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The inner ear of caviomorph rodents: phylogenetic implications and application to extinct West Indian taxa

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Abstract With their past and current diversities, West Indian caviomorph rodents dominate the terrestrial mammalian fauna of the Caribbean archipelago. Many of these species have recently become extinct, including the emblematic giant forms known as Heptaxodontidae. The higher-level systematics and content of this family have been widely disputed over the last decades (i.e., membership in Caviioidea *versus* Chinchilloidea *versus* Octodontoidea). Here we analyzed the phylogenetic signal provided by several characters of the caviomorph inner ear to address the phylogenetic affinities of the West Indian heptaxodontids. For this, we assembled an exhaustive taxonomic sampling ($N = 100$) of extant North and South American caviomorphs (including representatives of all families) and a wide array of West Indian forms among octodontoid echimyids (extant and extinct capromyines, as well as extinct heteropsomyines), and some heptaxodontid subfossil taxa such as *Amblyrhiza*, *Clidomys*, and *Elasmodontomys*. Geometric morphometrics and comparative phylogenetic methods were employed to explore shape differences of the inner ear and their potential systematic implications. Our results show that: (1) allometry is a major contributor to shape variation in the bony labyrinth; (2) shape variation bears a strong phylogenetic signal, providing diagnostic characters for Caviidae and Erethizontoidea; and (3) *Amblyrhiza* and *Clidomys* are morphologically closer to Chinchilloidea with which they have potential phylogenetic affinities. *Elasmodontomys* remains a problematic taxon as it exhibits inner ear features that are consistent with either Chinchilloidea or Octodontoidea, depending on how the allometric component is evaluated.

Keywords Allometry, Bony labyrinth, Caribbean islands, Fossils, Geometric morphometrics, Systematics

Statements and Declarations The authors declare no competing financial interests.

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Cardoso, and Quentin Martínez for their fruitful discussions and helping with the scanning of important specimens while they were visiting the Natural History Museum of London. Thanks to Andrés Rinderknecht for sharing his medical scan of *Josephoartigasia monesi* to attempt the extraction of its inner ear shape morphology. Marcelo R. Sánchez-Villagra, Alexandra Wegmann, Gabriel Aguirre Fernández, and Jorge D. Carrillo Briceño for helping us scanning the specimens housed at PIMUZ. We thank the 3D data repositories morphosource, DigiMorph, and their contributors. Three-dimensional data acquisitions were performed using the micro-computed tomography (μ CT) facilities of the MRI platform member of the national infrastructure France-BioImaging supported by the French *Agence Nationale de la Recherche* (Grant ANR-10-INBS-04, “*Investissements d’Avenir*”), and those of the Laboratoire d’Excellence (LabEx) Centre Méditerranéen de l’Environnement et de la Biodiversité (LabEx CeMEB, ANR10-LABX-0004). Finally, we thank the two anonymous reviewers for their insightful comments that enhanced the final version of the manuscript. This is ISEM publication ISEM 2023-116 SUD.

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Data Availability Statement

The landmark coordinates data and R code used for the GMM analyses are available on GitHub (https://github.com/Lea-dcnh/2023_Caviomorpha_InnerEar). The 3D surfaces models of *Amblyrhiza*, *Clidomys*, and *Elasmodontomys* are available on MorphoMuseum. The remaining 3D surfaces will be used for further analyses and are available upon request to the corresponding author.

Introduction

With their astonishing past and present biodiversity, islands are often considered as evolutionary laboratories (MacArthur and Wilson 1967). The study of island biotas has played a significant role in the emergence of major ecological and evolutionary theories (Darwin 1859; Wallace 1880), and shed light on the deterministic processes that shape biological diversity (Losos and Ricklefs 2009). On remote islands, resources availability and intra- and inter-specific interactions are often different from those found on mainlands. In such environmental contexts, new colonizing lineages may exhibit unique ecological and morphological characteristics compared to their mainland counterparts, a phenomenon known as the “island syndrome” (Losos and Ricklefs 2009). Rapid rates of morphological evolution and major morphological changes in insular lineages may obscure their relationships (e.g., Millien 2006; van den Hoek Ostende 2018; Delsuc et al. 2019). In mammals, well-documented island syndromes are characterized by major morphological changes with increased rates of morphological evolution (Millien 2006) and exceptional cases of gigantism and nanism (Foster 1964; Lomolino 1985, 2005; Brown et al. 2004; Hennekam et al. 2020). For the case of the West Indies, although the Quaternary fossil record is reasonably well sampled for mammals, the systematic positions of certain taxa remain controversial, reflecting the complexity of island lineage evolution.

The current diversity of West Indian terrestrial mammals is a pale reflection of that recorded from the late Quaternary (Davalos and Turvey 2012; Turvey et al. 2017). Nowadays, only two surviving threatened groups survive in the region: the solenodons (Solenodontidae, Eulipotyphla) and hutias (Capromyinae, Echimyidae, Octodontoidea, Caviomorpha, Rodentia). Extinct lineages of Antillean mammals are numerous, and include megalocnid sloths (e.g., MacPhee and Iturralde-Vinent 1994; Delsuc et al. 2019; Presslee et al. 2019; Viñola-López et al. 2022a), platyrrhine primates (e.g., Ford 1990; MacPhee and Iturralde-Vinent 1994; Horovitz and MacPhee 1999; MacPhee and Horovitz 2004; Cooke et al. 2011; Rosenberger 2011, 2013), eulipotyphlan insectivores (Nesophontidae and several Solenodontidae; e.g., Silva et al. 2007; Morgan et al. 2019; Buckley et al. 2020), echimid rodents (Heteropsomyinae and most Capromyinae; e.g., Anthony 1916; Miller 1916; Woods et al. 2001; MacPhee et al. 2003; MacPhee 2009; Viñola-López et al. 2022b), as well as the

giant rodents that are one of the topic of this paper, and traditionally grouped as members of the paraphyletic family Heptaxodontidae (for a summary, see MacPhee 2011). Except for Capromyinae and Solenodontidae, most of these West Indian mammal lineages were recently extirpated (Morgan and Woods 1986; MacPhee 2009; Turvey et al. 2017; Orihuela et al. 2020; Viñola-López et al. 2022b). For various reasons, both the extant and the subfossil taxa composing these groups have proven to be difficult to classify, although this is changing with the increasing utilization of modern and ancient genomics and proteomics in phylogeny construction (e.g., Fabre et al. 2014; Woods et al. 2018, 2021; Courcelle et al. 2019; Delsuc et al. 2019; Presslee et al. 2019).

Among these insular species, extinct and extant West Indian caviomorph rodents constitute a phylogenetic conundrum. For example, hutias have been traditionally considered as a separate family (i.e., Capromyidae), closely related but not part of monophyletic Echimyidae (e.g., Woods and Howland 1979; Verzi et al. 2014). Molecular data have conclusively shown that hutias are nested within Echimyidae (Fabre et al. 2014, 2017; Upham and Patterson 2015) and warrant no more than subfamily recognition (i.e., Capromyinae; Courcelle et al. 2019). On the other hand, in the absence of biomolecular evidence, the relationship of several extinct mammals continues to be problematic because several of them have not been included in phylogenetic analyses and their morphology is highly derived. This applies *a fortiori* to the recently extinct Heptaxodontidae, a group whose membership varies by author, but that traditionally includes *Amblyrhiza inundata* (Anguilla, St. Martin, and St. Barthélemy), *Elasmodontomys obliquus* (Puerto Rico), and *Clidomys osborni* (Jamaica), as well as poorly known taxa such as *Quemisia gravis* (Hispaniola), *Xaymaca fulvopulvis* (Jamaica), and *Tainotherium valei* (Puerto Rico). Anthony (1916, 1917) initially considered Heptaxodontidae as a subfamily of Chinchillidae on the basis of the multilamellar organization of their maxillary teeth. Based on the same tooth characters and their large body size, Simpson (1945) extended the family to include mid-Cenozoic South American taxa as well. Although Patterson and Wood (1982) noticed potential affinities of nominal heptaxodontids with Capromyidae, they did not propose a more inclusive higher-level clade for the reception of the former, leaving them *incertae sedis* as to superfamily. Woods (1989) considered Heptaxodontidae as “giant hutias” and proposed to separate them into two subfamilies: Heptaxodontinae, with *Quemisia*, *Elasmodontomys*, and *Amblyrhiza*, and Clidomyinae, with *Clidomys*. Subsequently, McKenna and Bell (1997) considered

Heptaxodontidae to include *Elasmodontomys*, *Amblyrhiza*, and *Clidomys* (plus two other extinct Neogene chinchilloids taxa from Patagonia: *Tetrastylomys* and *Pentastylomys*) and to stand as a family of Octodontoidea. Based on basicranial morphology, MacPhee (2011) concluded that *Amblyrhiza* is strongly related to Chinchilloidea, whereas *Elasmodontomys* was left unallocated, “resembling a wide variety of other taxa”. Based on dental evidence, *Amblyrhiza* and *Elasmodontomys* were recently placed together within Chinchilloidea, to the exclusion of any affiliation with Echimyidae (Marivaux et al. 2020). By contrast, a recent molecular phylogeny by Woods et al. (2021) recently asserted that *Elasmodontomys* is sister to the Hispaniolan capromyine *Plagiodontia*, and thus nested within Capromyinae, using mitogenomic and nuclear gene evidence. This result markedly conflicts with studies of incisor enamel microstructure, which showed that *Elasmodontomys* displays the primitive subtype 1-2 of multiseriate Hunter-Schreger bands (HSBs) (Martin 1992, 1994a, 1997; Marivaux et al. 2020, 2022); whereas extant Octodontoidea, including echimyines and capromyines, display the derived subtype 3 instead (Martin 1992; Boivin et al. 2019a; Marivaux et al. 2022). Adding to the prevailing uncertainty concerning the systematic position of *Elasmodontomys* is the significance, if any, of showing some octodontoid postcranial similarities (Patterson and Wood 1982; Woods and Hermanson 1985), the unusual chinchilloid cheek tooth laminar pattern and heterogeneous enamel layer (Marivaux et al. 2020), and inconclusive basicranial features (MacPhee 2011). There are no other molecular data available for any of the other heptaxodontids, and the species *Quemisia gravis*, *Xaymaca fulvopulvis*, and *Tainotherium valei* are known from very few elements.

