, although framed within a general hystricomorphous plan. We used regressions, based on osteological linear and geometric morphometric proxies, to reconstruct proportions and sizes of masticatory muscles in extinct caviomorphs, and discussed their paleobiological implications. We interpret that, similar to extant ctenomyids, *Actenomys* and *Eucelophorus* possessed robust masticatory muscles, with proportionally large *temporalis* and small infraorbital portion of the *zygomaticomandibularis*, suggesting tooth-digging capabilities, especially for *Eucelophorus*. *Eumysops* was also similar to ctenomyids, although with a smaller *masseter superficialis* and larger infraorbital portion of the *zygomaticomandibularis*, interpreted as more related to hard-food consumption than to tooth-digging. *Telicomys* converged with extant caviids possessing very large *masseter profundus* and *pterygoidei* (*pterygoideus lateralis* and *pt. medialis*), and small *temporalis*, which is associated with horizontal grinding and grass consumption. *Dolicavia* possessed these traits too, but with an unusually large infraorbital portion of the *zygomaticomandibularis* and a small *masseter superficialis*, similar to dipodoids. The light muscular development and emphasis on incisor biting efforts suggests a folivorous and granivorous diet. *Pithanotomys* possessed similar muscular proportions to *Dolicavia*, but with larger *temporalis* and zygomatic arch portion of the *zygomaticomandibularis*, that suggests some degree of tooth-digging capabilities and the consumption of hard- and tough-food items. *Prospaniomys* had a lightly built musculature with mainly generalized proportions but with large *pterygoidei*. This suggests a mixed diet, including leaves and diverse dietary items. The myological diversity of reconstructed extinct taxa falls within that of extant hystricomorphous rodents but extends beyond the range represented by extant caviomorph sample analyzed.

Keywords. Caviomorpha. Masticatory apparatus. Myology. Paleobiology. Regression analyses.

Resumen. RECONSTRUCCIÓN DE LA MUSCULATURA MASTICATORIA DE ROEDORES CAVIOMORFOS EXTINTOS Y SU IMPLICANCIA PALEOBIOLÓGICA. El aparato masticatorio de los caviomorfos tiene variantes miológicas relevantes dentro del plan histricomorfo. Nosotros usamos regresiones, basadas en indicadores osteológicos lineales y morfo-geométricos, para reconstruir proporciones y tamaños de músculos masticatorios en caviomorfos fósiles, discutiendo implicancias paleobiológicas. Similar a ctenómidos vivientes, *Actenomys* y *Eucelophorus* poseyeron musculatura voluminosa, con un *temporalis* grande, y una porción infraorbital del *zygomaticomandibularis* pequeña, sugiriendo habilidades dento-excavadoras, especialmente para *Eucelophorus*. *Eumysops* fue similar a ctenómidos, aunque con un *masseter superficialis* más pequeño y una porción infraorbital del *zygomaticomandibularis* más grande, vinculado al consumo de ítems dietarios duros y dento-excavación eventual. *Telicomys* convergió con cávidos poseyendo *masseter profundus* y *pterigoidei* (*pterygoideus medialis* y *pt. lateralis*) grandes, y *temporalis* pequeño, en asociación con molienda horizontalizada y consumo de pastos. *Dolicavia* poseyó también estos rasgos, pero junto a una porción infraorbital del *zygomaticomandibularis* inusualmente grande, y un pequeño *masseter superficialis*, similar a dipodoideos. La constitución muscular ligera y el énfasis en esfuerzos incisivos sugiere una dieta folívora y granívora. *Pithanotomys* poseyó proporciones similares a *Dolicavia*, pero con una musculatura más voluminosa, *temporalis* y una porción de arco cigomático del *zygomaticomandibularis* más grandes, sugiriendo cierto grado de habilidades dento-excavadoras y consumo de ítems dietarios duros y

resistentes. *Prospaniomys* tuvo una constitución muscular ligera con proporciones mayormente generalizadas pero *pterigoidei* grandes. Esto sugiere una dieta mixta, incluyendo hojas y diversos ítems. La diversidad miológica de los taxones reconstruidos está incluida en la de los roedores histricomorfos actuales, aunque no completamente contenida por la de los caviomorfos actuales analizados.

Palabras clave. Caviomorpha. Aparato masticatorio. Miología. Paleobiología. Análisis de regresión.

Introduction

Caviomorphs are a group of rodents that evolved in South America during, at least, the last 30 million years (Campbell et al., 2021; for an older estimation see Antoine et al., 2012), mostly in a context of continental isolation. Their radiation occurred alongside other native mammals, such as marsupials and extinct relatives, South American ungulates, xenarthrans, and New World monkeys (Vucetich et al., 1999; Pascual & Ortiz-Jaureguizar, 2007; Vassallo & Antenucci, 2015a). They went through taxonomic and morphological diversification events, generally associated with drastic changes in climate and environments, such as those recorded during the Eocene-Oligocene (EOT) and the middle–late Miocene climate transitions (Vucetich et al., 1999, 2015; Pérez & Pol, 2012; Upham & Patterson, 2015; Verzi et al., 2016; Álvarez et al., 2017; Boivin et al., 2019). Caviomorphs present a large ecomorphological diversity in terms of body sizes, substrate preference, locomotion types, and social systems (Patton et al., 2015; Vassallo & Antenucci, 2015b; Wilson et al., 2016). However, they are restricted in terms of their diet, which is mostly herbivorous, with occasional omnivory reported in some extant echimyids and inferred for some extinct forms (Vucetich & Verzi, 1996; Borroto Páez & Woods, 2012; Wilson et al., 2016). The predominantly herbivorous diet of caviomorphs (already established in earlier representatives) may have been a key factor to explain the success of these rodents during the development of new, more open environments, such as savannahs or shrublands, especially during the EOT and the late Oligocene, when a migration to high latitudes is recorded (see Mess et al., 2001: 201; Vucetich et al., 2010). Regarding the morphology of their masticatory apparatus, all caviomorph rodents correspond to a single masticatory osteo-myological morphotype: hystricomorphy.

Hystricomorphy is a topographical reorganization of masticatory muscles and related bony structures that was acquired in a few rodent groups (Hautier et al., 2015; Swanson et al., 2019; Potapova, 2020; but see Naples & Martin, 2000). This configuration increases the volume and available surface for the attachment of the most anterior layer of the *zygomaticomandibularis*, expanding the area of origin of the muscle towards the rostrum: the infraorbital portion (Woods, 1972; Potapova, 2020). This morphology is associated with the capability to produce large vertical forces, which functionally suggests either a collaboration with, or greater capacity than, the *temporalis* in the execution of vertical forces, resulting in a shift of the vertical resultant line of action to a more anterior location (Herrel et al., 2012; Cox, 2017). In turn, hystricomorphy implies lesser strain on the cranium when biting compared to other derived rodent configurations (Cox, 2017). Hystricomorphy relates, to some extent, with a limitation of the gape which could restrict the size of ingested food items (Herring & Herring, 1974; Cox, 2017). Additionally, several hystricomorphous rodents, including all caviomorphs, possess a *masseter superficialis* mainly originating from a small area on the anterior root of the zygomatic arch which inserts onto a broadly extended area on the medial surface of the mandible. This would extend the contractile, horizontalized portion of that muscle (*e.g.*, Álvarez et al., 2023). When the mandible is in a forward position, the tendon of origin will be arranged in a mostly vertical orientation contributing to vertical efforts. Thus, the hystricomorphous configuration is linked to gnawing but also to chewing modes that frequently include a large antero-posterior component, and even a preponderant horizontal (grinding) component, frequently related to the consumption of hard and fibrous food items (Hiiemae, 1971; Cox, 2008; Druzinsky et al., 2011; Potapova, 2020).

Among hystricomorphous rodents, three large morphotypes have been recognized (bathyergomorphs, generalist hystricomorphs, and specialist hystricomorphs) that, in turn, could represent part of a continuum between forms with diverse muscle proportions (Ercoli et al., 2023). These morphotypes vary from having a very well-developed *temporalis* and reduced/atrophied infraorbital portion of the *zygomaticomandibularis* (bathyergomorphs) to reduced *temporalis* and highly-developed infraorbital portion of the *zygomaticomandibularis* (specialist hystricomorphs), among other features. The generalist hystricomorph morphotype, which includes caviomorph rodents and some dipodoids, is characterized by intermediate proportions compared to the other hystricomorphous morphotypes (Ercoli et al., 2023). Its representatives demonstrate a great ecological versatility regarding dietary strategies, chewing movements, and functions, ranging from crushing to grinding forms, from grass eaters, omnivores to seed and insect eaters, and including chisel-tooth digging taxa (Wilkins & Cunningham, 1993; Hautier et al., 2012; Becerra et al., 2014; Álvarez et al., 2020, 2023; Potapova, 2020). Particularly for caviomorphs, they present important disparity in their osteo-muscular configurations. The infraorbital portion of the *zygomaticomandibularis* has different proportions, including a marked reduction in some Caviinae, and different configurations regarding its site of insertion (*e.g.*, Woods, 1972; Álvarez & Pérez, 2019). Differences in other muscle proportions and bone structures associated with masticatory muscle attachment are notable. Among them, the lateralization of the angular process and the ventral masseteric crest (*i.e.*, hystricognathy) is well marked in some clades, such as ctenomyids, while it is very reduced in others, such as caviids (almost a reversion to sciurognathy according to some authors; *e.g.*, Hautier et al., 2011), although this does not imply the modification of the muscular configuration (see Álvarez et al., 2023).

The fossil record of caviomorphs is very rich, and it has a good taxonomic representation of the different clades from the beginning of their diversification. However, it is infrequent to find crania and mandibles with such a degree of preservation that reconstruction of the complete musculature can be undertaken. There are only a few attempts in the literature to reconstruct masticatory myological traits (De Santis & Moreira, 2000; Fernández et al., 2000; Álvarez & Arnal, 2015; Álvarez & Pérez, 2019) or, even less so, those in which they are quantified (Blanco et al., 2012; Rinderknecht et al., 2019; Bogel et al., 2025).

The interpretation of the myological diversity of extinct caviomorphs is an incompletely explored topic, including the existence or extinction of certain variants, and whether past masticatory diversity can be contained within current morphological diversity. In this work, we set out to reconstruct the muscular proportions and absolute muscle masses of the main masticatory muscles in several extinct taxa represented by complete fossil materials. The functional and paleobiological implications of the myological reconstructions obtained are discussed in the comparative context of the diversity of hystricomorphous configurations currently recognized, and in light of the information previously available for the extinct taxa.

Institutional abbreviations. IANIGLA-PV, Paleovertebrate collection of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Mendoza, Argentina; MACN PV/CH, Paleovertebrate/ Chubut, respectively, collections of the Museo Argentino de Ciencias Naturales, CABA, Argentina; MEF-PV, Paleovertebrate collection of the Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina. MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Buenos Aires, Argentina.

Anatomical and other abbreviations. CrL, cranium, lateral view; CrD, cranium, dorsal view; CrV, cranium, ventral view; MandL, mandible, lateral view. APS, angular process shape; BL, basicranial length; CE, coronoid process extension; IFE, infraorbital fossa extension; MME_L, masticatory muscle extension, lateral view; MME_M, masticatory muscle extension, mandible; MME_V, masticatory muscle extension, ventral view; MPA, *masseter profundus* advancement; PAE, *pterygoidei* (*pterygoideus lateralis* and *pterygoideus medialis*) attachment extension; PAH, *pterygoidei* attachment height; PPP, paraoccipital process position; TFL, temporal fossa length; TFW, temporal fossa width; VRH, vertical ramus height; ZA, *zygomaticomandibularis* advancement; ZAE, zygomatic arch elevation; ZAS, zygomatic arch shape; ZAW, zygomatic arch width. PC, principal component; Rel, relativized values.

Materials and Methods

Materials. In order to assess the masticatory muscle proportions and sizes in extinct caviomorph rodents, we used 13 specimens corresponding to six species: *Actenomys priscus* (N = 3; Ctenomyidae), *Dolicavia* sp. (N = 2; Caviidae), *Eucelophorus chapalmalensis* (N = 1; Ctenomyidae), *Eumysops* sp. (N = 3; Echimyidae), *Pithanotomys chapalmalensis* (N = 2; Octodontidae), *Prospaniomys priscus* (N = 2; Abrocomidae) (see further details in Supplementary Online Information 1). Additionally, we included the extinct giant rodent *Telicomys giganteus* (Dinomyidae), which was reconstructed in the original formulation of the equations applied here (Ercoli et al., 2025). The selection and analysis of the extinct species were conditioned by the preservation of all relevant muscular scars of the masticatory apparatus which is a requirement for the quantification of proxies.