Relationship hypotheses are best tested with other phylogenies based on different character sets and approaches so that their relative performance when confronted with new data can be meaningfully assessed. In the case of the giant Antillean rodents and their putative relatives, additional sources of morphological information may serve this purpose. Petrosal bones often survive fossilization due to their high density and, as such, they represent a crucial source of information for paleontological studies. Microtomography-assisted analysis of the inner ear has proven to be of value for inferring phylogenetic affinities and ecological correlates in a number of mammalian groups such as primates (e.g., Spoor et al. 2007; Lebrun et al. 2010; Benoit et al. 2013; Ekdale 2013; Perier et al. 2016; del Río et al. 2021), artiodactyls (Orliac et al. 2012; Costeur 2014; Mennecart and Costeur 2016), cetaceans (e.g., Geisler and Luo 1996; Ekdale 2013, 2016; Mourlam and Orliac 2017),

xenarthrans (e.g., Billet et al. 2012, 2015a; Boscaini et al. 2018), carnivorans (e.g., Ekdale 2013; Grohé et al. 2016; Schwab et al. 2019), marsupials (Alloing-Séguier et al. 2013), and rodents (Ekdale 2013; Arnaudo et al. 2020). With reference to the latter, Ekdale (2013) has demonstrated that caviomorph cochleas are notably elongated in comparison to those of other mammals. Arnaudo et al. (2020) have shown that in some octodontoid caviomorphs, the length and number of turns of the cochlea are probably subject to phylogenetic constraints. Along with other indicators, observations like these suggest that caviomorph inner ear structures may contain a strong phylogenetic signal. To test this proposition, we analyzed here inner ear features across an extensive taxon sample, utilizing a molecular backbone approach (Upham and Patterson 2015; Upham et al. 2019) and comparative phylogenetic methods (Blomberg et al. 2003) as a basis for identifying potentially informative characters. We also used geometric morphometrics to explore interspecific variation in inner ear features in extant caviomorph rodents. As caviomorphs have undergone unparalleled body size variation compared to mammals generally (e.g., Álvarez et al. 2017), we expect this to provide a good model for studying allometric trends in inner ear shape with a special focus on Heptaxodontidae.

Material and methods

Institutional abbreviations

The specimens analyzed in this study come from the American Museum of Natural History (AMNH, New York, USA), the *Senckenberg Naturhistorische Sammlungen* (B, Dresden, Germany), the *Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia* (CAPPA/UFAC, Universidade Federal de Santa Maria, Brazil), the *Centre de Biologie et de Gestion des Populations* (CBGP, Montpellier, France), Lázaro W. Viñola Field collection (CLV, Matanzas, Cuba), the *Museo Argentino de Ciencias Naturales* (MACN, Buenos Aires, Argentina), the *Fundação Zoobotânica do Rio Grande do Sul* (MCN, Rio Grande do Sul, Brazil), the *Naturhistorisches Museum Basel* (NMB, Basel, Switzerland), Natural History Museum of London (NHMUK, London, UK), the *Universität Zürich Paläontologisches Institut und Museum* (PIMUZ, Zürich, Switzerland), the University of Florida Vertebrate Paleontology Collection (UF, Gainesville, USA), the *Universidade Federal do Acre* (UFAC,

Rio Branco, Brazil), the *Université de Montpellier* (UM, Montpellier, France), the Smithsonian Institution National Museum of Natural History (USNM, Washington, USA), the collection of Sabine Begal, the Witmer Lab of Ohio University (WitmerLab, Athens, USA), and the *Museum für Naturkunde Berlin* (ZMB, Berlin, Germany) (Online Resource 1 and 2).

Specimens

We studied the inner ears of 113 extant ($N = 100$) and extinct ($N = 13$) caviomorph species (Online Resource 1). With this sampling, around 95% of the generic diversity of extant caviomorphs was covered (52 of the 55 known genera; [Mammal Diversity Database 2022](#)), encompassing all families and subfamilies, represented by at least one specimen (Fig. 1; Online Resource 1). Analyzed individuals included both males and females, mostly of unknown age. Although the development of caviomorph inner ears was not separately studied, age does not seem to appreciably affect inner ear morphology in Phiomorpha (e.g., *Fukomys*, [Lindenlaub and Burda 1993](#); *Heterocephalus*, [Mason et al. 2016](#)), nor mammals in general (e.g., [Hoyte 1961](#); [Jeffery and Spoor 2004](#); [Ekdale 2013](#); [Mason et al. 2016](#); [Menecart and Costeur 2016](#); [Thean et al. 2017](#); but see [Sánchez-Villagra and Schmelzle 2007](#)). Regarding fossil taxa, our sample includes a total of eleven different extinct species from the West Indies ($N = 12$ specimens) and South American mainland ($N = 1$ specimen). Heptaxodontids sampled include *Amblyrhiza inundata* found on the Anguilla Bank (AMNH 11842; presumably from either Anguilla or St. Martin; see [MacPhee 2011](#)), *Elasmodontomys obliquus* found in Puerto Rico (AMNH 17127; Morovis; [Anthony 1918](#)), and *Clidomys* sp. from Jamaica (from AMNH collections, without number). Extinct West Indian echimyid octodontoids sampled include heteropsomyines, with *Heteropsomys insulans* collected in Puerto Rico (AMNH 14172, type; Ceiba cave, near Utuado; [Anthony 1916](#)), *Boromys torrei* (CLV 1240; Cueva Afan; CLV 974, 1746; Cueva de los Nesophontes) and *Boromys offella* (CLV without number, Cantera J-4) from Cuba, *Brotomys voratus* from Haiti (UF 490660; Trouing Jean Paul), as well as capromyines as *Rhizoplagiodontia lemkei* (UF 73921; Trouing Jérémie #5, Haiti), *Hexolobodon phenax* (UF 454000; Trouing Jérémie #5), and *Isolobodon portoricensis* (M 86668) from Hispaniola. All these aforementioned extinct rodents from the West Indies come from Quaternary deposits ([McFarlane et al. 1998](#); [Flemming and MacPhee](#)

1999; McFarlane 1999; MacPhee et al. 2000; Steadman and Takano 2013; Cooke and Crowley 2018; Viñola-López et al. 2022b). Finally, we also included the extinct neopiblemid chinchilloid, *Neoepiblema acrensis*, a giant taxon from the Late Miocene of mainland South America (UFAC 4515; Niterói, Acre River, Solimões Formation, Brazil; Late Miocene; Kerber et al. 2019).

Three-dimensional (3D) data acquisition

The 3D data acquisition focused on the skull and petrosal bone using X-ray microtomography (Fig. 1; Online Resource 3: Figs. S1-S4). Specimens from NHMUK were scanned using a Nikon Metrology HMX ST 225 and those from B, NMB, PIMUZ, and ZM using a Nikon XT H 225 ST. Two specimens of *Pattonomys carrikeri* were borrowed from the USNM and were scanned along the specimens from CBGP, CBUN and UM using an EasyTom 150 hosted in the *Institut des Sciences de l'Évolution de Montpellier* (MRI; ISE-M, Montpellier, France). Fossil taxa from AMNH were scanned using a GE Phoenix vtomex s240 and those from CLV and UF with a GE Phoenix vtomex m240 hosted at the Nanoscale Research Facility of the University of Florida (NRF, Gainesville, USA). Specimens from CAPP and MCN were scanned using a Skyscan™ 1173 hosted at the *Laboratório de Sedimentologia e Petrologia of the Pontifícia Universidade Católica do Rio Grande do Sul* (PUCRS, Porto Alegre, Brazil), and those from UFAC with a GE Medical CT Scan.

Scanning resolution of the sample ranged from 11 to 104 μm (Online Resource 1). Due to the heterogeneous origin of the scans (multiple scanning facilities), it was not possible to ascertain the orientation of all specimens, potentially leading to mirrored 3D reconstructions (Fig. 1; Online Resource 4: Figs. S1-S4). However, several studies (Cerio and Witmer 2019; Lebrun et al. 2021; Ward et al. 2021) performed on inner ear asymmetry showed that the effect of asymmetry was much smaller than intraspecific variation. Segmentation of the left or right bony labyrinth for each individual was performed using Avizo 7.1. Right specimens were mirrored when needed using MorphoDig 1.5.3 (Lebrun 2018) to work preferably on left-oriented inner ears.

Semilandmark and linear measurements protocol

The inner ear being a highly curved and coiled structure, we digitized a total of five 3D curves using MorphoDig 1.5.3 (Lebrun 2018; Online Resource 2), which correspond to the first 2.5 turns of the cochlea (the minimum observed in our sample; Online Resources 1 and 2), the lateral (LSC), anterior (ASC) and posterior (PSC) semicircular canals, as well as the common crus (Online Resource 2). These curves were placed at the center of the lumen of the semicircular canals and the cochlea in order to minimize segmentation errors on self-interpretation of grey shades as part of the structure. Moreover, this positioning ensured that errors induced by inter-scanner variability and other parameters such as slice thickness and tube currents were minimized (Larue et al. 2017). For each curve, we extracted a set number of equidistant semilandmarks (Online Resource 2), for a total of $N = 80$ semilandmarks, and slid them along the tangent of the curve to minimize Procrustes distances between each specimen (Bookstein 1991, 1997; Gunz and Mitteroecker 2013). This allowed correction for the artificial part of the shape variation generated by the arbitrary spacing of semilandmarks. In order to compare the inner ear shape variation across all species, we performed a Generalized Procrustes Analysis (GPA; Rohlf and Slice 1990), which executed rotation, translation, and scaling operations in order to remove size and other non-shape differences in the semilandmark configurations. This step enabled the extraction of inner ear size component (centroid size) and Procrustes shape coordinates for each species in our sample. Additional linear measurements of the inner ear were made for the cochlea and SCs (Online Resource 2) in order to compensate for cochlea bias and to visualize them in different phylogenetic scenarios.

All geometric morphometric analyses were performed using R 3.6.3 (R Core Team 2020) with the “geomorph 4.0” package (Baken et al. 2021; Adams et al. 2022).