The ctenomyids *Actenomys* and *Eucelophorus* present similar morphologies that, to some extent, resemble those of extant *Ctenomys* (*e.g.*, Fernández et al., 2000; Reig & Quintana, 1992). A body size comparable to those of the largest species of the latter genus (1-2 kg; *i.e.*, *C. conoveri*; Wilson et al., 2016) was estimated for *Actenomys* (1.3 kg; Fernández et al., 2000). In the case of *Eucelophorus*, its largest species (*E. cabrerai*) was compared (without size estimation) to one of the largest species of *Ctenomys* (*C. tuconax*, which weighs around 600 gr; Reig & Quintana 1992; Wilson et al., 2016). They are recorded in Pliocene (*Actenomys*) and Pliocene-to-Pleistocene (*Eucelophorus*) layers along the Atlantic coasts of Buenos Aires province (Argentina; Fig. 1). They have been inferred as semi-fossorial/fossorial or specialized burrowers, respectively (Genise, 1989; Reig & Quintana, 1992; De Santis & Moreira, 2000; Bogel et al., 2025). The octodontid *Pithanotomys* (Pliocene-to-Pleistocene strata of Central and Northwestern Argentina; but see Candela et al., 2023 for a probable late Miocene record) was possible similar sized to that of largest *Ctenomys* (e.g., *C. conoveri*) and other medium-sized caviomorphs such as dasyproctids and some erethizontids (~ 1 kg). *Pithanotomys* has been reconstructed in alternative ways: as fossorial or cursorial (Olivares et al., 2010a; Fernández Villoldo et al., 2020). The abrocomid *Prospaniomys* (early Miocene of the Argentinean Patagonia; Arnal & Kramarz, 2011; Fig. 1) was reconstructed as an omnivore-generalized herbivore, larger than *Abrocoma* (~ 200 gr; Wilson et al., 2016) and similar to the caviid *Cavia* (~ 500 gr; Wilson et al., 2016) (Álvarez & Arnal, 2015; Boivin et al., 2024). The echimyid *Eumysops* (Pliocene-Pleistocene; Olivares *et al*., 2020; Fig. 1) was likely an epigean, open-habitat adapted taxon, with a body size larger than other myocastorines (~ 250-500 gr; Wilson et al., 2016), except for *Myocastor* (6-7 kg; Wilson et al., 2016), and similar to the caviid *Cavia* (Olivares et al., 2010b, 2020; Boivin et al., 2024). The caviid *Dolicavia* (Pliocene

layers of Buenos Aires province, Argentina; Quintana, 1997; Fig. 1) was a cavy-like taxon, with cranial morphology similar to *Microcavia* (Quintana, 1997; Álvarez & Verzi, 2014). The dinomyid *Telicomys* (late Miocene-Pliocene from Argentina and Peru; Rinderknecht et al., 2019; Fig. 1) was a large-sized (~ 100 kg, larger than capybaras which weigh up to 65 kg; Wilson et al., 2016), mixed-feeder (Rinderknecht et al., 2019), whose musculature was recently reconstructed by Ercoli et al. (2025).

Methods.

We analyzed the myological configuration of these seven fossil taxa in a comparative morpho-functional framework and in the context of the diversity of caviomorphs and other extant hystricomorphous rodents (*e.g.*, dipodoids). The addition of the latter allowed increasing the extant models considered in order to consider that extinct caviomorph taxa might differ from extant ones and resemble other hystricomorphous rodents in some myological and/or ecomorphological features. In order to reconstruct myological features of the main muscle units of the masticatory apparatus, we used two sets of equations proposed by Ercoli et al. (2025). To reconstruct myological proportions, we used the "Path 1" equations (Supplementary Online Information 2). The "Path 1" equations considered only taxa located in the region of a myospace named Pathway 1 by Ercoli et al. (2023), to which all extant hystricomorphous species are assigned, and also included suinomorphs, protrogomorphs and bathyergomorphs, and equidomorphs. Additionally, the "Total-sampled equation" from Ercoli et al. (2025) was used to reconstruct the proportion of the *pterygoideus medialis* in *Prospaniomys*, because a negative, nearly zero value (-0.4%), was obtained with the Path 1 equation, and as such, an unreliable prediction. Beyond this particular case, the "Path 1" equations for the remaining taxa have smaller predictive errors (ranging from 8.6 to 18.5%) compared to the Total-Sampled equations (ranging from

20.1 to 57.1%; Ercoli et al., 2025); therefore, the former was preferred for reconstructing myological proportions. To reconstruct the total absolute muscular masses, we used the equation designed by Ercoli et al. (2025; Supplementary Online Information 2). Following a correction on the corresponding script (replacing "predict" by "predictMultstep" in line 226) given by Ercoli et al. (2025: supplementary material 5) we present here the corrected value for the total muscle mass estimated for *Telicomys giganteus* (correcting that presented by Ercoli et al., 2025).

Following Ercoli et al. (2025), we digitized 17 measurements and two landmark configurations required as osteological proxies (Fig. 2; Supplementary Online Information 3, 4). Measurements and landmarks were digitized on photographs. The vast majority of these images were taken by the authors and some are from cited bibliographic sources or taken upon request by colleagues (Supplementary Online Information 1). The linear and geometric-morphometric proxies were designed to represent the available space and main morphological changes of the attachment sites for main units of the masticatory muscles of herbivorous mammals (*masseter superficialis*, *masseter profundus*, zygomatic arch portion of the *zygomaticomandibularis*, infraorbital portion of the *zygomaticomandibularis*, *temporalis*, *pterygoideus medialis*, and *pterygoideus lateralis*). Photographs were scaled and measurements were digitized using TPS software (Rohlf, 2015). Considering that almost all extinct taxa were represented by several specimens (except *Eucelophorus*; Supplementary Online Information 1), we checked the correspondence in the general sizes of crania and mandibles in each taxon. In relation with that, two additional measurements were taken in the longitudinal plane (*i.e.*, the distance between the anterior border of the glenoid fossa and the anterior end of the incisors in the cranium, and the same measurement between the condyle and incisors in the mandible). We

confirmed that all specimens of each taxon were similar in these measurements relative to the threshold of +/-10%, following the criterion established by Ercoli et al. (2025; result not shown). These measurements were not included in the predictive equation. Mean values of proxies for each taxon were computed and used for further analyses.

The raw linear measurements were transformed following the procedure in Ercoli et al. (2025). First, we computed the geometric mean (GM) values for a subset of the raw measurements, including those that do not contain values that are zero or near zero ("Data for regressions to estimate absolute muscle masses" in Supplementary Online Information 3). Then, ratios between raw measurements and GM were computed. Both geometric morphometric datasets were projected in the corresponding principal component spaces (see Ercoli et al., 2025).

For the estimation of muscle proportions in fossils, their relativized linear measurements together with their scores on the principal components (see Supplementary Online Information 3) were included in the corresponding equations ("Path 1", "Total-sampled"). Given that the original muscle proportions were logit-transformed to serve as response variables during the construction of the regression equations (see Ercoli et al., 2025), the output of the estimations based on these logit regressions was re-transformed to obtain the proportions of main units and subunits of the masticatory muscles for fossils. Once the predictions for fossils were obtained, the sum of all muscle proportions for each taxon was rescaled to add up to 100% (correcting deviations, in all cases lesser than 3%).

For the total absolute mass estimations, the log10-transformed measurements were included as predictor variables in the corresponding equations ("Path 1", "Total-sampled"; see above). It is important to highlight that, when we refer to the value of total masticatory adductor mass, it means the combination of zygomasseteric complex +

temporalis + *pterygoidei* (*i.e.*, *pterygoideus lateralis* and *pterygoideus medialis*) of one side of the masticatory apparatus.

The combination of both results (*i.e.*, total absolute adductor mass and proportions of each bundle and muscles) allowed us to infer the absolute mass of each main unit and subunit. All other methodological details, software used, and decision fundamentals were explained in detail by Ercoli et al. (2025).

The reconstructed proportions of each extinct caviomorph were projected onto the myospace (*i.e.*, morphospace built up exclusively from myological variables) presented by Ercoli et al. (2023), in order to evaluate the correspondence between these inferences and extant morphotypes. Additionally, the reconstructed proportions of each extinct taxon analyzed, together with the proportions of selected extant dipodoids, were projected in a second myospace constructed only on the basis of extant caviomorphs (Table 1). This projection was made using the R environment (R Core Team, 2024). In this second myospace, we delimited the morphospace grouping taxa by their habits considering diet and fossorial abilities, following bibliographic sources (Wilson et al., 2016; Álvarez et al., 2020; see Table 1). The categories were defined as follows: tough-food eaters are taxa that typically include a large quantity of fibrous items, such as grasses, in their diet (*i.e.*, caviids); hard food eaters are taxa that typically include hard to break plant materials, such as seeds or stems, in their diet (*i.e.*, chinchillids); tooth diggers/strong-biters are taxa that use their masticatory apparatuses for digging or other activities that demand higher efforts, such bark gnawing (*i.e.*, ctenomyids, some echimyids); generalists are taxa that include a wide variety of dietary ítems (*i.e.*, some octodontids), without a specialization to the other categories defined above. To evaluate the correspondence between myological proportions and the dietary classes proposed here for extant caviomorphs (Table 1), we calculated the intraclass correlation

coefficient (ICC). This analysis was run using the ICC package (version 2.4.0; Wolak et al., 2012), and the result was interpreted following Koo & Li (2016).

The reconstructed myological configurations were compared with previous inferences for each taxon, when available. Additionally, the ecomorphological information about masticatory configuration, diet, and other paleobiological aspects was considered in the paleobiological interpretation of each taxon.

Results

Masticatory muscle sizes and proportions

Except for *Telicomys*, all extinct taxa analyzed were small-sized caviomorphs although they presented dissimilar values for total masticatory muscle mass (Table 2). *Prospaniomys* was reconstructed as possessing the smallest masticatory muscles (3.776 gr), followed by *Dolicavia* (4.917 gr), both values are similar to that of some extant cavies (*e.g.*, *Galea leucoblephara*, 3.254 gr), chinchillas (*Chinchilla lanigera*, 3.366 gr), and some ctenomyids (*e.g.*, *Ctenomys australis*, 4.922 gr) (Table 1). *Actenomys*, *Eucelophorus*, and *Eumysops* were reconstructed with the highest values (9.095 gr, 7.062 gr, and 8.959 gr, respectively; Table 2) surpassing the value presented by largest extant cavies (*e.g.*, *Cavia aperea*, 6.645 gr). *Telicomys* was reconstructed as possessing a total muscle mass of 354.983 gr.

The reconstructed proportions for extinct taxa indicate that, in comparison to the other caviomorphs, the ctenomyids *Actenomys* and *Eucelophorus* possessed high values for the *masseter superficialis* and *temporalis*, and moderate to low values for other masseter bundles, infraorbital part of the *zygomaticomandibularis* and *pterygoideus medialis*, similar to extant ctenomyids (Tables 1, 2). The proportions reconstructed for

Eucelophorus stood out by their more extreme configuration in comparison to *Actenomys* and other ctenomyids.

The reconstructed proportions for *Dolicavia* stand out among caviomorphs by the high development of the *masseter profundus* and *pterygoidei*, and low values for the *masseter superficialis*, *temporalis*, and zygomatic arch portion of the *zygomaticomandibularis* (Tables 1, 2). The reconstructed proportions for this taxon were similar to extant caviids and those reconstructed for *Telicomys* by Ercoli et al. (2025). *Dolicavia* differs from other caviids by the presence of a well-developed infraorbital portion of the *zygomaticomandibularis* and extreme reduction of the *masseter superficialis*.

Eumysops, *Pithanotomys*, and *Prospaniomys* were reconstructed with intermediate and more generalized myological proportions. *Eumysops*, and in lesser degree *Pithanotomys*, were highlighted by a well-developed infraorbital portion of the *zygomaticomandibularis* as well as the *temporalis*. On the other hand, *Prospaniomys* and *Pithanotomys* were characterized by well-developed bundles of the *masseter* originating from the zygomatic arch, while *Pithanotomys* with a particularly reduced *masseter superficialis* (Tables 1, 2).

Herbivorous myospace

In the herbivorous myospace (Fig. 3A), morphotypes that positioned at positive values of the first two principal components (PC1, PC2) correspond to myological proportions with high values for the bundles of the *masseter* that originate from the zygomatic arch and infraorbital portion of the *zygomaticomandibularis*, and low values for the *temporalis* (see Ercoli et al., 2023 for detailed description and discussion of this myospace). Most of the extinct caviomorphs were placed within the polygon that

corresponds to generalized hystricomorphs which, in turn, includes all extant caviomorphs. PC1 accounted for most of the myological variation among the extinct taxa. The ctenomyids *Actenomys* and *Eucelophorus* were placed towards the lowest values on PC1. *Dolicavia* exhibited the highest values of PC1 outside that polygon and was located close to the polygon that included the specialized hystricomorphs. *Eumysops*, *Pithanotomys*, *Prospaniomys*, and *Telicomys* were placed at intermediate values between the aforementioned fossils and high values of PC1, within the generalized hystricomorph polygon.

Caviomorph myospace

The first two axes of the myospace defined by extant caviomorphs explained 85.79% of the total myological variance of the sample (Fig. 3B). Towards positive values of PC1 (69.75%), the main changes were related to larger proportions of *masseter superficialis* and secondarily *zygomaticomandibularis* bundles and *temporalis*, and lower proportions of *masseter profundus* (Table 3). Towards positive values of PC2 (16.04%), the main changes were related to larger proportions of the infraorbital portion of the *zygomaticomandibularis* and *pterygoideus medialis*, and lower proportions of *temporalis* and *masseter superficialis*, and secondarily, the *masseter profundus* (Table 3). These axes showed a clear segregation between extant taxa with different life habits (Fig. 3B). Those which are tough-food eaters (which typically include a large quantity of grasses in their diet; *i.e*., caviids) exhibited negative values of PC1; fossorial, subterranean, and other strong-biting taxa (*i.e.*, *Ctenomys* spp., *Euryzygomatomys*, *Myocastor*) showed positive values of PC1. Taxa that include hard food items in their diet (*i.e.*, *Chinchilla*, dipodoids) presented positive values of the PC2. The single taxon here analyzed that possesses intermediate and generalized life habits, *Octodon*, was

found near to the center of the myospace. Regarding extinct taxa, *Telicomys* fell near to tough-food eaters. *Actenomys* and *Eucelophorus* were associated with tooth-diggers and strong-biters, falling inside or possessing even more extreme myological proportions than extant representative with these habits. *Dolicavia*, *Pithanotomys*, and *Prospaniomys* were distributed along the space between grazer and hard-food-eating taxa, while *Eumysops* was positioned between the latter group and strong-biters. In accordance with the extant species distribution in the morphospace, the correlation between myological proportions and dietary classes was very high (ICC = 0.91), a value that suggests an excellent association between variables (see Koo & Li, 2016).

Discussion

There are some previous attempts to quantitatively reconstruct the myological configurations in several extinct caviomorph rodents (*Actenomys*, *Josephoartigasia* and *Telicomys*; Blanco et al., 2011; Cox et al., 2015; Rinderknecht et al., 2017; Bogel et al., 2025). These are valuable contributions because they contribute to a practically unexplored field in caviomorphs. However, these reconstructions, although give the quantification of muscular variables, are largely based on qualitative, expert-driven estimations (e.g., volumes modelling is the result of decision taken by the user on the base of its expertise) rather than a standardized quantitative framework (*e.g.*, predictive equations) to constrain muscle volumes/masses. In this study we present the first reconstruction of myological proportions and muscle sizes of the masticatory apparatus in several extinct caviomorph taxa that relies on quantitative predictive models. The implemented method, based on a broad comparative framework and with statistical support, represents a step forward in comparison with previous inferences.

The reconstructed muscle proportions of extinct caviomorphs fell within the range of the values known for extant hystricomorphous rodents. Particularly they grouped with generalized hystricomorphs, and extant caviomorphs, which likely reflects a more or less persistent hystricomorphous myological plan. Our results reveal that for some extinct taxa (*Dolicavia*, *Eumysops*, and *Pithanotomys*), the infraorbital portion of the *zygomaticomandibularis* was reconstructed as being larger than that present in extant caviomorphs. Accordingly, the infraorbital fossa of these taxa is larger, and particularly taller, than in extant related species, supporting these reconstructions and suggesting an interesting variation in the myological configuration when compared to extant caviomorph representatives.

The ctenomyids *Actenomys* and *Eucelophorus* were reconstructed as possessing robust masticatory musculature and with similar muscle proportions to extant *Ctenomys* and *Euryzygomatomys*, which possess fossorial or subterranean habits and, in the case of the latter taxon, bark gnawing habits, and *Myocastor* which has semi-aquatic habits but constructs its own burrows and resting platforms made of sticks and other vegetation (D'Adamo et al., 2000; Wilson et al., 2016). Remarkably, these extinct forms were inferred as possessing the largest *temporalis* among caviomorphs, including *Ctenomys* species. An enlarged zygomatic arch portion of the *zygomaticomandibularis* was also reconstructed for these ctenomyids, particularly *Eucelophorus*. This is partially comparable and consistent with the results obtained by Bogel et al. (2025, fig. 6) who estimated large cross-sectional areas for both muscles in *Actenomys*. Both *temporalis* and zygomatic arch portion of the *zygomaticomandibularis* are dedicated to exert vertical forces so they are linked to functions such as incisive biting and/or orthal chewing (Turnbull, 1970; Becerra et al., 2014; McIntosh & Cox, 2016; Potapova, 2020). Considering the flattened cheek teeth and procumbent, deeply inserted incisors

458 of ctenomyids, the first option is a more suitable explanation in relation to tooth-digging
459 activities and aggressive encounters described for extant species (Becerra et al., 2014;
460 Becerra, 2015; McIntosh & Cox, 2016). Additionally, the *temporalis* allows a marked
461 retraction of the jaw and is suitable for resisting pulling efforts which may be required
462 when removing objects during digging (Hiiemae, 1971; Vassallo, 1998; Cox et al.,
463 2020; Potapova, 2020 and references therein).

464 *Masseter superficialis* was highly developed in *Actenomys* and *Eucelophorus*, as
465 also occurs in extant ctenomyids. The line of action of this muscle is forward and tilted
466 anteriorly, contributing to horizontal movements during chewing and to powerful
467 incisive biting, but without restricting gape as other zygomasseteric bundles may do
468 (Cox, 2017; Álvarez et al., 2023), which is functionally relevant when tooth-digging
469 capabilities and/or powerful biting are needed. On the other hand, the infraorbital
470 portion of the *zygomaticomandibularis*, which also has a forward line of action but
471 restricts gape to a greater degree (Cox, 2017), is not well developed in hystricomorph
472 rodents that are specialized in tooth-digging habits (*e.g.*, Becerra *et al*., 2011, 2014;
473 McIntosh & Cox, 2016; Cox et al., 2020), and was reconstructed similarly in extinct
474 representatives (Table 2; De Santis & Moreira, 2000).

475 Considering the ecomorphology of extant ctenomyids (which are burrowers and
476 grass-eaters; Comparatore et al., 1995; Wilson et al., 2016), the relatively poor
477 development of *pterygoidei* and *masseter profundus* should be interpreted as linked to
478 the increment of other masticatory bundles, as the *masseter superficialis* and *temporalis*
479 (in relation to digging specializations; see McIntosh & Cox, 2016), instead of reflecting
480 a lesser importance of horizontal movements dedicated to chewing, which is the
481 common pattern in caviomorphs. Even more, these caviomorphs have a diet containing
482 grasses and/or other fibrous elements that require considerable effort to masticate.

Finally and in support of our muscular inferences, the cranio-mandibular bony anatomy that characterizes *Actenomys* and *Eucelophorus*, as well as extant ctenomyids is characterized by a robust skull with broad surface for muscular attachments, procumbent and deeply inserted incisors, high coronoid and condylar processes, and robust and tall zygomatic arches (Reig & Quintana, 1992; Verzi & Olivares, 2006; Bogel et al., 2025). However, some differences between the two fossils can be denoted. Previous studies suggested a high specialization for tooth-digging and subterranean habits for *Eucelophorus* (Reig & Quintana, 1992; Verzi & Olivares, 2006; Vieytes et al., 2007). On the other hand, *Actenomys* possessed more slender incisors, less marked tooth-digging capabilities, probably accompanied with scratch-digging specializations. Beyond the mode of excavation, it is assumed that the latter taxon made its own burrows (Genise, 1989; De Santis & Moreira, 2000; Fernández et al., 2000; Verzi & Olivares, 2006; Elissamburu et al., 2011; Bogel et al., 2025). Muscle proportions inferred in this work fit with life habit differentiation between both genera. In all muscles, when compared with other caviomorphs, *Eucelophorus* was more specialized in tooth-digging: it had larger *temporalis*, zygomatic arch portion of *zygomaticomandibularis*, and *masseter superficialis*, and smaller *masseter profundus* and *pterygoidei*. The extreme configuration of the masticatory myology of *Eucelophorus* (Fig. 3B) is consistent with the interpretation that this taxon is the South American rodent with the strongest specialized morphology for tooth-digging (Verzi & Olivares, 2006). On the other hand, *Actenomys* was reconstructed with larger *masseter profundus* and *pterygoidei* than *Eucelophorus*, which suggests a probable higher proportion of fibrous items in its diet, even though the proportions of *Eucelophorus* could be a by-product of the modifications for tooth-digging displayed by this genus. The latter can be considered a speculation that posits tooth-digging as the leading

adaptive process and that dietary adaptions would be subject to the freedoms that the former allows.

The reconstructed muscle proportions for the extinct caviid *Dolicavia* stand out because of the presence of some values similar to those of extant caviids, such as a large *masseter profundus* and a small *temporalis*, but with a notably small *masseter superficialis* and an unusually large infraorbital portion of the *zygomaticomandibularis*. These latter features resemble those of the dipodoids considered here and, to a lesser degree, to other hystricomorphous rodents with large infraorbital portion, such as pedetids (Gambaryan et al., 1980; Offermans & de Vree, 1993). This explains the intermediate position of *Dolicavia* in the myospaces between those taxa and caviids (Fig. 3). A large infraorbital portion of the *zygomaticomandibularis* is related to strong biting effort by the incisors or the anterior cheek teeth and, ultimately, the consumption of hard dietary items (*e.g.*, Herrel et al., 2012; Cox, 2017). The muscular morphotype of *Dolicavia* is not represented among the caviomorph morphotypes studied here (Fig. 3) but *Dolicavia´*s cranial and dental morphology resembles that of the caviid *Microcavia*. These genera share more gracile skulls, large orbits, less extended temporal fossa, and generalized heart-shaped lobe tooth morphology in the context of caviids, which are the caviomorphs with diets more specialized for including large amounts of grasses (Quintana, 1997; Prado et al., 1998; Álvarez & Verzi, 2014; Boivin et al., 2022). *Microcavia* has a mainly folivorous diet which may also include stems, seeds, small fruits, and represents the least specialized grass-eating taxon among extant caviines (Tognelli et al., 1999; Sassi et al., 2007; Larramendy, 2020). Accordingly, *Dolicavia* displayed a non-fossorial morphotype (although it used burrows opportunistically; Genise, 1989; Elissamburu et al., 2011), with a reduced *temporalis* and a large infraorbitalis portion of the *zygomaticomandibularis*. This configuration would shift

anteriorly the resultant of the forces exerted by masticatory muscles to enhance the action of the incisors or anterior cheek teeth. This suggests a diet with a large proportion of hard, but small items, such as stems, small fruits, and seeds, as well as grasses, although without a specialization on the latter item.

The reconstructed proportions for the extinct dinomyid *Telicomys* (see also Ercoli et al., 2025) matched, in several aspects, with those recorded for extant caviomorphs whose diet include a large proportion of fibrous items, including grass (*e.g.*, caviids; Fig. 3; Guichón & Cassini, 1998; Tognelli et al., 1999; Sassi et al., 2007; Larramendy, 2020). The reconstructed proportions for *Telicomys* indicate the presence of small *temporalis*, *masseter superficialis* and zygomatic arch portion of the *zygomaticomandibularis*, and a large *masseter profundus*, resembling extant caviids. These myological traits can be related to the prevalence of horizontal grinding movements and to a lesser importance of powerful incisor biting and retraction forces, and the absence of tooth-digging specializations (Cox, 2017; Álvarez et al., 2023). Previous studies, in contrast, suggested that this taxon would have displayed a powerful incisive biting because of the estimation of high forces and very robust incisors (Rinderknecht et al., 2019). The large size of this taxon could explain large muscular masses and hence large bite forces. More specifically, Rinderknecht et al. (2019) reconstructed a very large cross-section area for the infraorbital portion of the *zygomaticomandibularis* because of the presence of four deep premaxillary fossae that would have increased muscle volume. The estimation of larger forces is probably linked to this feature. The reconstructed proportions in our study support the inference for *Telicomys* as probable grass-eating taxon. However, although in the literature extinct dinomyids are generally not described as having strict grazing diets but rather as mixed feeders, including twigs or branches (Candela et al., 2013; Rinderknecht et al., 2019),

the cheek teeth morphology, which is euhypsodont and include aligned lophes, does not contradict an important grass component in the diet, as we inferred through muscular proportions.

The reconstructed proportions of the abrocomid *Prospaniomys* reflect a particular combination of traits. On one hand, it is inferred as possessing large *pterygoidei*, a small zygomatic arch portion of the *zygomaticomandibularis*, and moderately to small *masseter superficialis*, traits typically observed in grass-eaters such as caviids (Fig. 3B; Table 2; Álvarez et al., 2023). On the other hand, *Prospaniomys* was reconstructed with a very well-developed infraorbital portion of the *zygomaticomandibularis*, more similar to generalized forms. The moderate to large *masseter profundus* and *temporalis* in addition to a lightly-built masticatory musculature indicate an intermediate configuration between grass-eater taxa and generalized ones, which conflicts with the possibility of the prevalence of strong horizontal masticatory movements and dependence on consumption of fibrous items. This reconstruction partially agrees with that proposed by Álvarez & Arnal (2015) who described *Prospaniomys* as presenting a relatively well-developed *temporalis*, including a large infraorbital portion of the *zygomaticomandibularis*, and moderate to large *masseter profundus*. Based on these traits and the presence of a brachydont and bunodont dentition those authors suggested an omnivorous-generalized herbivorous diet for this taxon. In summary, considering the osteo-myological data available for *Prospaniomys*, it can be understood as a caviomorph species with generalized masticatory apparatus, with a mixed diet that would include leaves and a wide variety of dietary items, with *Octodon* being a suitable extant caviomorph analogue.