Visualization of shape variation and statistical analyses

Mean shape and size were used when at least two specimens were sampled for the same species. To visualize the allometric effect on inner ear shape, we performed a simple multivariate linear regression of Procrustes shapes on the \log_{10} of centroid size (Online

Resource 4: Table S1a) followed by Procrustes MANOVAs, considering superfamilies (Goodall 1991) with a resampling of 10,000 random permutations to test for significant allometric effect (Fig. 2; Table 1; Online Resource 4: Tables S1b-S2). For taxonomic purposes, we performed a homogeneity of slopes test (HOS), which consisted in an analysis of covariance (MANCOVA) between size, taxonomic groups (i.e., superfamilies) and the interaction of size and groups on inner ear shape, thereby assessing whether some superfamilies are characterized by unique allometries or shared a common allometry (Online Resource 4: Table S4). Pairwise comparisons enabled us to detect superfamilies that showed differences in slope angles (direction of shape change with size) and lengths (amount of shape change with size) of allometric trajectories (Online Resource 4: Tables S5-S6). We assessed significance with a resampling of 10,000 random permutations and applied a Bonferroni (Bonferroni 1936) and Holm-Bonferroni (Holm 1979) correction to account for multiple comparisons. Then, a principal component analysis (PCA) was performed to visualize shape variations among sampled species in a multidimensional morphospace (Fig. 3), and in the case of a common allometric pattern between grouping factors, residuals from the multivariate regression of shape on the log of centroid size were used to correct the shape of all specimens for allometry, then analyzed in a second PCA (cf. allometry-free; Fig. 4). Additionally, a linear discriminant analysis (LDA) with a leave-one-out cross-validation algorithm was used in order to estimate the reliability of inner ear shape as a taxonomical marker (e.g., Evin et al. 2013; Ferreira-Cardoso et al. 2020; Online Resource 3: Figs. S9-S12 and Online Resource 4: Table S7), and perform class reattribution on fossil species (Online Resource 4: Table S8). Raw Procrustes coordinates of inner ear shape were used as dependent variables over principal components as posterior probabilities proved to be more accurate.

Post-hoc tests and LDA were performed using the “MASS” (Venables and Ripley 2002) and “caret” (Kuhn 2008) R packages.

Comparative phylogenetic analyses

The time-calibrated molecular phylogeny of Upham et al. (2019) was used as a topological backbone for comparative phylogenetic analyses (Fig. 1). Extinct and extant species not available in the molecular dated tree were removed from our dataset prior to pruning in order

to match our species sample ($N = 54$ species). We explored the nature of any given phylogenetic signal to the inner ear morphological variation. A phylogenetic signal can be defined as the tendency of a trait to be more similar between closely-related species than between distant ones (Blomberg et al. 2003). To measure it, we used Blomberg's K descriptive statistic as it is adapted to both univariate (K ; Blomberg et al. 2003) and highly-dimensional data (K_{mult} ; Adams 2014) on inner ear shape and centroid size (Online Resource 4: Table S9). Values of K and $K_{\text{mult}} < 1$ imply that taxa resemble each other phenotypically less than expected under Brownian motion, whereas values of K and $K_{\text{mult}} > 1$ imply that close relatives are more similar to one another phenotypically than expected under Brownian motion (Adams 2014). The significance of this K_{mult} was assessed using 10,000 random permutations of shape data among the tips of the phylogeny. Finally, a phylogenetic generalized least squares regression (PGLS) between mean shape and size variables was implemented to test the effect of evolutionary allometry (Klingenberg 2016; Online Resource 4: Table S3) taking into account the non-independence of species sharing a common phylogenetic history (Felsenstein 1985). We used a multivariate implementation of the PGLS in order to process our shape data ("procd.PGLS" function in "geomorph" package). Finally, phylogenetic character mapping of the cochlear ratio, relative size of the SCs (Online Resources 1 and 2), and centroid size depending on the relative position of *Elasmodontomys* within Chinchilloidea or Octodontoidea was established (Fig. 5; Online Resource 3: Figs. S13-S15). Fast estimation of maximum likelihood of ancestral states was used for visualizing the ancestral states of the characters on the different phylogenetic scenarios (Revell 2012). Additional geometric morphometric methods (GMM) and statistical analyses were carried out independently on the semicircular canals and the cochlea only (Online Resource 4: Table S9). All phylogenetic comparative analyses were performed using the following R packages: "ape" (Paradis et al. 2004), "geomorph" (Adams et al. 2022), and "phytools" (Revell 2012).

Results

Evolutionary allometry of the inner ear in caviomorph rodents

The multivariate regression of inner ear shape on the logarithm of size with superfamilies as grouping factors of all species with the exception of Heptaxodontidae showed a significant

effect of size ($F = 11.687$, $R^2 = 0.134$, $P < 0.001$) and superfamilies ($F = 4.858$, $R^2 = 0.167$, $P < 0.001$), but not interaction between size and superfamilies ($F = 1.304$, $R^2 = 0.045$, $P = 0.131$) (Table 1). The HOS test (Online Resource 4: Table S4) accepted the null hypothesis of parallel slopes and subsequent pairwise comparisons of allometric trajectories were congruent with these results (Online Resource 4: Tables S5-S6). In that context, it may be expected that caviomorph rodents possess a common allometric trajectory that does not depend on their suprafamilial affiliation (Fig. 2). When we accounted for phylogeny (Online Resource 4: Table S3), we found a non-significant effect of size on shape ($F = 1.815$, $R^2 = 0.034$, $P = 0.189$), meaning that size has an important phylogenetic component. Other multivariate regressions of all species including *Amblyrhiza*, *Clidomys*, and *Elasmodontomys* and of extant species only showed similar results of the effect of size on shape and the interaction between size and superfamilies (Online Resource 4: Tables S1-S2). Size-related changes in the minimum and maximum predicted shapes of inner ears in caviomorphs are mainly due to the more lateral orientation of the cochlea and a slight relative increase in PSC size (Figs. 2-3).

Interspecific variation of inner ear shape in extant and extinct caviomorphs

With allometry

The morphospace of each superfamily partially or fully overlaps and does not show straightforward patterns. The first two principal components of PCA with allometry (Fig. 3; see Online Resource 3 Figs. S5-S6 for additional axes) explain 40% of inner ear shape variation, with PC1 showing extreme size variation between species. In fact, labyrinthine centroid size clearly increases along the PC1, and the associated variation is expressed both in size and shape of the semicircular canals, as well as the orientation of the cochlea. Larger taxa on PC1 positive scores are characterized by a cochlea that is oriented more laterally and slightly larger semicircular canals, whereas smaller taxa on PC1 negative scores show a smaller PSC compared to the ASC, an oval-shaped ASC that is wider than higher, dorsal deviation of the posterior part of the LSC from mean plane configuration, and a ventrally oriented cochlea. On PC2, we observe variations in the size of the semicircular canals and common crus. From negative to positive scores, taxa with a relatively smaller common crus

and relatively larger ASC and LSC are separated along the PC2 from taxa with a larger common crus associated with relatively smaller ASC and LSC.

Among the four superfamilies, Octodontoidea has the highest specific diversity (Online Resource 1) and shows the highest amount of inner ear shape variance. Interestingly, the morphospaces of Abrocomidae, Ctenomyidae, and Octodontidae group exclusively on high negative PC1 scores and positive PC2 scores. Octodontoids are clearly separated from Echimyidae, which mostly have negative scores on PC2, with the exception of *Mesocapromys nanus*, *Myocastor coypus*, *Heteropsomys insulans*, *Hexolobodon phenax*, and *Rhizoplagiodontia lemkei*, which have positive PC2 scores (Fig. 3). Erethizontoidea has the lowest specific diversity (Online Resource 1) and show the smallest amount of shape variation among superfamilies. Erethizontoids have positive scores of PC1 and PC2. The morphospaces of cavioid Cuniculidae and Dasyproctidae are restricted to positive PC1 scores and around low PC2 scores. They overlap partially with the broader morphospace of Caviidae. Moreover, the inner ear shape of *Hydrochoerus hydrochaeris*, the largest extant rodent, is separated from the rest of the cavioids with high positive scores on PC2. Within Chinchilloidea, the high positive projection score of *Dinomys branickii* on PC2 distinguishes it from Chinchillidae and the extinct taxon *Neoepiblema acrensis*.

Concerning the Heptaxodontidae, the projection scores of *Amblyrhiza* and *Clidomys* are next to each other on high PC2 scores and fall outside the morphospace of all superfamilies. They are, however, closest to *Dinomys* and *Hydrochoerus*. In contrast, the position of *Elasmodontomys* occurs within the morphospace of Chinchilloidea, Caviioidea, and Erethizontoidea. It is worth noting that although *Elasmodontomys* is located outside the morphospace of octodontoids, it remains relatively close to the extinct heteropsomyine *Heteropsomys insulans* and capromyine *Hexolobodon phenax*.

Without allometry

With the acceptance of the hypothesis of a common allometric pattern among all superfamilies of caviomorph rodents, we were able to perform size correction on inner ear shape (Klingenberg 2016). Residuals from the multivariate regression of shape on size of all specimens were used to perform an allometry-free PCA (Fig. 4; see Online Resource 3: Figs. S7-S8 for additional axes). Variation of inner ear shape without allometric effect seems more

phylogenetically structured than variation with allometry (Fig. 3). The first two PCs corrected for allometry account for 37% of inner ear shape variation. The PC1 shows variation in the relative size and shape of the semicircular canals, common crus, and cochlea. From negative to positive projection scores, the size of the semicircular canals increases, while it decreases for the common crus and the cochlea. The semicircular canals also tend to have a more rounded shape. The PC2 shows variation in angular deviation of the semicircular canals and in orientation and coiling of the cochlea. Along the PC2, from negative to positive scores, the ASC deviates outwards and the PSC inwards. The cochlea flattens out, taking a more compact look than mean shape, and its orientation shifts ventrally.

The morphospace of Erethizontoidea, with low negative scores on PC2, clearly distinguishes it from all other caviomorph superfamilies, which greatly overlap around the origin. The morphospace of Caviidae, with the exception of *Dolichotis patagonum* and *Kerodon rupestris*, spans negative PC1 scores, apart from Cuniculidae and Dasyproctidae, which have PC1 positive scores. Within Chinchilloidea, *Dinomys* has negative scores of PC1 and PC2 and is clearly separated from the morphospace of Chinchillidae and the extinct Neoepiblemidae. Octodontoidea show the highest amount of shape variation in PC1. Abrocomidae, Ctenomyidae, and Octodontidae have high PC1 negative scores and around null PC2 scores. They stand apart from Capromyinae and other Echimyidae, which have positive and low PC1 negative scores, as well as low positive and negative PC2 scores.

Regarding heptaxodontids, the projection score of *Elasmodontomys* falls within the morphospace of the Caviioidea, Chinchilloidea, and Octodontoidea, with only West Indian octodontoids in immediate proximity. The species closest to *Elasmodontomys* are the extinct heteropsomyine *Boromys offella* and *Heteropsomys insulans*, the capromyine *Hexolobodon phenax* and *Rhizoplagiodontia lemkei*, and finally the extant capromyine *Mysateles prehensilis*. *Amblyrhiza* and *Clidomys* are found outside the morphospace of all superfamilies and have negative scores of PC1 and PC2. They are very close to each other, and then to *Dinomys branickii* (Dinomyidae, Chinchilloidea), as observed with the PCA with allometry (Fig. 3).

Phylogenetic relevance of the inner ear shape and size

The phylogenetic signal of shape data of the inner ear showed significant values (all $P < 0.001$; Online Resource 4: Table S9) close to 1 for the whole inner ear ($K_{\text{mult}} = 0.804$) and semicircular canals only ($K_{\text{mult}} = 0.812$), thereby revealing that closely related species have a strong phylogenetic inertia under Brownian motion for these traits. The cochlea ($K_{\text{mult}} = 0.637$) shows a somewhat lesser phylogenetic component. Size analyses revealed a phylogenetic signal higher than 1 (centroid size; $K_{\text{mult}} = 1.502$), thereby indicating that closely-related species are more similar than expected under a Brownian motion model, further emphasizing the phylogenetic component of caviomorph inner ear size. A direct observation of size variation mapped on a phylogenetic tree of caviomorphs reveals that this character is related to their evolutionary history (Online Resource 3: Fig. S13): the small size of octodontoids clearly distinguishes them from other superfamilies, such as cavioids which can be medium to very large sized, or erethizontoids and chinchilloids which are larger and whose size variation is comparatively smaller. The LDA performed on raw Procrustes coordinates retrieves posterior probabilities on group reattribution with an overall accuracy of 83.1% ($P < 0.001$; see Online Resource 4: Table S7 for details of the model). Superfamilies are well discriminated along LD1 (61.1%), LD2 (27.4%) and to a lesser extent LD3 (11.5%) (Online Resource 3: Figs. S10-S12). Erethizontoids are the only group to show high positive LD1 and LD3 values, and as such are well discriminated from the other superfamilies. In this LDA, the position of *Amblyrhiza* is predicted among chinchilloids, *Elasmodontomys* is considered as an octodontoid, and finally, *Clidomys* is attributed to erethizontoids (all posterior probabilities over 99%; Online Resource 4: Table S8).

Discussion

Size influences the inner ear shape variation in caviomorph rodents

The extreme body size variation of caviomorphs, ranging from tens of grams to hundreds of kilograms (taking into account fossil taxa; Rinderknecht and Blanco 2008; Antoine et al. 2012; Vucetich et al. 2015), compared to other mammalian orders can partially be explained

by the multiple diversification events and evolutionary rate changes experienced during their adaptive radiations (Álvarez et al. 2017). Álvarez et al. (2017) demonstrated that patterns of size evolution within caviomorphs were complex and heterogeneous. Cavioids and chinchilloids (and to a lesser extent erethizontoids) presented accelerated rates of evolution and an increase in body size, whereas it was the opposite for octodontoids with the exception of *Myocastor* and insular Capromyinae. Recurrent emergence of large-bodied species within Cavoidea, Chinchilloidea, and Erethizontoidea could be related to the colonization of new ecological niches (Raia et al. 2012). However, this pattern is generally not observed within most Octodontoidea, which remain small to medium-sized despite their great diversity and the large variety of habitats they occupy in the Neotropics (Upham and Patterson 2012). As we observed, size explains a significant portion of the total inner ear shape variation (Table 1), which was not retained after phylogenetic correction (Online Resource 4: Table S3). The HOS test revealed no group-specific influence of size on inner ear shape (Online Resource 4: Table S4), thereby allowing us to consider the existence of a common allometric trend of inner ear shape in Caviomorpha (Fig. 2). Comparisons between PCAs with (Fig. 3) and without allometric correction (Fig. 4) showed that inner ear shape is somewhat sensitive to allometry in caviomorphs, and thus critical from an evolutionary perspective (Online Resource 3: Fig. S13). Previous studies on inner ear shape allometry produced contrasting results depending on the mammalian orders examined. For example, the inner ear shape of Xenarthra (Billet et al. 2015b; Boscaini et al. 2018) and Carnivora (Musteloidea: Grohé et al. 2016; Canidae: Schweizer et al. 2017; Janssens et al. 2019) showed no significant and/or notable changes associated with allometry, whereas those of Diprotodontia (Alloing-Séguier et al. 2013) and Primates (Platyrrhini: del Río et al. 2020; Strepsirrhini: Lebrun et al. 2010) were influenced by allometry. The extreme size variation observed among Caviomorpha might explain the significance of our results. Based on our allometric results, increased body size is associated with lateralization of the cochlea, as well as a relative increase of PSC size (Fig. 2). Studies carried out on cochlear development in the human fetus suggested that cochlear orientation depends on the expansion of the cranial base and subsequent reorientation of the petrosal bone during fetal stages, before (and possibly after) the ossification of the otic capsule (e.g., Jeffery and Spoor 2004; Martínez-Monedero et al. 2011). How the cochlea develops in this regard in caviomorphs and other rodents (and mammals generally) is not known. In the event that this ontogenetic process is retained

among euarchontoglires, placentals, or mammals in general and is not clade-specific, then lateralization of the cochlea may be a convergent character associated with large body size and gigantism. Interestingly, previous studies on large mammals, including large-bodied marsupials (Alloing-Séguier et al. 2013), strepsirrhine primates (Lebrun 2010), and the extinct giant sloth *Megatherium* (Billet et al. 2013) have yielded similar results.

The West Indian Heptaxodontidae are known to have reached exceptionally large body sizes (e.g., Biknevicius et al. 1993; MacPhee 2009), and as such, they represent an outstanding case of insular gigantism. The inner ear morphology of the heptaxodontids *Amblyrhiza*, *Clidomys*, and *Elasmodontomys* is strongly influenced by allometry, as evidenced by the relative increase of PSC size and great lateralization of the cochlea (Online Resource 3: Figs. S1-S4 and S13). As a result, the allometric trajectory of their inner ear is found to be similar to that observed in extant caviomorph rodents from mainland South America and insular Caribbean Capromyinae (Fig. 2). With the exception of the increase in relative size, there is actually no evidence that the allometric pattern is specific to an insular *versus* mainland evolutionary context, and thus due to the island syndrome in particular.

Inner ear morphology partially reflects the systematics of extant Caviomorpha

Our comparative phylogenetic analyses indicate that a significant phylogenetic signal is carried by the inner ear of extant caviomorph rodents (Online Resource 4: Table S9). The shape of the whole inner ear, semicircular canals only, and cochlea only are phylogenetically relevant and almost identical across data pools, with and without allometry being considered.

Erethizontoidea is the most distinctive superfamily in terms of inner ear morphology in our sample. All species were found to lie in close proximity in both PCAs (Figs. 3-4) and were particularly well differentiated from other superfamilies in the PCA corrected for allometry (Fig. 4). Their morphology is characterized by an ASC that is wider than the PSC, an acute angle between the ASC and the PSC, a relatively small LSC that does not deviate from its linear axis, as well as a shortened cochlea with a low number of turns (Fig. 5; Online Resource 1 and Online Resource 3: Figs. S1, S3). The latter feature is commonly found

within mammals (Ekdale 2013), but within Caviomorpha it is a distinctive feature of Erethizontidae (Online Resource 1 and Online Resource 3: Fig. S1). Erethizontoids are considered to be the most conservative clade of caviomorphs because their skull morphology (Vucetich et al. 2015) and pentalophodont dentition (Candela 2002; Marivaux et al. 2002, 2004; Marivaux and Boivin 2019) are comparable to those of Asian-African basal hystricognaths. Also, their incisor enamel microstructure displays primitive subtype 1 to transitional subtype 1-2 multiserial HSB (e.g., Martin 1992; Marivaux et al. 2022). On the basis of these observations, we propose that a low cochlear ratio could be an autapomorphy of Erethizontidae in Caviomorpha (Fig. 5). The inclusion of the genus *Chaetomys* in the Erethizontidae has been a matter of debate since its initial description. Based on its dental pattern and adult retention of deciduous premolars (Patterson and Wood 1982), *Chaetomys* has often been placed within Echimyidae. However, phylogenetic analyses based on mitochondrial DNA (Villela et al. 2009), morpho-cranial anatomy (Voss and Angermann 1997) and incisor enamel microstructure (Martin 1994b) have substantiated its close affinities with Erethizontidae. The inner ear characteristics presented above also support the inclusion of *Chaetomys* within Erethizontoidea (Fig. 5).

Cavioidea occupy a broad morphospace in both PCAs (Figs. 3-4). They exhibit the largest number of cochlear turns in our sample. This feature is highly variable within Caviomorpha (ranging from 2.5 to 4.75 turns; Fig. 5; Online Resource 1). In our study, for methodological reasons, only the first 2.5 turns of the cochlea were sampled, which limited proper shape quantification using GMM (Online Resource 2). Although the morphology of the cavioid cochlea is highly distinctive (Online Resource 3: Fig. S1), this imposed limitation is likely one of the reasons why this clade is not well differentiated from other superfamilies in both PCAs. However, it is more informative for distinction between Caviidae and Dasyproctidae + Cuniculidae. On the PCA with allometry, morphological variation is greater along PC1 and primarily due to allometry (Fig. 3) whereas without allometry most of the variation is due to the relative size of the semicircular canals and basal turns of the cochlea. The latter is almost as wide as high in Caviidae whereas it is wider in the first turn than in the second turn in Dasyproctidae and Cuniculidae (Fig. 4). Looking at the anatomy of the inner ear of Cavioidea, the spiral of the cochlea has an elongated aspect (Online Resource 3: Fig. S1). Specifically, in Caviidae (*Cavia*, *Galea*, *Microcavia*, *Dolichotis*, *Kerodon*, and

Hydrochoerus) the cochlea has a “corkscrew-like” appearance, with individual turns having almost the same width, whereas in Dasyproctidae (*Myoprocta* and *Dasyprocta*) as well as Cuniculidae (*Cuniculus*) the cochlea is more “cone-shaped” with spiral width decreasing from base to apex. Ekdale (2013) previously suggested that the elongated aspect of the cochlea is a synapomorphy of Caviomorpha as compared to mammals. With a comprehensive taxonomic sample, our anatomical investigations show, however, that this character is far from being widespread within Caviomorpha (Fig 5). As it stands, the cochlear aspect is phylogenetically informative when there is extreme shortening or elongation (Fig. 5). The combination of an elongated cochlea that is also highly coiled may be a synapomorphy of Cavoidea. In contrast, the similar cochlear morphology in *Myocastor coypus* can be interpreted as a non-exclusive autapomorphy acquired by convergence (Fig. 5; Online Resource 3: Fig. S2).