In the case of the extinct octodontid *Pithanotomys*, the reconstructed proportions resemble, to some degree, those inferred for *Prospaniomys* (Fig. 3; Table 2). Among

these features, the presence of a large *masseter profundus* and a moderate development of the *pterygoidei*, are highlighted. However, *Pithanotomys* presented a smaller *masseter superficialis* and a larger development of the *temporalis* and both portions of the *zygomaticomandibularis*, muscles involved in vertical forces exerted at the level of incisors and anterior cheek teeth. Proportions inferred for this taxon were similar to those of generalized dipodoids, such as *Zapus*. This muscle configuration suggests strong incisors utilization, although the gape would have been limited due to the presence of a large infraorbital portion of the *zygomaticomandibularis*. This strong incisor biting ability would have been combined with moderate grinding, as inferred from the dental morphology of *Pithanotomys*, including misaligned occlusal relieves and enamel bands (Greaves, 1973; Becerra et al., 2012). All these features would suggest dietary habits more similar to taxa that eat stems, tubers, seeds, and small fruits, without ruling out fibrous items, such as grass, but without evidence of extreme specializations to grass consumption. Fossorial habits were previously suggested for this taxon (Olivares et al., 2010a). The presence of a large infraorbital portion of the *zygomaticomandibularis* is not found in extant subterranean caviomorphs for which muscular data is available (*i.e.*, *Ctenomys*; Becerra et al., 2011, 2014; Ercoli et al., 2023), which could contradict the inference of fossorial habits. However, a large infraorbital portion of the *zygomaticomandibularis* does appear to occur when examining at the cranial morphology of some fossorial taxa, for example in *Lagostomus* (Álvarez, 2012), that combine scratch- and tooth-digging modes to construct their burrows (Fernández, 1949; Morgan et al., 2007). This myological feature, together with skull shape traits such as small eye perimeter and narrowness of incisive foramina (the latter related to the strengthening of the cranium; Olivares et al., 2010a), would indicate fossorial habits for this taxon. Our reconstruction lies between two previous proposals

608 that are contradictory to some extent: fossorial habits had been proposed through linear
609 measurements on the skull (Olivares et al., 2010a), and cursorial habits similar to those
610 of *Octomys*, through the study of endocranial anatomy (Fernández Villoldo et al., 2020).
611 In summary, the ability to consume tough and/or fibrous items, but without a dominance
612 of grasses in the diet, is proposed for *Pithanotomys*, as well as occasional digging
613 activities with incisors, without being a strict tooth-digger.
614 Muscle proportions reconstructed for the echimyid *Eumysops*, which differ
615 markedly from other caviomorphs in the sample, caused this genus to be located in a
616 position not shared with any other taxon in the caviomorph myospace (Fig. 3B).
617 *Eumysops* would have presented a relatively large *temporalis* and a moderately
618 developed *masseter profundus*, both traits similar to that observed in burrower
619 caviomorphs. However, the relatively large infraorbital portion of the
620 *zygomaticomandibularis* and the skull morphology (*e.g.*, large orbits, low mandibular
621 condyle; both traits interrelated and associated with the occupation of open
622 environments according to Olivares et al. [2020]) challenge the possibility that this
623 taxon was a specialized subterranean taxon (*e.g.*, *Ctenomys*). In turn, Elissamburu et al.
624 (2011) and Genise (1989) recorded the presence of *Eumysops* in paleocaves, but they
625 doubted whether this rodent actually dug them, stating instead that it more likely
626 occupied the burrows made by other taxa, such as *Actenomys*. Although an affinity to
627 specialized burrower, and particularly subterranean morphotypes, can be rule out, and
628 open-habitat preference was inferred for this taxon (Olivares et al., 2020), some degree
629 of fossoriality can not be discarded and other factors might also explain the particular
630 configuration of *Eumysops*. A large infraorbital portion of the *zygomaticomandibularis*,
631 together with a small *masseter superficialis*, suggest that *Eumysops* was close to extant
632 taxa that eat stems, seeds, and small fruits, which require great incisive effort and little

633 grinding (i.e., there is no sign that *Eumysops* would have included grass in its diet), such
634 as *Chinchilla* and dipodoids.

635 In summary, studied extinct caviomorphs mostly grouped with extant
636 hystricomorphs, but several of them presented myological peculiarities not present in
637 extant caviomorphs. For example, *Dolicavia*, *Eumysops*, and *Pithanotomys* would have
638 possessed an infraorbital portion of the *zygomaticomandibularis* representing more than
639 20% of the total adductor mass, a value not reached by extant caviomorph
640 representatives with available data (Becerra et al., 2011, 2014; Cox & Jeffery, 2011;
641 Álvarez et al., 2023; Ercoli et al., 2023 and references therein). In addition, these taxa
642 possessed a remarkably reduced *masseter superficialis* (16.3% in *Eumysops*, and near or
643 less than 7% in *Dolicavia* and *Pithanotomys*). In this sense, these three extinct
644 caviomorphs are inferred as possessing proportions similar to less-derived dipodoids
645 (*e.g.*, Gambaryan et al., 1980; Ercoli et al., 2023). Thus, at least some extinct South
646 American caviomorphs seem to occupy a partially different region of the myospace of
647 extant caviomorph forms (having central values for PC1 and positive values for PC2,
648 Fig. 3B). It is worth noting that *Chinchilla* is the only extant caviomorph with available
649 data that is close to those values (Becerra *et al*., 2014). Cranial shape analysis that
650 included the infraorbital fossa indicated that probably it and other chinchillids, such as
651 *Lagidium* and *Lagostomus*, would possess an infraorbital part of the
652 *zygomaticomandibularis* even larger than the extant taxa analyzed (Álvarez, 2012;
653 Álvarez & Ercoli, 2025). The still scarce data available for extant caviomorphs
654 precludes the development of a more comprehensive scenario beyond these preliminary
655 observations.

656

657 **Conclusions**

658 The values obtained in the reconstruction of proportions and sizes of the masticatory
659 muscles of extinct caviomorphs seem robust considering that the obtained value fell
660 within the range of extant caviomorphs and other hystricomorphous rodents and the
661 observed variants are in line with previous inferences based on other proxies. These
662 results allowed us to discuss novel, as well as previously proposed, inferences about
663 different aspects of life habits of the analyzed extinct taxa. For *Actenomys* and
664 *Eucelophorus*, we conclude that their masticatory configuration agrees with tooth-
665 digging capabilities, which are especially exaggerated in *Eucelophorus*. For *Eumysops*,
666 we suggest a diet based on hard-food items and eventual fossorial activities. *Telicomys´*
667 masticatory muscle configuration seems to have been associated with horizontal
668 grinding and grass consumption. For *Dolicavia*, we propose a folivorous and
669 granivorous diet, without a specialization for grass consumption. The masticatory
670 configuration reconstructed for *Pithanotomys* implies some degree of tooth-digging
671 capabilities and the consumption of hard- and tough-food items. For *Prospaniomys*, we
672 propose a mixed diet, including leaves and probably several other dietary items. The
673 reconstruction of a relatively large infraorbital portion of the *zygomaticomandibularis*
674 for some caviomorph extinct taxa, with proportions not found in extant representatives
675 with available data, indicates that the myological diversity of the reconstructed extinct
676 taxa fell within that of extant hystricomorphous rodents considered as a whole, but
677 exceeded that found in the extant caviomorphs analyzed here. More data on extant
678 caviomorphs are needed for a comprehensive understanding of the myological diversity
679 within the group.
680

681 **Acknowledgments**

We would like to thank the following people for granting access to material under their care: M. Taglioretti (MMP); A. Kramarz (former Curator), M. Ezcurra, B. von Baczko (MACN). We thank I. Olivares (MLP) who kindly provided us photographs of *Pithanotomys*. We thank the Associate Editor A. Forasiepi and three anonymous reviewers for their comments that improved the original manuscript. This research was financially supported by PICT-2018-01237, PICT-2021-I-INVI-00406, PICT-2020-SERIEA-02985 Agencia I+D-i (Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación), UNLP SN006 (Universidad Nacional de La Plata), and PIP GI 11220210100278CO CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas).

References

Álvarez, A. (2012). *Diversidad morfológica del aparato masticatorio en roedores caviomorfos: un análisis de patrones adaptativos y restricciones* (Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata).

Álvarez, A., & Arnal, M. (2015). First approach to the paleobiology of extinct *Prospaniomys* (Rodentia, Hystricognathi, Octodontoidea) through head muscle reconstruction and the study of craniomandibular shape variation. *Journal of Mammalian Evolution, 22*, 519–533.

Álvarez, A., & Ercoli, M. D. (2025). Shape, integration, and morpho-functional trade-offs in the anterior cranium of cavioids in the context of caviomorph rodents. *Mastozoología Neotropical, 32*, e01121.

Álvarez, A., Ercoli, M. D., Boivin, M., Ortiz Tejerina, A. M., & Moyano, S. R. (2023). Head myology of wild cavies (Caviidae, Caviomorpha) and functional

implications of hystricomorphous and hystricognathous configurations. *Journal of Mammalian Evolution, 30*, 747–771.

Álvarez, A., Ercoli, M. D., & Verzi, D. H. (2020). Integration and diversity of the caviomorph mandible (Hystricomorpha, Rodentia): accessing to the evolutionary history through fossils and ancestral shape reconstructions. *Zoological Journal of the Linnean Society, 188*, 276–301.

Álvarez, A., Moyers Arévalo, R. L., & Verzi, D. H. (2017). Diversification patterns and size evolution in caviomorph rodents. *Biological Journal of the Linnean Society, 121*, 907–922.

Álvarez, A., & Pérez, M. E. (2019). Deep changes in masticatory patterns and masseteric musculature configurations accompanied the eco-morphological evolution of cavioid rodents (Hystricognathi, Caviomorpha). *Mammalian Biology, 96*, 53–60.

Álvarez, A., & Verzi, D. H. (2014). Ontogenetic allometry as a key dimension to understand cranial shape of †*Dolicavia minuscula* (Rodentia, Caviidae). 4th International Palaeontological Congress (p. 643). Mendoza.

Antoine, P.-O., Marivaux, L., Croft, D. A., Billet, G., Ganerød, M., Jaramillo, C., Martin, T., Orliac, M. J., Tejada, J., Altamirano, A. J., Duranthon, F., Fanjat, G., Rousse, S., & Gismondi, R. S. (2012). Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. *Proceedings of the Royal Society B, 279*, 1319–1326.

Arnal, M., & Kramarz, A. G. (2011). First complete skull of an octodontoid (Rodentia, Caviomorpha) from the early Miocene of South America and its bearing in the early evolution of Octodontoidea. *Geobios, 44*, 435–444.

Becerra, F. (2015). Aparato masticatorio en roedores caviomorfos (Rodentia, Hystricognathi): análisis morfofuncional, con énfasis en el género *Ctenomys* (Ctenomyidae) (Tesis Doctoral, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata).

Becerra, F., Echeverría, A. I., Casinos, A., & Vassallo, A. I. (2014). Another one bites the dust: bite force and ecology in three caviomorph rodents (Rodentia, Hystricognathi). *Journal of Experimental Zoology, Series A Ecology, Genetics, and Physiology*, *321*, 220–232.

Becerra, F., Echeverría, A. I., Vassallo, A. I., & Casinos, A. (2011). Bite force and jaw biomechanics in the subterranean rodent Talas tuco-tuco (*Ctenomys talarum*) (Caviomorpha: Octodontoidea). *Canadian Journal of Zoology*, *89*, 334–342.

Becerra, F., Vassallo, A. I., Echeverría, A. I., & Casinos, A. (2012). Scaling and adaptations of incisors and cheek teeth in caviomorph rodents (Rodentia, Hystricognathi). *Journal of Morphology*, *273*, 1150–1162.

Blanco, R. E., Rinderknecht, A., & Lecuona, G. (2012). The bite force of the largest fossil rodent (Hystricognathi, Caviomorpha, Dinomyidae). *Lethaia, 45*, 157–163.

Bogel, F., Vassallo, A. I., & Becerra, F. (2025). Musculoskeletal reconstruction and morphofunctional and palaeoecological analysis of the extinct †*Actenomys priscus* (Rodentia: Ctenomyidae). *Biological Journal of the Linnean Society, 145*, blaf041.

Boivin, M., Álvarez, A., & Ercoli, M. D. (2022). Integration patterns of cheek teeth and ecomorphological evolution in grinding herbivores: the case of caviine rodents (Caviomorpha: Caviidae). *Zoological Journal of the Linnean Society, 196*, 1094–1116.

Boivin, M., Álvarez, A., Ercoli, M. D., Moyano, S. R., Salgado-Ahumada, J. S., Ortiz Tejerina, A. M., & Cassini, G. H. (2024). Body mass estimation from cheek tooth

measurements in extinct caviomorphs (Ctenohystrica, Hystricognathi): the importance of predictor, reference sample and method. *Journal of Mammalian Evolution, 31*, 43.