Chinchilloids also have a bony labyrinth influenced by allometry, although the shared allometric pattern (Fig. 2) prevents clear definition of characters related to its shape. The PCAs reveal a difference between Chinchillidae and Dinomyidae, which is mainly expressed by PC2 in both cases. It is due to a relative decrease in the size of the common crus for the semicircular canals and slightly larger than higher basal turns of the cochlea in the Chinchillidae, whereas the opposite is true in Dinomyidae. Several anatomical features seem to stand out such as the combination of a large ASC relative to other semicircular canals with an acute angle between the ASC and PSC (Online Resource 1) and coupled with a flattening of the last turn of the cochlea at the apex (Online Resource 3: Fig. S1). This flattening, particularly marked in Chinchillidae, also appears in Octodontoidea among Octochinchilloi (*sensu* Boivin 2019, in Boivin et al. 2019b; Online Resource 3: Figs. S1-S2). Within Chinchilloidea, Dinomyidae (*Dinomys*) is characterized by acute angles between the semicircular canals, as well as by the relatively small size of their SCs with respect to the height of the inner ear (Online Resource 1 and Online Resource 3: Fig. S15). Dinomyids are also characterized by a low cochlear ratio paired with an increased number of cochlear turns; this brings them close to the large extinct taxa *Amblyrhiza* and *Clidomys* (Fig. 5). The Early Miocene *Prospaniomys priscus*, sister taxon to crown Octodontoidea (*sensu* Arnaudo et al. 2020), exhibits a low to intermediate number of cochlear turns (2.5-3 turns) and an intermediate cochlear ratio compared to extant Caviomorpha (Arnaudo et al. 2020). These observations are consistent with the ancestral state of the cochlear ratio (Fig. 5) and number

of turns (Online Resource 3: Fig. S14) recovered at the root of the caviomorph tree, which lead us to interpret them as plesiomorphic conditions in caviomorph rodents.

Within Octodontoidea the large morphospace of the inner ear shape is difficult to capture as a whole (Figs. 3-4). The Abrocomidae, Ctenomyidae, and Octodontidae are found close to each other in negative PCA scores without allometry, and are distinguished as a group by the size of their relatively small SCs in regard to the total size of the bony labyrinth in both PCAs (Figs. 3-4; Online Resource 3: Fig. S15), and the large size of the ASC relative to the PSC and LSC. The angle between the ASC and the PSC is obtuse, the LSC deviates dorsally (except for the Abrocomidae) in its posterior part, and the common crus is well developed. The cochlea is longer than wider with the exception of Ctenomyidae, oriented more anteroventrally, and stockier in appearance (Online Resource 3: Fig. S2). These common features of the bony labyrinth support the monophyly and phylogenetic proximity of Ctenomyidae and Octodontidae, a result consistent with morpho-paleontological (e.g., Verzi et al. 2014; Arnal and Vucetich 2015) and molecular (e.g., Fabre et al. 2012, 2013; Upham et al. 2019) data. However, the proximity of *Abrocoma* to the morphospace of these two families in both PCAs (Figs. 3-4), as well as morphological similarities in inner ear morphology (Online Resource 3: Figs. S1, S3 and S15), may hint at convergence in these features due to their similar ecologies: Abrocomidae, Ctenomyidae and Octodontidae all live to varying degrees in subterranean habitats (Vassallo 1998; Álvarez et al. 2011; Hautier et al. 2011, 2012; Verde Arregoitia et al. 2020). These taxa show postcranial features linked to fossoriality, such as moderately to very robust humeri, radius, ulna and autopodium, humeri with developed tubercles and medial epicondyles, and marked curvature of the radius and ulna (Morgan et al. 2015). In contrast, Echimyidae exhibits highly variable bony labyrinth shapes, preventing characterization of this family by means of traits of this structure (Online Resource 3: Figs. S1-S4). This pattern seems to be linked to specific aspects of their adaptive radiation (Fabre et al. 2013, 2015; Emmons et al. 2015). However, bony labyrinth features observed in echimyids tend to correlate with expected phylogenetic relationships at the subfamilial level. This is particularly the case for the relative size of the semicircular canals (Online Resource 3: Fig. S15), which segregate most arboreal echimyines (Echimyini; *Mesomys*, *Isothrix*, *Pattonomys*, *Makalata*, *Phyllomys*, *Kannabateomys*, *Callistomys*, and *Diplomys*) from other taxa in positive PC1 scores in both PCAs (Figs. 3-4). The Euryzygomatomyinae (*Euryzygomatomys*, *Clyomys*, and *Trinomys*) are not distinguishable

from other Echimyidae with the exception of *Clyomys laticeps* due to its extreme cochlear ratio (Fig. 5). The Greater Antillean Capromyinae have an intermediate bony labyrinth shape, as evidenced by their central positioning in the inner ear shape morphospace (Figs. 3-4), and average values of the cochlear ratio and number of turns of the cochlea (Fig. 5). We did not identify any characteristics that would allow them to be distinguished from other families. Carterodontinae (*Carterodon*) lies close to Capromyinae in the inner ear morphospace without allometry (Fig. 4). This result is consistent with gene-based phylogenies (Fabre et al. 2014, 2017; Courcelle et al. 2019; Woods et al. 2021), but when allometry was considered this positioning was not retrieved (Fig. 3). *Carterodon* has a large LSC relative to the ASC and PSC (Online Resource 3: Figs. S2, S4), similar to conditions in Euryzygomatomyinae (*Euryzygomatomys* and *Clyomys*; Online Resource 3: Figs. S1-S4), and also agrees with this taxon in dental morphology (Carvalho and Salles 2004; Candela and Rasia 2012). The position of *Carterodon* is a major point of debate as it appears to be a convergent taxon with the semi-fossorial forms of Euryzygomatomyinae (*Clyomys* and *Euryzygomatomys*) with respect to its dental morphology (Carvalho and Salles 2004; Candela and Rasia 2012). In view of the genomic data, it is likely that the similarities in SCs morphology between the Euryzygomatomyinae and Carterodontinae are homoplasies, possibly a result of their shared semi-fossorial lifestyles or inherited from their ancestors.

Phylogenetic and biogeographical implications for Heptaxodontidae of the West Indies

Linear discriminant analysis (LDA) results in the attribution of *Amblyrhiza* to Chinchilloidea, *Clidomys* to Erethizontoidea, and *Elasmodontomys* to Octodontoidea, were obtained from a model with 83% accuracy (Online Resource 3: Figs. S10-S12 and Online Resource, Table S7). From an anatomical viewpoint, the assignment of *Clidomys* to Erethizontoidea seem quite unlikely, and may result from an inadvertent methodological bias in characterizing only one part of the shape of the cochlea (Online Resource 2). Moreover, LDA appears to be a controversial method for assigning fossil taxa to systematic and ecological categories (Panciroli et al. 2017). For this reason, we refrain from using these results in the superfamilial attribution of heptaxodontid taxa. Although we were able to identify many diagnostic features for extant subfamilies, families and superfamilies of Caviomorpha, results for

Heptaxodontidae are more difficult to interpret, particularly because of the strong allometric effect of large body size in *Amblyrhiza inundata*, *Clidomys* and *Elasmodontomys obliquus*, as previously discussed (see [Biknevičius et al. 1993](#); [MacPhee 2009](#)).

Amblyrhiza and *Clidomys* share a very similar conformation of the bony labyrinth (Fig. 1; Online Resource 1 and Online Resource 3: Figs. S1, S3) in having a particularly acute angle between the ASC and the PSC, as well as between the PSC and the LSC compared to other taxa (Fig. 1; Online Resource 1). Their PSC and LSC are also very similar in having a round-shaped PSC and slightly oval-shaped LSC along its length (Online Resource 3: Figs. S1, S3). The short and tightly coiled cochlea is almost identical in the two species. Also, in both PCAs, *Amblyrhiza* and *Clidomys* are consistently found close to each other, outside the morphospaces of most extant superfamilies, but close to *Dinomys branickii* (Dinomyidae, Chinchilloidea) (Figs. 3-4). The inner ear morphology of *Dinomys* is markedly similar to that of *Amblyrhiza*, with virtually identical cochlea, common crus and LSC. The ASC and PSC are roughly similar in shape and size, but differ in orientation. *Dinomys* also resembles *Clidomys* in cochlear configuration and slightly smaller LSC (Fig. 1; Online Resource 3: Figs. S1, S3). Because the common crus of *Dinomys* is smaller than that of *Clidomys*, the PSC appears different, even though it is of similar size and shape. In contrast, their ASCs are a distinguishing feature of the two taxa, being round-shaped in *Clidomys* but oval (breadthwise) in *Dinomys*. [MacPhee \(2011\)](#) previously highlighted apparently homologous characters of the auditory region shared by *Amblyrhiza* and Chinchillidae (i.e., an elongated acoustic canal and fused ectotympanic-ectotympanic suture in the adult, as well as a conspicuous tympanic window in the bullar wall), although features related to basicranial vasculature (i.e., connection between ramus post-tympanicus and ramus stapedia posterior) appear to be identical in *Amblyrhiza* and *Dinomys*. He proposed that if *Amblyrhiza* turns out to be the sister group of Chinchillidae, vascular characters of the basicranium shared by the former and *Dinomys* would have to be considered as the result of a convergence, or as primitive traits lost by chinchillids during their evolution. [MacPhee \(2011\)](#), however, resolved the problem by considering *Amblyrhiza* to be sister to both extant families of Chinchilloidea (Chinchillidae and Dinomyidae). Our results strongly support the inclusion of this iconic giant West Indian taxon among the Chinchilloidea, a conclusion also recently reached based on dental morphology and incisor enamel microstructure ([Marivaux et al. 2020, 2022](#)). Moreover, the present paper offers novel insights regarding the position of

Clidomys, as we recovered this taxon close to *Amblyrhiza*, and by extension to other Chinchilloidea, notably Dinomyidae and Neopiblemidae. Comparative studies including *Amblyrhiza* and *Clidomys* have primarily focused on the teeth, as these are the structures most frequently preserved in the fossil record (DeSalle 2009). *Amblyrhiza* displays a dental pattern characterized by laminae with a heterogeneous thickness of the enamel layer, a condition found in several Chinchilloidea (Chinchillinae, Lagostominae, Dinomyidae; e.g., Kramarz et al. 2013; Marivaux et al. 2020). *Clidomys* exhibits lamellar lophs without enamel layer heterogeneity, a condition reminiscent to that found in some extinct chinchilloids such as the Neopiblemidae (e.g., *Neopiblema*, *Phoberomys*), but also convergently in two independent lineages of Echimyidae (Octodontoidea), the genera *Diplomys* and *Phyllomys* (e.g., Emmons 2005; Fabre et al. 2017).