Boivin, M., Marivaux, L., & Antoine, P.-O. (2019). L'apport du registre paléogène d'Amazonie sur la diversification initiale des Caviomorpha (Hystricognathi, Rodentia): implications phylogénétiques, macroévolutives et paléobiogéographiques. *Geodiversitas, 41*, 143–245.

Borroto Paez, R., & Woods, C. A. (2012). Recent species studies: feeding habits of the capromyid rodents. In R. Borroto Paez, C. A. Woods & F. E. Sergile (Eds.), *Terrestrial mammals of the West Indies, contributions* (pp. 71–91). Florida Museum of Natural History and Wacahoota Press.

Campbell, K. E. Jr., O'Sullivan, P. B., Fleagle, J. G., De Vries, D., & Seiffert, E. R. (2021). An early Oligocene age for the oldest known monkeys and rodents of South America. *Proceedings of National Academy Sciences, USA, 118*, e2105956118.

Candela, A. M., Abello, M. A., Reguero, M. A., García Esponda, C. M., Pardiñas, U. F. J., Zurita, A. A., Pujos, F., Miño-Boilini, A., Quiñones, S., Galli, C. I., Luna, C., Voglino, D., De los Reyes, M., & Quaranta, P. (2023). The Late Miocene mammals from the Humahuaca Basin (northwestern Argentina) provide new evidence on the initial stages of the Great American Biotic Interchange. *Papers in Palaeontology, 9*, e1527.

Candela, A. M., Cassini, G. H., & Nasif, N. L. (2013). Fractal dimension and cheek teeth crown complexity in the giant rodent *Eumegamys paranensis*. *Lethaia, 46*, 369–377.

780 Comparatore, V. M., Cid, M. S., & Busch, C. (1995). Dietary preferences of two
781 sympatric subterranean rodent populations in Argentina. *Revista Chilena de*
782 *Historia Natural, 68*, 197–206.
783 Cox, P. G. (2008). A quantitative analysis of the eutherian orbit: correlations with
784 masticatory apparatus. *Biological Reviews, 83*, 35–69.
785 Cox, P. G. (2017). The jaw is a second-class lever in *Pedetes capensis* (Rodentia:
786 Pedetidae). *PeerJ, 5*, e3741.
787 Cox, P. G., & Jeffery, N. (2011). Reviewing the morphology of the jaw-closing
788 musculature in squirrels, rats, and guinea pigs with contrast-enhanced microCT.
789 *The Anatomical Record, 294*, 915–928.
790 Cox, P. G., Faulkes, C. G., & Bennett, N. C. (2020). Masticatory musculature of the
791 African mole-rats (Rodentia: Bathyergidae). *PeerJ, 8*, e8847.
792 D'Adamo, P., Guichón, M. L., Bó, R. F, & Cassini, M. H. (2000). Habitat use of the
793 coypu (*Myocastor coypus*) in agro-systems of the Argentinean pampas. *Acta*
794 *Theriologica*, *45*, 25–33.
795 De Santis, L. J. M., & Moreira, G. J. (2000). El aparato masticador del género extinto
796 *Actenomys* Burmeister, 1888 (Rodentia, Ctenomyidae): inferencias sobre su modo
797 de vida. *Estudios Geológicos, 56*, 63–72.
798 Druzinsky, R. E., Doherty, A. H., & De Vree, F. L. (2011). Mammalian masticatory
799 muscles: homology, nomenclature, and diversification. *Integrative and*
800 *Comparative Biology, 51*, 224–234.
801 Elissamburu, A., Dondas, A., & De Santis, L. (2011). Morfometría de las paleocuevas
802 de la "Fm." Chapadmalal y su asignación a *Actenomys* (Rodentia), *Paedotherium*
803 (Notoungulata) y otros mamíferos fósiles hospedantes. *Mastozoología Neotropical*,
804 *18*, 227–238.

Ercoli, M. D., Álvarez, A., Cassini, G. H., Kuznetsov, A., Quentin-Derlich, J., & Warburton, N. M. (2025). An easy-to-apply method to reconstruct proportions and sizes of masticatory muscles in extinct herbivorous mammals. *Journal of Mammalian Evolution, 32*, 42.

Ercoli, M. D., Álvarez, A., Warburton, N., Janis, C. M., Potapova, E. G., Herring, S. W., Cassini, G. H., Tarquini, J., & Kuznetsov, A. (2023). Myology of the masticatory apparatus of herbivorous mammals and a novel classification for a better understanding of herbivore diversity. *Zoological Journal of the Linnean Society, 198*, 1106–1155.

Fernández, M. (1949). Sobre la vizcacha (*Lagostomus trichodactylus* Brooks) sus viviendas y su protección. *Boletín de la Academia Nacional de Ciencias, 38*, 348–379.

Fernández, M. E., Vassallo, A. I., & Zárate, M. (2000). Functional morphology and palaeobiology of the Pliocene rodent *Actenomys* (Caviomorpha: Octodontidae): the evolution to a subterranean mode of life. *Biological Journal of the Linnean Society, 71*, 71–90.

Fernández Villoldo, A., Perez, S. I., & Verzi, D. H. (2020). Análisis del endocráneo de *Pithanotomys* en el contexto de octodontoideos vivientes (Rodentia). *PE-APA, Supplemento de Resúmenes, 20*, R79.

Gambaryan, P. P., Potapova, E. G., & Fokin, I. M. (1980). Morphofunctional features of the muscular apparatus of the head in the jerboas (to the justification of the natural system of Dipodoidea, Rodentia, Mammalia). *Trudy Zoologicheskogo Instituta AN SSSR, 91*, 3–51.

828 Genise, J. F. (1989). Las cuevas con Actenomys (Rodentia, Octodontidae) de la
829 formación Chapadmalal (Plioceno Superior) de Mar del Plata y Miramar
830 (Provincia de Buenos Aires). Ameghiniana, 26, 33–42.
831 Greaves, W. S. (1973). The inference of jaw motion from tooth wear facets. *Journal of*
832 *Paleontology, 47,* 1000–1001.
833 Guichón, M. L., & Cassini, M. H. (1998). Role of diet selection in the use of habitat by
834 pampas cavies *Cavia aperea pamparum* (Mammalia, Rodentia). *Mammalia, 62,*
835 23–35.
836 Hautier, L., Cox, P. G., & Renaud, L. (2015). Grades and clades among rodents: the
837 promise of geometric morphometrics. In P. G. Cox & L. Hautier (Eds.), *Evolution*
838 *of the rodents: advances in phylogeny, functional morphology, and development*
839 (pp. 277–299). Cambridge University Press.
840 Hautier, L., Lebrun, R., & Cox, P. G. (2012). Patterns of covariation in the masticatory
841 apparatus of hystricognathous rodents: implications for evolution and
842 diversification. *Journal of Morphology, 273,* 1319–1337.
843 Hautier, L., Lebrun, R., Saksiri, S., Michaux, J. J., Vianey-Liaud, M., & Marivaux, L.
844 (2011). Hystricognathy vs sciurognathy in the rodent jaw: A new morphometric
845 assessment of hystricognathy applied to living fossil *Laonastes* (Rodentia,
846 Diatomyidae). *PLoS One, 6,* e18698.
847 Herrel, A., Fabre, A.-C., Hugot, J.-P., Keovichit, K., Adriaens, D., Brabant, L., Van
848 Hoorebeke, L., & Cornette, R. (2012). Ontogeny of the cranial system in
849 *Laonastes aenigmamus. Journal of Anatomy, 221,* 128–137.
850 Herring, S. W., & Herring, S. E. (1974). The superficial masseter and gape in mammals.
851 *The American Naturalist, 108,* 561–576.

852 Hiiemae, K. (1971). The structure and function of the jaw muscles in the rat (*Rattus*
853 *norvegicus* L.) III. The mechanics of the muscles. *Zoological Journal of the*
854 *Linnean Society, 50*, 111–132.
855 Koo, T., & Li, M. (2016). A guideline of selecting and reporting Intraclass Correlation
856 Coefficients for reliability research. *Journal of Chiropractic Medicine, 15*, 155–
857 163.
858 Larramendy, L. (2020). *Distribución espacial y diversidad vegetal en la biodeposición*
859 *de* Galea leucoblephara *y* Microcavia maenas *en un área protegida y un campo*
860 *pastoreado, Ñacuñán, Mendoza*. Tesis de Licenciatura, Facultad de Ciencias
861 Agrarias, Universidad Nacional de Cuyo, Luján de Cuyo, Mendoza). Available
862 from https://bdigital.uncu.edu.ar/.
863 McIntosh, A. F., & Cox, P. G. (2016). Functional implications of craniomandibular
864 morphology in African mole-rats (Rodentia: Bathyergidae). *Biological Journal of*
865 *the Linnean Society, 117*, 447–462.
866 Mess, A., Bohr, B., & Thomas, M. (2001). Evolutionary transformations of
867 hystricognath Rodentia and the climatic change in the Eocene to Late Oligocene
868 time interval. *Mitteilungen Museum für Naturkunde, Berlin, Zoologischer Reihe,*
869 *77*, 193–206.
870 Morgan, C. C., Olivares, A. I., Álvarez, A., & Verzi, D. H. (2007). Myoskeletal
871 specializations for digging in the rodent *Lagostomus maximus* (Caviomorpha,
872 Chinchillidae). *IX Congreso de Ciencias Morfológicas* (pp. 55). La Plata.
873 Naples, V. L., & Martin, L. D. (2000). Evolution of hystricomorphy in the Nimravidae
874 (Carnivora; Barbourofelinae): evidence for complex character convergence with
875 rodents. *Historical Biology, 14*, 169–188.

876 Offermans, M., & de Vree, F. (1993). Electromyography and mechanics of mastication
877 in the springhare, *Pedetes capensis* (Rodentia, Pedetidae). *Belgian Journal of*
878 *Zoology, 123*, 231–261.
879 Olivares, A. I., Álvarez, A., Verzi, D. H., Perez, S. I., & De Santi, N. A. (2020).
880 Unravelling the distinctive craniomandibular morphology of the Plio-Pleistocene
881 *Eumysops* in the evolutionary setting of South American octodontoid rodents
882 (Hystricomorpha). *Palaeontology, 63*, 443–458.
883 Olivares, A. I., Morgan, C. C., & Verzi, D. H. (2010b). Skeletal specializations of the
884 extinct South American echimyid rodent *Eumysops* (Hystricognathi). *9th*
885 *International Congress of Vertebrate Morphology*. Punta del Este.
886 Olivares, A. I., Morgan, C. C., Álvarez, A., & Verzi, D. H. (2010a). Análisis
887 morfométrico e inferencia de los hábitos del roedor †*Pithanotomys*
888 (Hystricomorpha: Octodontidae). Primer Encuentro de Morfometría, abstracts (p.
889 16). La Plata.
890 Pascual, R., & Ortiz-Jaureguizar, E. (2007). The Gondwanan and South American
891 episodes: two major and unrelated moments in the history of the South American
892 mammals. *Journal of Mammalian Evolution, 14*, 75–137.
893 Patton, J. L., Pardiñas, U. F. J., & D'Elía, G. (Eds.). (2015). *Mammals of South*
894 *America: Vol. 2. Rodents*. University of Chicago Press.
895 Pérez, M. E., & Pol, D. (2012). Major radiations in the evolution of caviid rodents:
896 reconciling fossils, ghost lineages, and relaxed molecular clocks. *PLoS One, 7*,
897 e48380.
898 Potapova, E. G. (2020). Morphofunctional transformations of the jaw muscles in rodent
899 evolution. *Biology Bulletin Reviews, 10*, 394–406.

Prado, J. L., Chiesa, J., Tognelli, G., Cerdeño, E., & Strasser, E. (1998). Los mamíferos de la Formación Río Quinto (Plioceno), provincia de San Luis (Argentina). Aspectos bioestratigráficos, zoogeográficos y paleoambientales. *Estudios Geológicos, 54*, 153–160.

Quintana, C. (1997). El roedor *Dolicavia minuscula* (Caviomorpha, Caviidae) del Plioceno Superior de la provincia de Buenos Aires, Argentina. *Historia Animalium, 3*, 55–71.

R Core Team. (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.r-project.org/.

Reig, O. A., & Quintana, C. A. (1992). Fossil ctenomyine rodents of the genus *Eucelophorus* from the Pliocene and Early Pleistocene of Argentina (Caviomorpha: Octodontidae). *Ameghiniana, 29*, 363–380.

Rinderknecht, A., Jones, W. W., Araújo, N., Grinspan, G., & Blanco, R. E. (2019). Bite force and body mass of the fossil rodent *Telicomys giganteus* (Caviomorpha, Dinomyidae). *Historical Biology, 31*, 644–652.

Rohlf, F. J. (2015). The tps series of software. *Hystrix, 26*, 9–12.

Sassi, P. L., Borghi, C. E., Dacar, M. A., & Bozinovic, F. (2011). Geographic and seasonal variability in feeding behavior of a small herbivorous rodent. *Acta Theriologica, 56*, 35–43.