Regarding *Elasmodontomys obliquus*, this taxon was interpreted as a member of either Octodontoidea, based on a postcranial character (i.e., elongation of the acromion process of the scapula; Woods 1984; Woods and Hermanson 1985), or Chinchilloidea, based on dental characters (i.e., taeniodont lower and upper teeth, a multi-laminar occlusal pattern, laminae with a heterogeneous thickness of the enamel layer, narrow interlaminar space, etc.; Marivaux et al. 2020) and incisor enamel microstructure (i.e., subtype 1-2 of multiserial HSBs; Martin 1992; Marivaux et al. 2020, 2022). Using the several characters of the ibony labyrinth, the phylogenetic affiliation of *Elasmodontomys* is also difficult to interpret, as we found contrasting results depending on whether or not allometric effects on inner ear shape were considered. For example, on the PCA with allometry, *Elasmodontomys* falls within the overlapping morphospace embracing large cavioids, chinchilloids and erethizontoids (Fig. 3). Species closest to the morphospace of *Elasmodontomys* include *Dolichotis salinicola* and *Kerodon rupestris* as well as *Chaetomys subspinosus*, *Coendou prehensilis* and *Coendou spinosus*. Chinchilloids as represented by *Lagostomus maximus* and *Dinomys branickii*, are more spatially distant, with the latter being nearest to the morphospace of *Elasmodontomys*. Finally, and perhaps most interestingly, the West Indian echimyid octodontoids, *Heteropsomys insulans* and *Hexolobodon phenax* are the species nearest to *Elasmodontomys* in our results. However, the lack of clear proximity of the morphology of *Elasmodontomys* to one superfamily rather than another is most likely due to the high degree of allometry affecting the latter taxon, which makes it difficult to draw conclusions. The PCA without allometry provides another perspective on this problem (Fig. 4): even though

Elasmodontomys falls within the overlapping morphospace of cavioids, chinchilloids and octodontoids, it is close to the center of the morphospace of capromyines and heteropsomyines such as *Boromys offella*, *Heteropsomys insulans*, *Hexolobodon phenax*, *Mysateles prehensilis* and *Rhizoplagiodontia lemkei*. It is also worth noting that the position of *Elasmodontomys*, well away from the other two Heptaxodontidae, *Amblyrhiza* and *Clidomys* on both PCAs (Figs. 3-4), implies that the inner ear of *Elasmodontomys* differs substantially from those of its two alleged counterparts. The comparative anatomy of *Elasmodontomys* shows an increased relative size of the ASC compared to the LSC and PSC, and a dorsal deviation of the LSC posteriorly (Fig. 1; Online Resource 3: Figs. S1, S3). These character states are not observed in *Dinomys*, *Amblyrhiza* or *Clidomys*, whereas they are present in extinct capromyines (*Hexolobodon phenax*, *Isolobodon portoricensis*, *Plagiodontia aedium*, *Plagiodontia ipnaeum*, and *Rhizoplagiodontia lemkei*; Online Resource 3: Figs. S2, S4). Only the low cochlear ratio places *Elasmodontomys* close to *Amblyrhiza* and *Clidomys* (Fig. 5a; Online Resource 3: Fig. S1), but also to *Heteropsomys insulans* (Online Resource 3: Fig. S4). MacPhee (2011) reached a similar conclusion on the basis of basicranial anatomy and mentioned that *Elasmodontomys* resembles “a wide variety of other taxa— but not *Amblyrhiza* in particular or chinchilloids in general”. This ambiguous, somewhat complex situation for *Elasmodontomys* is echoed by other morpho-anatomical analyses. The conflicting clues given by the morphology of the inner ear do not allow us to ascertain a suprafamilial attribution for *Elasmodontomys* as to whether it should be regarded as a chinchilloid and thus a close relative of the heptaxodontids *Amblyrhiza* and *Clidomys* (Fig. 5a), or as an octodontoid, closely related to extant capromyines (Fig. 5b) and to extinct heteropsomyines. We hypothesize that the unique and complex association of Octochinchilloi morphological characters observed in *Elasmodontomys* (i.e., orientation, size and shape of the cochlea similar to *Amblyrhiza* and *Clidomys*, and similarity in shape and size of the semicircular canals with extant and extinct capromyines and heteropsomyines) could perhaps be explained by an island syndrome that affected inner ear morphology differently from other heptaxodontids. Otherwise, we are perhaps also today unable to recognize how allometry affects large-bodied octodontoids, as most extant and extinct species from mainland South America remained small-sized throughout their evolutionary history (Álvarez et al. 2017).

Recently, the molecular phylogenetic results published by Woods et al. (2021) placed *Elasmodontomys* within echimyids as a sister-lineage to the Hispaniolan *Plagiodontia*, together with other hutias (*Capromys*, *Geocapromys*, *Mesocapromys*, and *Mysateles*) and some West Indian echimyid subfossil taxa (*Boromys* and *Brotomys*). Previous morphological inferences (MacPhee 2011) and our inner ear results for *Elasmodontomys* do not clearly contradict these molecular results. However, Woods et al. (2021) went further, proposing in both their title and abstract that one colonization event might account for the origin of the endemic caviomorph radiation in the West Indies. If this hypothesis is correct (but see Marivaux et al. 2022), the antiquity of this radiation must go back to the late Paleogene, as *Borikenomys*, recently discovered in the early Oligocene of Puerto Rico displays potential affinity with heptaxodontids, all of which share a similar enamel microstructure pattern not documented in any echimyids or capromyines that is unlikely to be due to homoplasy (Marivaux et al. 2020). One consequence of the phylogenetic argument of Woods et al. (2021) is that placing the split between Capromyinae and South American Echimyidae in the Early Miocene is either far too young and at least inconsistent with a single colonization event (e.g., Upham and Patterson 2015; Fabre et al. 2017; Courcelle et al. 2019; Woods et al. 2021), or, alternatively, that the early colonization of Puerto Rico by the ancestor of the *Borikenomys* lineage was quickly followed by its extinction. This alternative is somewhat difficult to envisage if we consider the hypothesis of a phylogenetic link of this taxon with the Heptaxodontidae (*Amblyrhiza*, *Elasmodontomys*, *Quemisia*, etc., sensu Marivaux et al. 2020, 2022). On dental grounds, *Borikenomys* from Puerto Rico displays stronger affinities with Chinchilloidea than with Octodontoidea (Marivaux et al. 2020, 2022), and to date, no rodent fossils from this ancient epoch and geographical area have been found or identified as documenting octodontoid presence (Marivaux et al. 2021). As our inner ear results and several other lines of morphological evidence strongly support the placement of *Amblyrhiza* within Chinchilloidea, a single colonization event of the West Indies by caviomorphs as advocated by Woods et al. (2021) seems doubtful. To conclude, we acknowledge that island evolution has fostered remarkably distinctive living and extinct forms (Losos and Ricklefs 2009; van der Geer et al. 2011) including West Indian mammals. Relationships and potential monophyly of both West Indian Primates (Horovitz and MacPhee 1999; MacPhee and Horovitz 2004; Cooke et al. 2011; Woods et al. 2018) and heptaxodontid rodents (MacPhee 2011; Fabre et al. 2015; Marivaux et al. 2020, 2022; Woods et al. 2021) are still in doubt. In

West Indian xenarthrans, both paleoproteins and ancient DNA have deciphered their relationships and significantly altered their past classifications (Delsuc et al. 2019; Presslee et al. 2019). West Indian rodents also display a rather unusual set of derived and plesiomorphic morphological characters that hinder the resolution of their phylogenetic relationships. In view of these morphological discrepancies along with our inconclusive inner ear results for *Elasmodontomys*, we call for further assessments of Western Indian caviomorph relationships using more paleoproteins or ancient DNA to further test their phylogenetic relationships and to understand both the pattern of their morphological evolution and their colonization history.

Conclusion

Our results show that the inner ear proved to be a suitable structure to characterize the phylogenetic relationships of caviomorph rodents at the family-level, and that part of the morphological variation of this structure is due to allometry. A lateralization of the cochlea as well as a slight relative increase of the PSC size may be typical of large taxa in mammals and should therefore be considered in character matrices for future cladistic analyses. We identified that shape combined with the number of turns of the cochlea are excellent markers for Erethizontoidea and Caviidae, respectively. Namely, Erethizontoidea are characterized by an extreme shortening of the cochlea that was probably conserved from their ancestry with African hystricognathous rodents and by a low number of turns. Caviidae are, for their part, extremely derived, showing a thin and elongated cochlea with a high number of turns. Further studies are needed to investigate the developmental process behind the extreme coiling of the cochlea in Caviioidea and lateralization of the cochlea in larger taxa to better understand how these features appeared and evolved. Our study also offers interesting insights into the ecological components of the inner ear, as the relative size of the SCs on the height of the inner ear appears to be particularly relevant for differentiating fossorial taxa from arboreal ones. Preliminary analyses of the ecological patterns of the inner ear sound promising for locating adaptive morphology through caviomorphs evolution and inferring possible morpho-functional causes that could explain its great diversity.

Additionally, our results on the characterization of the morphological variation of the inner ear in extant caviomorphs have been used to assess the suprafamilial affinities of the West Indian extinct heptaxodontids *Amblyrhiza*, *Clidomys* and *Elasmodontomys*. Our results demonstrate that *Amblyrhiza* and *Clidomys* are more similar to each other than to *Dinomys*, an extant chinchilloid, and that *Elasmodontomys* displays a mosaic of characters that places this taxon between Chinchilloidea and Octodontoidea. We therefore consider *Elasmodontomys* as a representative of Octochinchilloi, which does not allow us to support one or the other hypotheses regarding the suprafamilial affinities of this taxon, nor to provide additional information on the chronology and number of dispersal events that led to the diversification of the Heptaxodontidae in the Caribbean islands. The next step would be to integrate extinct giant chinchilloids (dinomyids and other neoepiblemids) from the South American mainland to test if the allometric pattern observed in the Caribbean islands occurs in the same way, and if there are similar evolutionary trends among West Indian heptaxodontids. Finally, adding Old World hystricognaths such as extinct Phiomorpha, Thryonomyoidea and Hystricoidea, and possibly Ctenodactylidae, as well as studying other phylogenetically relevant structures of the inner ear that were not investigated here (e.g., the vestibular aqueduct and endolymphatic sac) should help refining and polarizing the inner ear characters for future cladistic assessments and paleontological applications.

Competing interests

The authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

Author's contributions

LDC, RL, LM and PHF conceived the study. LWVL, LK and PHF collected CT-scan data and LDC segmented and conducted morphometric analyses with assistance of LH, PHF and RL. LWVL, JVJ, POA, MB and LM collected and identified field specimens and provided paleontological information. LWVL, RDEM, LK, JVJ, POA, MB, LH and RL supplied specimen information, identifications and commentary on the manuscript. LDC, LM and PHF wrote the manuscript with inputs from all authors.

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Figure captions

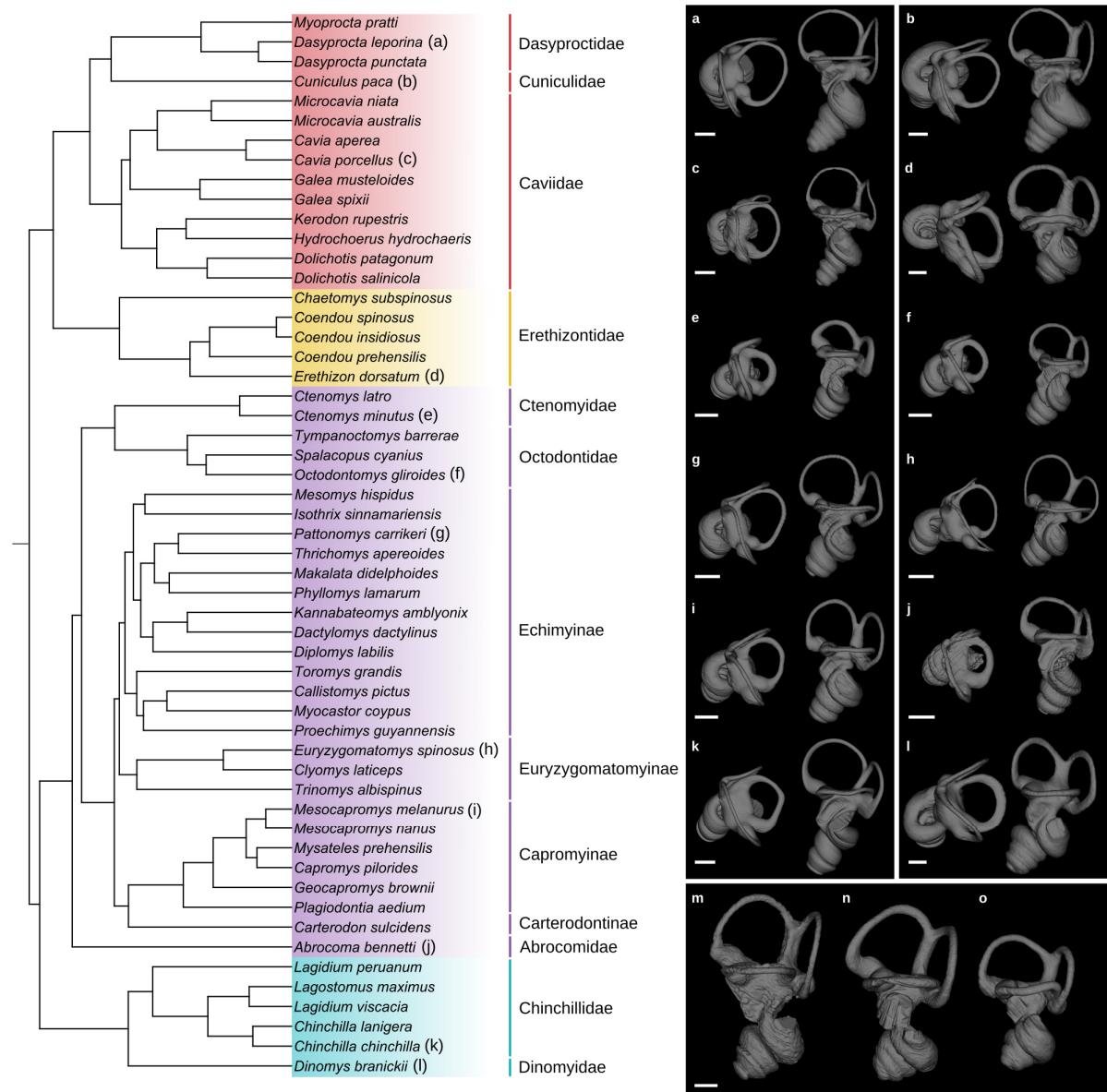


Fig. 1 Phylogeny and morphological diversity of the inner ear of caviomorph rodents. The phylogenetic tree of sampled extant species is derived from Upham et al. (2019) and associated with three-dimensional reconstructions of the inner ear of selected extant and extinct species used in this study (a-o). The inner ear morphology of one specimen of each extant family of caviomorph rodents represented all in the dorsal (left) and lateral (right) views (a-l). The inner ear morphology of the subfossil heptaxodontids from the West Indies: (m) *Amblyrhiza inundata*, (n) *Clidomys* sp. and (o) *Elasmodontomys obliquus*. Scale bars = 1.5 mm.

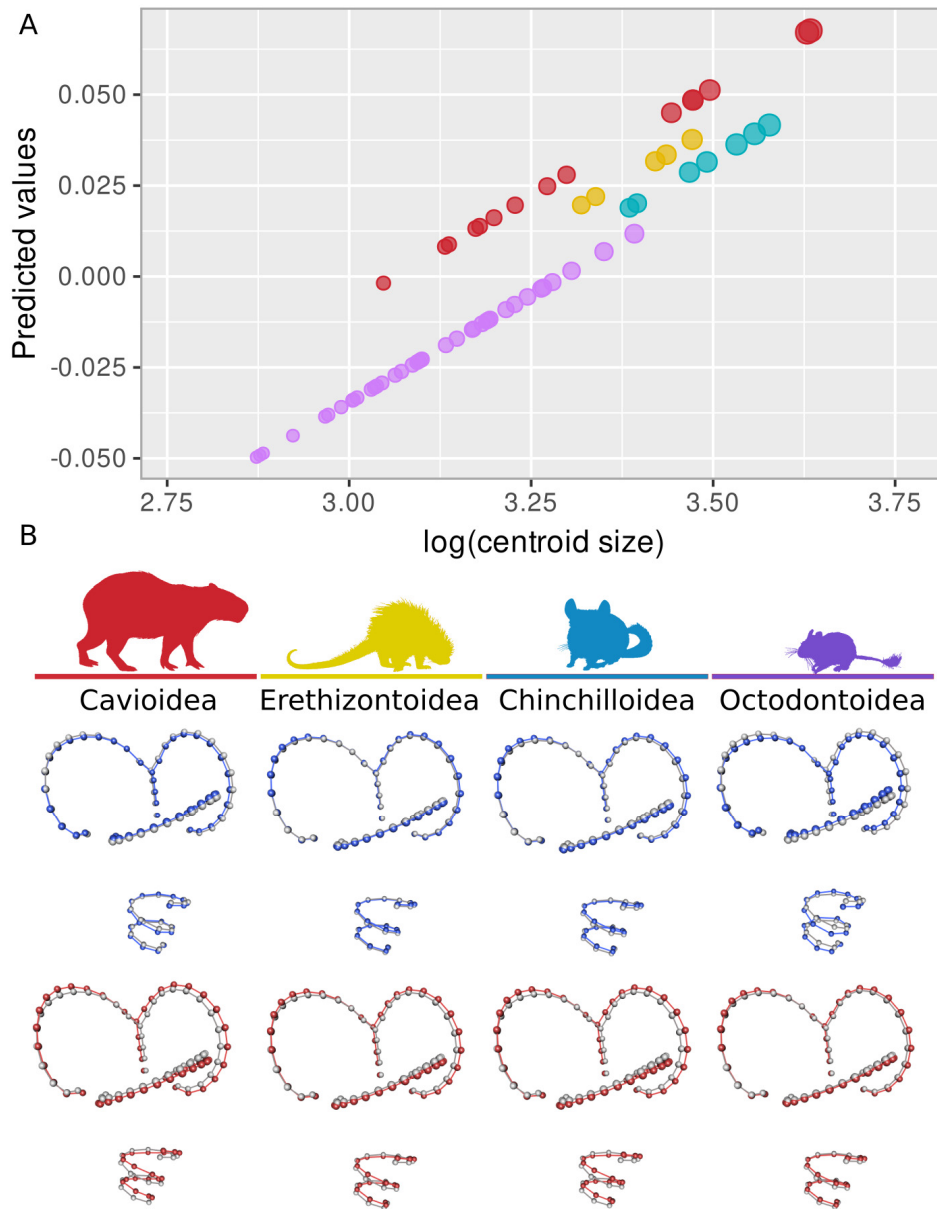


Fig. 2 Evolutionary allometry of extant superfamilies of caviomorph rodents. **a.** Linear regression of the PC1 of predicted values of the multivariate regression of inner ear shape on the logarithm of centroid size. **b.** Predicted inner ear shapes from the multivariate regression model of shape on size for the smallest (top; blue lines), and largest inner ear (bottom; red lines) of each caviomorph superfamily. Grey lines represent the mean shape of the inner ears in our sample, with the exception of the Heptaxodontidae.