Tognelli, M. F., Borghi, C. E., & Campos, C. M. (1999). Effect of gnawing by *Microcavia australis* (Rodentia, Caviidae) on *Geoffroea decorticans* (Leguminosae) plants. *Journal of Arid Environments, 41*, 79–85.

Turnbull, W. D. (1970). *Mammalian masticatory apparatus*. Fieldiana (Geology), 18, 147–356.

924 Upham, N. S., & Patterson, B. D. (2015). Phylogeny and evolution of caviomorph
925 rodents: a complete timetree for living genera. In A. I. Vassallo & D. Antenucci
926 (Eds.), *Biology of caviomorph rodents: diversity and evolution* (pp. 63–120).
927 Sociedad Argentina para el Estudio de los Mamíferos (SAREM).
928 Vassallo, A. I. (1998). Functional morphology, comparative behaviour, and adaptation
929 in two sympatric subterranean rodents genus *Ctenomys* (Caviomorpha:
930 Octodontidae). *Journal of Zoology, 244*, 415–427.
931 Vassallo, A. I., & Antenucci, D. (2015a). Introduction. In A. I. Vassallo & D. Antenucci
932 (Eds.), *Biology of caviomorph rodents: diversity and evolution* (pp. 1–10).
933 Sociedad Argentina para el Estudio de los Mamíferos (SAREM).
934 Vassallo, A. I., & Antenucci, D. (Eds.). (2015b). *Biology of caviomorph rodents:*
935 *diversity and evolution*. Sociedad Argentina para el Estudio de los Mamíferos
936 (SAREM).
937 Verzi, D. H., & Olivares, A. I. (2006). Craniomandibular joint in South American
938 burrowing rodents (Ctenomyidae): adaptations and constraints related to a
939 specialised mandibular position in digging. *Journal of Zoology, 270*, 488–501.
940 Verzi, D. H., Olivares, A. I., Morgan, C. C., & Álvarez, A. (2016). Contrasting
941 phylogenetic and diversity patterns in octodontoid rodents and a new definition of
942 the family Abrocomidae. *Journal of Mammalian Evolution, 23*, 93–115.
943 Vieytes, E. C., Morgan, C. C., & Verzi, D. H. (2007). Adaptive diversity of incisor
944 enamel microstructure in South American burrowing rodents (Family
945 Ctenomyidae, Caviomorpha). *Journal of Anatomy, 211*, 296–302.
946 Vucetich, M. G., Arnal, M., Deschamps, C. M., Pérez, M. E., & Vieytes, C. E. (2015).
947 A brief history of caviomorph rodents as told by the fossil record. In A. I. Vassallo

948 & D. Antenucci (Eds.), *Biology of caviomorph rodents: diversity and evolution*
949 (pp. 11–62). Sociedad Argentina para el Estudio de los Mamíferos (SAREM).
950 Vucetich, M. G., & Verzi, D. H. (1996). A peculiar octodontoid (Rodentia,
951 Caviomorpha) with terraced molars from the Lower Miocene of Patagonia
952 (Argentina). *Journal of Vertebrate Paleontology, 16*, 297–302.
953 Vucetich, M. G., Verzi, D. H., & Hartenberger, J. L. (1999). Review and analysis of the
954 radiation of the South American Hystricognathi (Mammalia. Rodentia). *Comptes*
955 *Rendus de l'Académie des Sciences, 329*, 763–769.
956 Vucetich, M. G., Vieytes, E. C., Pérez, M. E., & Carlini, A. A. (2010). The rodents from
957 La Cantera and the early evolution of caviomorph in South America. In R. H.
958 Madden, A. A. Carlini, M. G. Vucetich & R. F. Kay (Eds.), *The paleontology of*
959 *Gran Barranca: evolution and environmental change through the Middle Cenozoic*
960 *of Patagonia* (pp. 189–201). Cambridge University Press.
961 Wilkins, K. T., & Cunningham, L. L. (1993). Relationship of cranial and dental features
962 to direction of mastication in tuco–tucos (Rodentia: Ctenomys). *Journal of*
963 *Mammalogy, 74*, 383–390.
964 Wilson, D. E., Lacher, T. E. Jr., & Mittermeier, R. A. (Eds.). (2016). *Handbook of*
965 *Mammals of the World: Vol 6. Lagomorphs and Rodents I*. Lynx Edicions.
966 Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating
967 repeatability. *Methods in Ecology and Evolution, 3*, 129–137.
968 Woods, C. A. (1972). Comparative myology of jaw, hyoid and pectoral appendicular
969 regions of New and Old World hystricomorph rodents. *Bulletin of the American*
970 *Museum of Natural History, 147*, 115–198.
971
972

Figure captions

Figure 1. Schematic phylogeny of caviomorph rodents, considering the molecular phylogeny of Álvarez et al. (2017) and further modifications of Álvarez et al. (2020). Biochrons of caviomorph families and extinct taxa here studied are indicated.

Figure 2. Measurements and landmarks and semilandmarks configurations for each extant and extinct analyzed specimen represented in a skull of *Myocastor coypus* (MLP 30.XII.02.72). See Main text for abbreviations. For details and variable definitions see table 1 in Ercoli *et al.* (2025). Light blue (large) circles, landmarks; yellow, light orange, orange circles, sets of semilandmarks. ZAE equals 0 in the case of *Myocastor* so it is represented by a point. Scale bar equals 1 cm.

Figure 3. Myological morphospaces on which reconstructed proportions of extinct caviomorph rodents were projected (star symbols, see Table 2). **A**, myo-space of herbivorous mammals indicating some of the major myological morphotypes and paths following Ercoli *et al.* (2023). Morphotypes of the "Path 1", which are included in the regression analyses, are illustrated with colored polygons; **B**, myo-space of caviomorph rodents. Main ecological groups are indicated. The proportions of two dipodoids were also projected.

Tables

Table 1. Proportions of masticatory muscles and total masticatory muscle mass (in grams) and life habits of extant caviomorphs and two additional hystricomorphous rodents (Dipodoidea). Mass sup, *masseter superficialis*; Mass prof, *masseter profundus*; Pt lat, *pterygoideus lateralis*; Pt med, *pterygoideus medialis*; Temp, *temporalis*; ZMd, zygomatic arch portion of the *zygomaticomandibularis*; ZMd io, infraorbital portion of the *zygomaticomandibularis*. Data for muscles are compiled from Álvarez et al. (2023) and Ercoli et al. (2023).

Caviomorph rodents	Mass sup	Mass prof	ZMd	ZMd io	Temp	Pt lat	Pt med	Total mass	Body mass (g)	Life habits
Cavia aperea	16.20%	44.70%	3.50%	6.20%	17.80%	1.70%	9.90%	6.645	600	Tough-food eater
Cavia porcellus	20.10%	52.20%	4.30%	4.40%	6.30%	1.70%	11.00%	-	1200	Tough-food eater
Chinchilla lanigera	22.30%	32.30%	9.30%	17.60%	5.10%	2.90%	10.50%	3.366	400	Hard-food eater
Ctenomys australis	30.90	29.30	9.20%	11.70	14.00	1.10	3.90%	4.922	400	Tooth-digger/str

	%	%		%	%	%				ong biter
Ctenomys talarum	28.00%	29.30%	11.20%	11.40%	9.50%	2.30%	8.30%	1.98	130	Tooth-digger/strong biter
Euryzygomatomys spinosus	26.80%	20.00%	7.40%	19.30%	14.20%	5.30%	6.90%	-	200	Tooth-digger/strong biter
Galea leucoblephara	17.40%	40.00%	6.30%	9.00%	6.30%	1.20%	19.70%	3.254	400	Tough-food eater
Hydrochoerus hydrochaeris	15.30%	39.70%	10.60%	11.90%	5.50%	2.40%	14.50%	181.68	50000	Tough-food eater
Myocastor coypus	34.40%	24.00%	8.80%	8.70%	14.10%	3.10%	6.90%	42.96	6500	Tooth-digger/strong biter
Octodon degus	21.40%	34.70%	9.90%	15.30%	11.30%	1.60%	5.90%	2.317	200	Generalist

Additional hystricomorphos rodents										
Dipus sagitta	9.80%	25.60%	4.20%	40.40%	4.10%	4.50%	11.30%	-	100	Hard-food eater
Zapus hudsonius	9.40%	33.80%	4.70%	20.00%	17.80%	4.40%	9.90%	-	20	Hard-food eater

1003

1004

1005 **Table 2.** Predictions of proportions of masticatory muscles and total masticatory muscle
1006 mass (in grams) for each reconstructed extinct caviomorph rodent. For the total absolute
1007 muscle mass, mean value, upper and lower quantiles are presented. Mass sup, *masseter*
1008 *superficialis*; Mass prof, *masseter profundus*; Pt lat, *pterygoideus lateralis*; Pt med,
1009 *pterygoideus medialis*; Temp, *temporalis*; ZMd, zygomatic arch portion of the
1010 *zygomaticomandibularis*; ZMd io, infraorbital portion of the *zygomaticomandibularis*.
1011 Qup, upper quantiles; Qlow, lower quantiles. Data for the proportions of masticatory
1012 muscles of *Telicomys* are taken from Ercoli *et al*. (2025).
1013

	Proportions and absolute masses for masticatory muscles								Total mass	
Taxon	Mass sup	Mass prof	ZMd	ZMd io	Temp	Pt lat	Pt med		Mean value	(Qup/Qlow)
Actenomys priscus	24.52% /2.230	27.62%/ 2.512	6.30% /0.573	14.02% /1.275	19.22 %/1.7 48	7.22% /0.656	1.11% /0.101		9.095	2.781 / 19.723
Dolicavia sp	6.07%/ 0.298	42.12%/ 2.071	3.32% /0.163	29.79% /1.465	8.73% /0.429	4.20% /0.207	5.76% /0.283		4.917	1.437 / 10.036
Eucelophorus chapalmalensis	32.79% /2.316	15.06%/ 1.064	10.62 %/0.7 50	13.89% /0.981	21.69 %/1.5 31	2.75% /0.194	3.20% /0.226		7.062	2.119 / 14.938
Eumysops sp	16.32% /1.462	27.62%/ 2.475	6.58% /0.589	28.31% /2.537	15.43 %/1.3 82	4.78% /0.428	0.96% /0.086		8.959	2.736 / 19.400
Pithanotomys chapalmalensis	7.08%/ 0.595	36.64%/ 3.082	10.57 %/0.8 89	20.27% /1.704	15.98 %/1.3 44	5.72% /0.481	3.75% /0.315		8.411	2.557 / 18.099
Prospaniomys priscus	19.09% /0.721	38.06%/ 1.437	4.43% /0.167	16.53% /0.624	11.60 %/0.4 38	3.59% /0.136	6.70% /0.253		3.776	1.082 / 7.509
Telicomys giganteus	13.55% /48.106	45.47%/ 161.419	7.61% /27.00 5	13.60% /48.275	8.82% /31.29 9	1.63% /5.793	9.32% /33.08 6		354.983	142.258 / 1103.618

1014

Table 3. Factor loadings for the described principal components of the caviomorph myospace (see Fig. 3B). Abbreviations: Mass sup, *masseter superficialis*; Mass prof, *masseter profundus*; Pt lat, *pterygoideus lateralis*; Pt med, *pterygoideus medialis*; Temp, *temporalis*; ZMd, zygomatic arch portion of the *zygomaticomandibularis*; ZMd io, infraorbital portion of the *zygomaticomandibularis*.

	PC1	PC2
Mass sup	0.45633562	-0.41491845
Mass prof	-0.7879738	-0.26978503
ZMd	0.12018626	0.20052134
ZMd io	0.24779785	0.53735329
Temp	0.16189108	-0.51644281
Pt lat	0.05958571	0.06357893
Pt med	-0.2554357	0.39413944

Supplementary Online Information

Supplementary Online Information 1. List of fossil specimens analyzed. “x” indicates in which cranial and mandibular view each specimen was included. Sources other than own photographs are indicated. Abbreviations: CrL, lateral view of cranium; CrD, dorsal view of cranium; CrV, ventral view of cranium; MandL, lateral view of mandible.

Supplementary Online Information 2. Coefficients of regression models for each muscle proportion ("Path 1" equations, see Materials and Methods), and total adductor mass of the masticatory apparatus. MSS=*masseter*, ZMd=*zygomaticomandibularis*, and Pt=*pterygoideus*. For PC's variables, associated statistics, other data, and scripts to transform variables and run equations, see Supplementary Online Information S3 of this article and download free available Supplementary Online Sources of Ercoli et al. (2025, https://doi.org/10.1007/s10914-025-09787-y).

Supplementary Online Information 3. Variables used in regression analyses. Data for regressions to estimate relative muscle masses include the relativized values for each cranio-mandibular variable, and scores on principal components of geometric morphometric analyses (see Material and methods section). Data for regressions to estimate absolute muscle masses include the raw values of selected cranio-mandibular variables. Geometric mean (GM) of these variables is presented.

Supplementary Online Information 4. Aligned landmarks and semilandmarks coordinates for studied fossils for zygomatic arch shape (ZAS) and angular process shape (APS) analyses.

Figure 1. Schematic phylogeny of caviomorph rodents, considering the molecular phylogeny of Álvarez et al. (2017) and further modifications of Álvarez et al. (2020). Biochrons of caviomorph families and extinct taxa here studied are indicated.

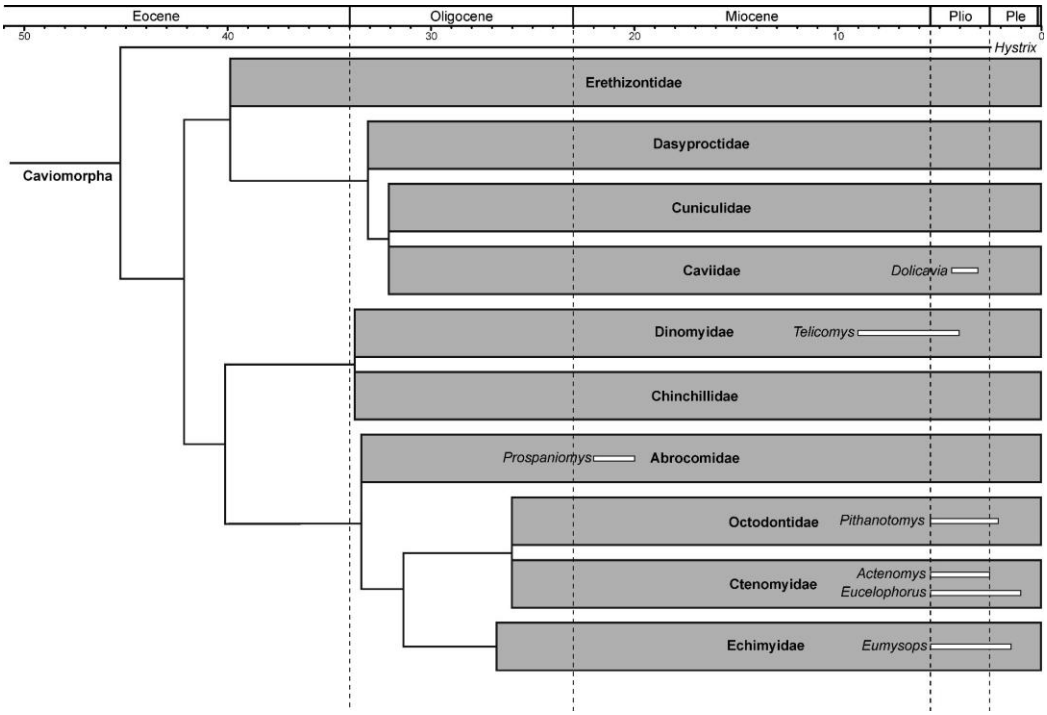


Figure 2. Measurements and landmarks and semilandmarks configurations for each extant and extinct analyzed specimen represented in a skull of *Myocastor coypus* (MLP 30.XII.02.72). For details and variable definitions see table 1 in Ercoli *et al.* (2025). Light blue (large) circles, landmarks; yellow, light orange, orange circles, sets of semilandmarks. APS, angular process shape; BL, basicranial length; CE, coronoid process extension; IFE, infraorbital fossa extension; MME_L, masticatory muscle extension, lateral view; MME_M, masticatory muscle extension, mandible; MME_V, masticatory muscle extension, ventral view; MPA, *masseter profundus* advancement; PAE, *pterygoidei* (lateral pterygoideus and medial pterygoideus) attachment extension; PAH, *pterygoidei* attachment height; PPP, paraoccipital process position; TFL, temporal fossa length; TFW, temporal fossa width; VRH, vertical ramus height; ZA, *zygomaticomandibularis* advancement; ZAE, zygomatic arch elevation; ZAS, zygomatic arch shape; ZAW, zygomatic arch width. ZAE equals 0 in the case of *Myocastor* so it is represented by a point. Scale bar equals 1 cm.

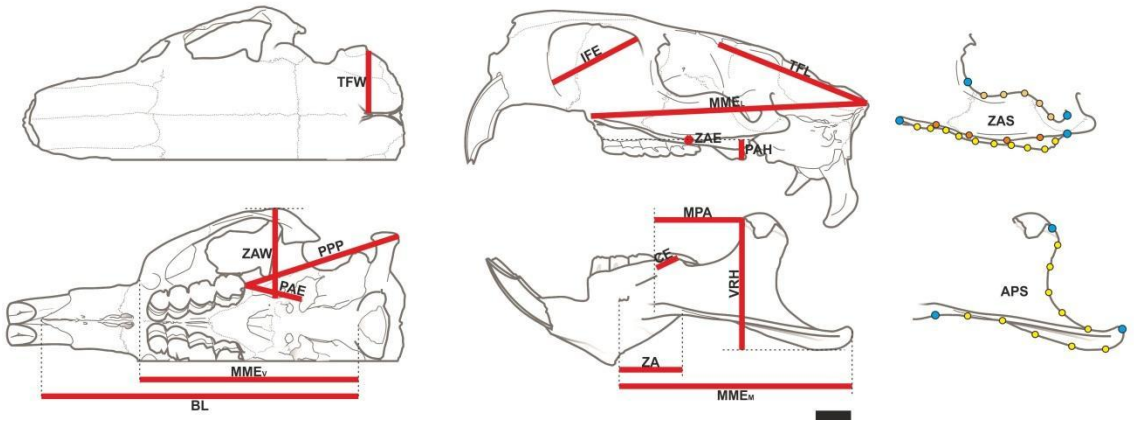
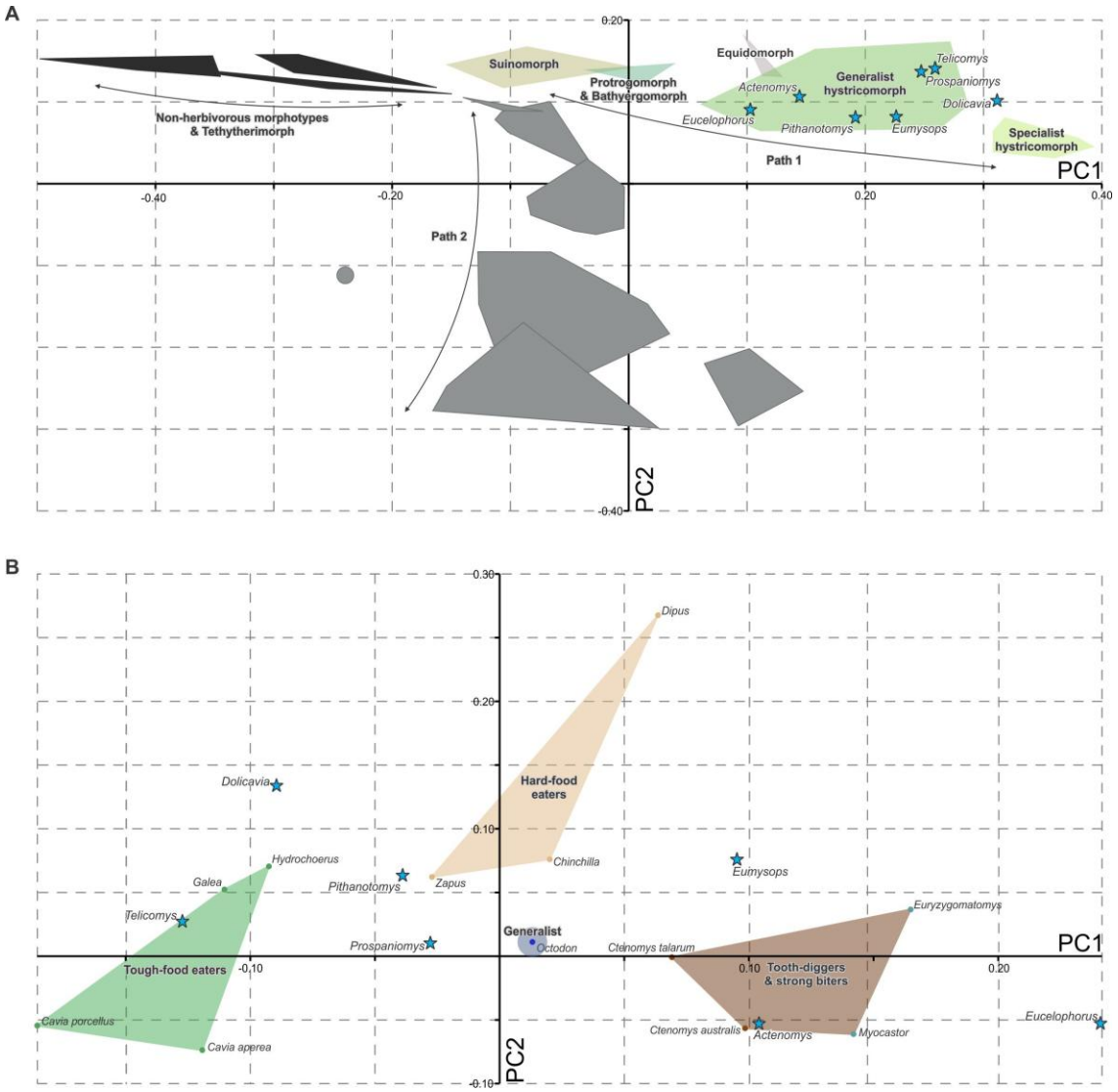
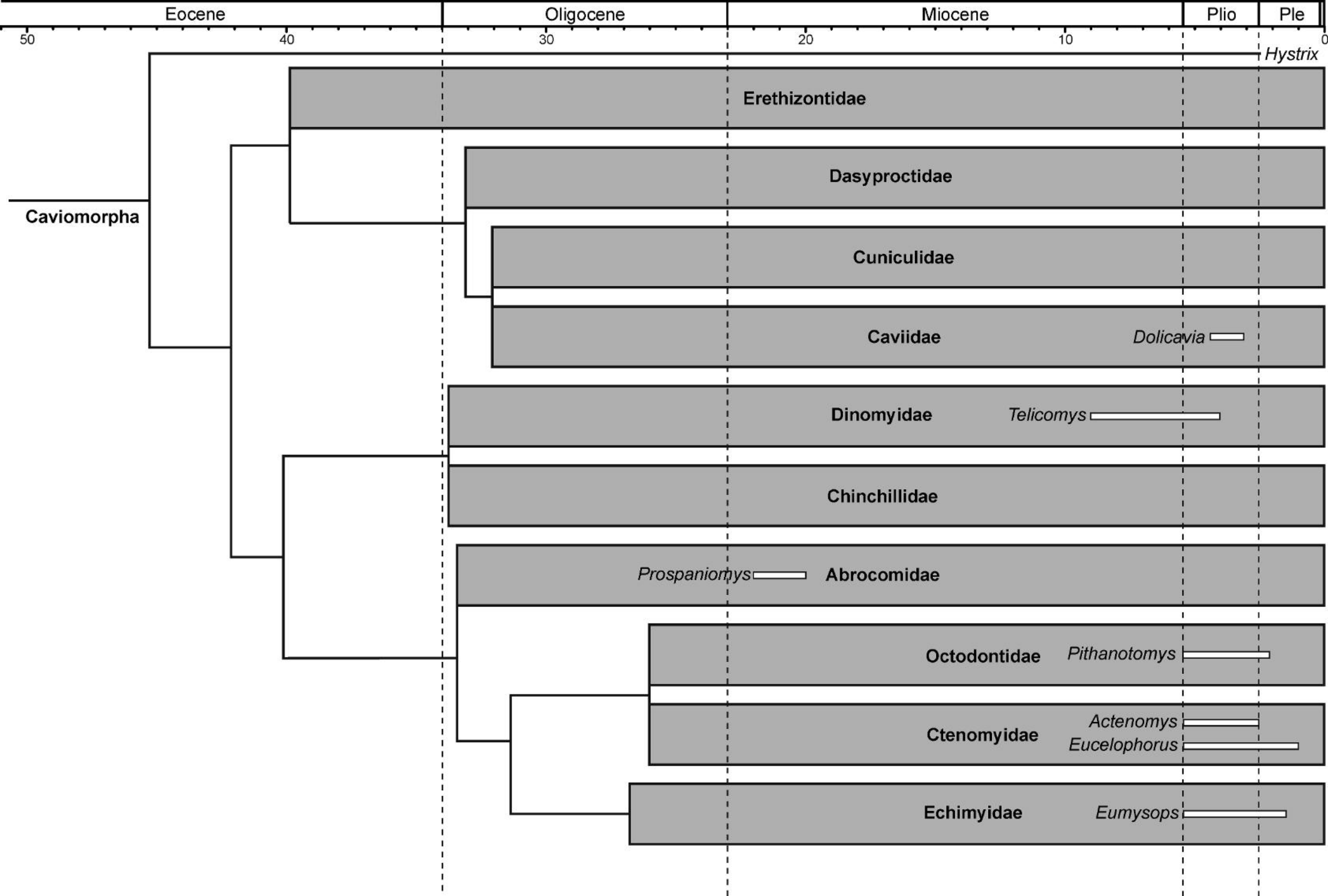
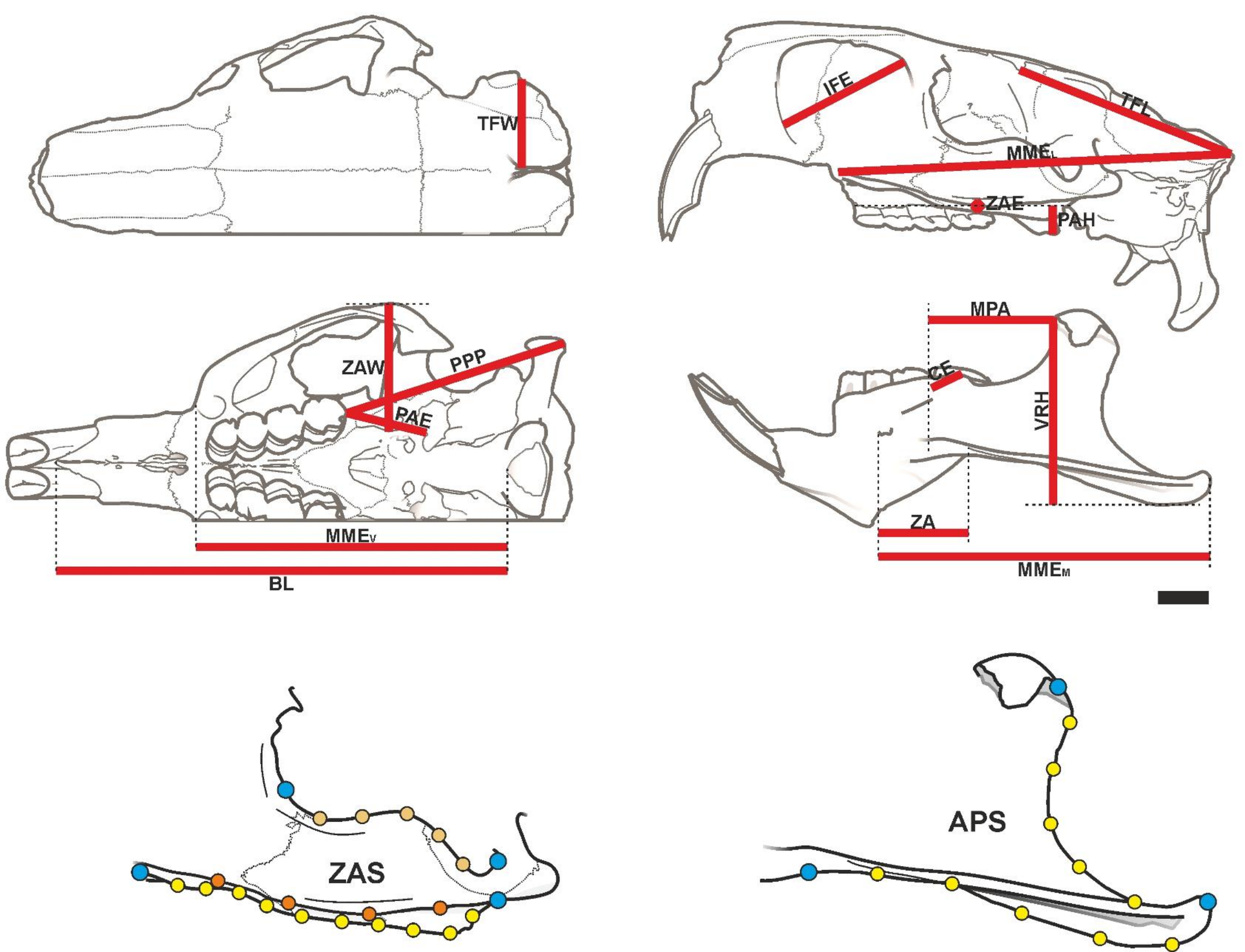