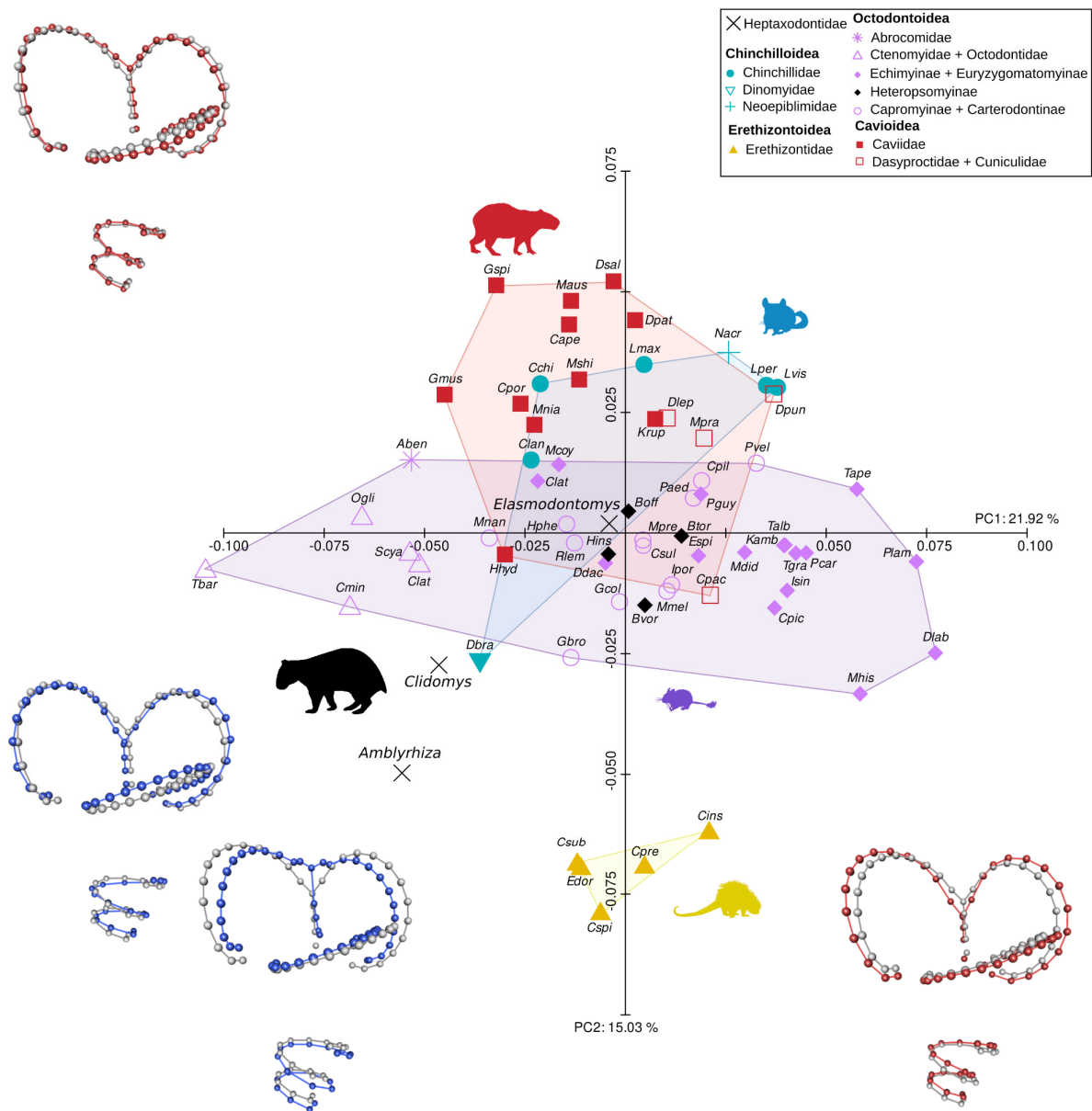


Fig. 4 Principal component analysis (PCA) of inner ear shape of Cavimorpha corrected for allometry and associated lines representing its morphological variation. Bottom inner ears represents extreme shape variation on PC1 and left inner ears on PC2. Minimum shape is represented in a blue line, maximum shape in a red line, and mean shape in a grey line. Abbreviations for the species in the figure can be found in the Online Resource 1.

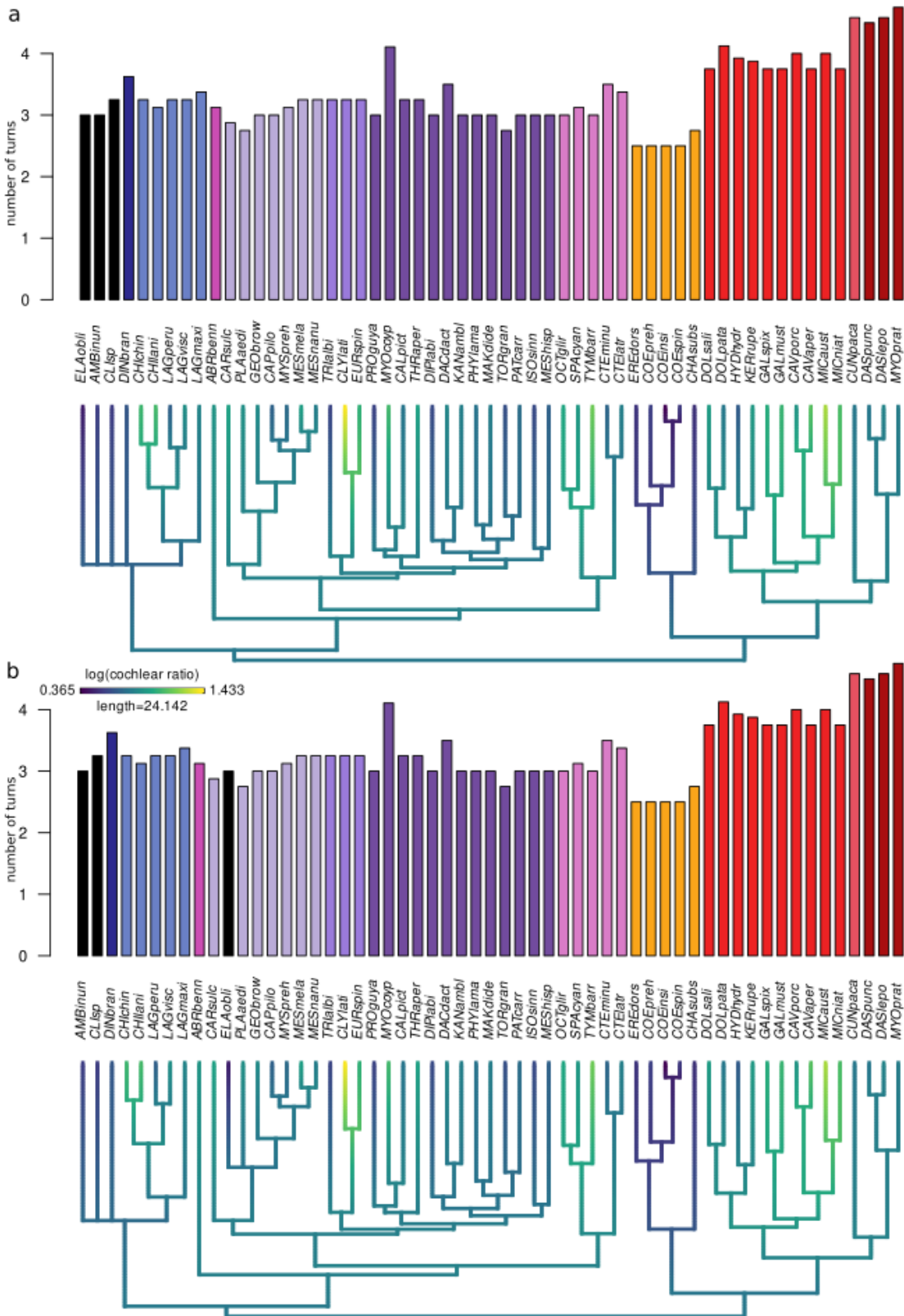


Fig. 5 Phylogenetic character mapping of the logarithm of the cochlear ratio combined with the number of turns of the cochlea. The phylogenetic tree of sampled extant species is derived

from Upham et al. (2019). The Heptaxodontidae are represented in black and were manually added to the phylogeny in order to illustrate the two evolutive scenarios for the Heptaxodontidae: **a.** a monophyletic scenario with *Elasmodontomys obliquus* being part of the Chinchilloidea; **b.** a polyphyletic scenario with *Elasmodontomys obliquus* being part of the Octodontoidea. Colors of the histogram correspond to the different clades of Caviomorpha. From left to right: dark blue: Dinomyidae; blue: Chinchillidae; dark pink: Abrocomidae; light purple: Capromyinae + Carterodontinae; purple: Euryzygomatomyinae; dark purple: Echimyinae; pink: Octodontidae + Ctenomyidae; orange: Erethizontidae; red: Caviidae; light red: Cuniculidae; dark red: Dasyproctidae. Abbreviations for the species in the figure can be found in the Online Resource 1.

Table caption

Table 1 Manova of mean shape (Procrustes coordinates) ~ log(centroid size) * superfamily of all species except Heptaxodontidae. Abbreviations: *Df*, degrees of freedom.

	<i>Df.</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
Log(cs)	1	0.134	11.687	<0.0001*
Superfamily	3	0.167	4.858	<0.0001*
Log(cs):superfamily	3	0.045	1.304	0.131
Residuals	57	0.654	-	-
Total	64	-	-	-

Df, degrees of freedom; *F*, *F*-statistics; *R*², coefficient of correlation; *P*, *P*-value; * statistically significant *P* (*P* ≤ 0.05)

Supplementary Material

<https://link.springer.com/article/10.1007/s10914-023-09675-3#Sec23>

Online Resource 1 Specimens table

Online Resource 2 Linear measurements and GMM protocol

Online Resource 3 Additional figures

Online Resource 4 Additional statistical tables