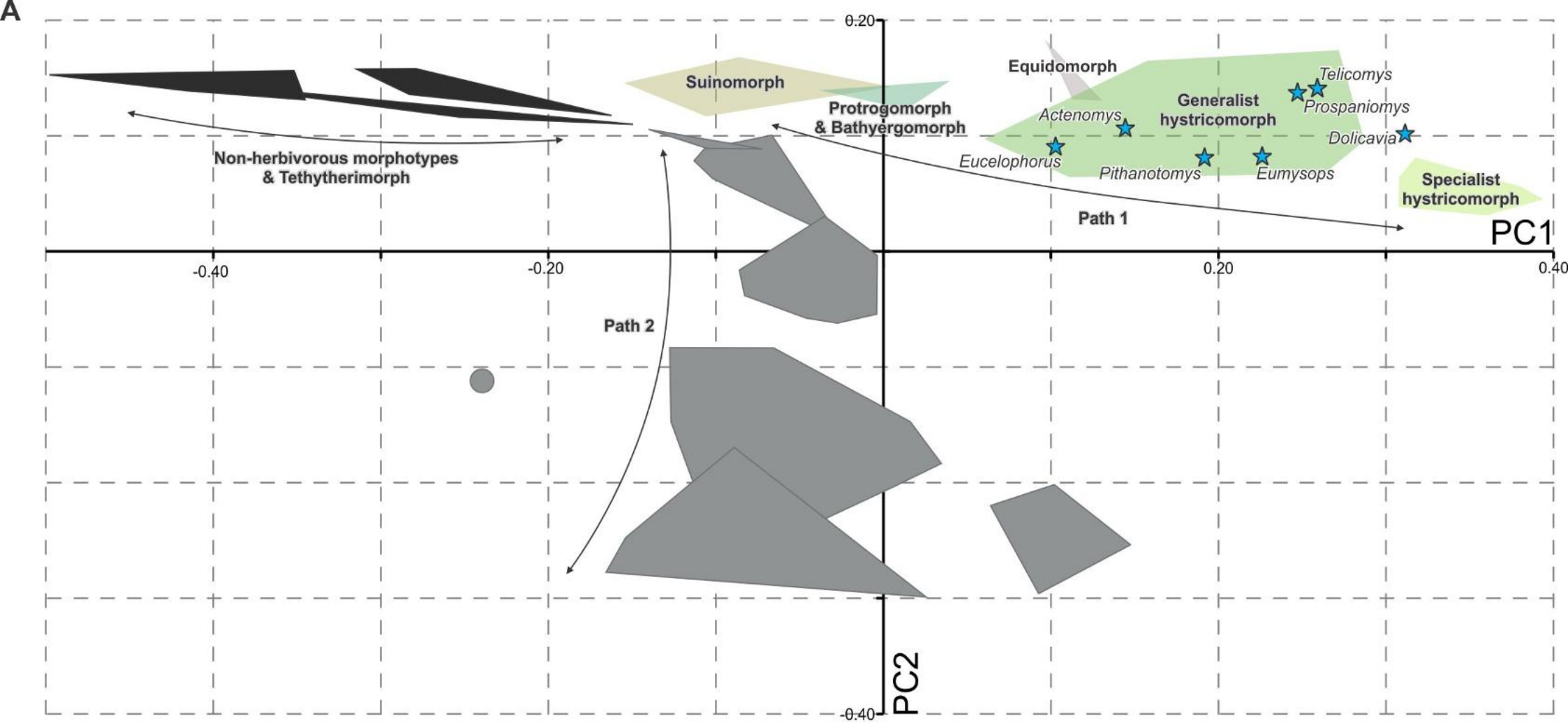
Figure 3. Myological morphospaces on which reconstructed proportions of extinct caviomorph rodents were projected (star symbols, see Table 2). **A**, myo-space of herbivorous mammals indicating some of the major myological morphotypes and paths following Ercoli et al. (2023). Morphotypes of the "Path 1", which are included in the regression analyses, are illustrated with colored polygons; **B**, myo-space of caviomorph rodents. Main ecological groups are indicated. The proportions of two dipodoids were also projected.



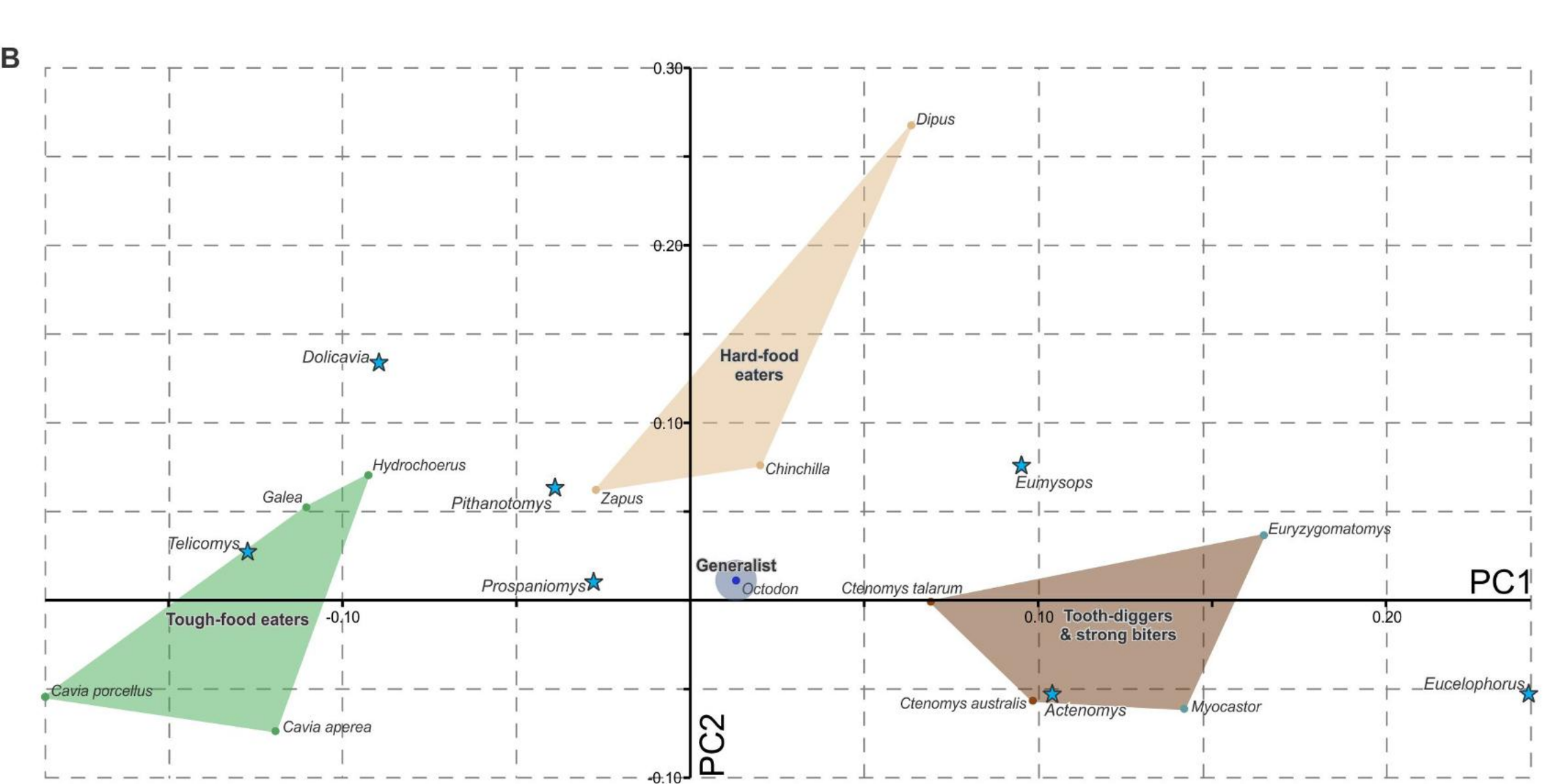

Eocene
Oligocene
Miocene
Plio
Ple
50
40
30
20
10
0
Hystrix
Erethizontidae
Dasyproctidae
Caviomorpha
Cuniculidae
Caviidae
Dolicavia
Dinomyidae
Telicomys
Chinchillidae
Prospaniomys
Abrocomidae
Octodontidae
Pithanotomys
Ctenomyidae
Actenomys
Eucelophorus
Echimyidae
Eumysops


TFW
IFE
TFL
MME_L
ZAE
PAH
ZAW
PPP
PAE
MME_V
BL
MPA
CF
VRH
ZA
MME_M
ZAS
APS

A


0.20
-0.40
-0.20
0.20
0.40
-0.40
PC1
PC2
Suinomorph
Protrogomorph
& Bathyergomorph
Equidomorph
Generalist
hystricomorph
Specialist
hystricomorph
Non-herbivorous morphotypes
& Tethytherimorph
Path 1
Path 2
Telicomys
Prospaniomys
Dolicavia
Actenomys
Eucelophorus
Pithanotomys
Eumysops

B


0.30
0.20
0.10
-0.10
-0.10
0.10
0.20
PC1
PC2
Dipus
Hard-food
eaters
Chinchilla
Zapus
Dolicavia
Hydrochoerus
Galea
Telicomys
Pithanotomys
Prospaniomys
Eumysops
Euryzygomatomys
Generalist
Octodon
Ctenomys talarum
Tough-food eaters
Tooth-diggers
& strong biters
Cavia porcellus
Cavia aperea
Ctenomys australis
Actenomys
Myocastor
Eucelophorus