



Allometry, Function and Shape Diversification in the Inner Ear of Platyrrhine Primates

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Abstract

The diversification of anatomical structures with functional importance during the branching process of a clade is a widely studied phenomenon in evolutionary biology. In recent years, there is a growing interest in the study of the inner ear, a structure associated with hearing, locomotion, and indirectly, with body size. These studies have been particularly important in primates. The platyrrhine radiation is an ideal system in which to study inner ear diversification because it is one of the major groups of living primates and an example of an adaptive radiation related to body size and ecological characteristics. In this work, we used micro-tomography, 3D geometric morphometrics, and phylogenetic comparative methods to explore the pattern of shape variation in the inner ear of platyrrhines and to assess whether this variation is related to size, locomotion, and vocalization. Our main results suggest that (1) diversification of inner ear morphology was achieved early in the radiation, particularly for the shape of the semicircular canals and the relative size of the cochlea; (2) inner ear shape diversification is generally not associated with changes in vocalization features or locomotion behaviors; and (3) conversely, body size is a strong predictor of inner ear shape. This last result contrasts with recent studies indicating that allometry has weak effects on platyrrhine cranial diversification and suggests complex factors driving inner ear diversification in the clade.

Keywords Phylogenetic structure · Adaptive radiation · Microtomography · Geometric morphometrics · Phylogenetic comparative method

Introduction

The relationship between form and function, as well as the ecological relevance of morphological characters, has been widely explored in ecological and evolutionary studies since the

nineteenth century (e.g., Darwin 1859; van der Klaauw 1948; Radinsky 1987; Losos and Mahler 2010). The conceptual basis to understand this relationship was established early in Darwin's studies and then systematized in several disciplines, such as in Anthropology (Moss and Young 1960), Mammalogy and Paleobiology (Radinsky 1987). The main question underlying the relationship between form and function in different disciplines can be summarized as: when are deterministic factors, related to functional or ecological variation, more important to explain morphological diversity than purely random factors (Butler and King 2004; Gavrillets and Losos 2009)?

In this context, the evolutionary diversification of anatomical structures with functional importance –such as Darwin's finches' beaks, limb size and shape in *Anolis* lizards on the Caribbean islands, and body shape in East African cichlids (Gavrillets and Losos 2009) – has been widely studied (Simpson 1944; Gavrillets and Losos 2009). Building on paleontological significance and technological advances (i.e., microtomography, μ CT), there is a recent and growing interest in studying the inner ear in the otic capsule, a structure with

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specific ecologically relevant functions (Spoor et al. 2007; Kirk and Gosselin-Ildari 2009; Lebrun et al. 2010; Ekdale 2016). Particularly, this structure has two main features: the cochlea – involved in sound perception – and the semicircular canals – three bony tubes related to balance maintenance during locomotion (Spoor et al. 2007; Kirk and Gosselin-Ildari 2009; Ekdale 2016).

Considering these functional characteristics, several studies have explored the macroevolutionary relationship between size and shape diversification of the inner ear and changes in locomotion and hearing capabilities in different mammalian clades (see review in Ekdale 2016). In primates, for example, where locomotion and communication through vocalizations are fundamental ecological factors (Fleagle 2013), it has been suggested that changes in cochlear size and shape may be related to shifts in audible frequencies. Particularly, a relative increase in cochlea size and in the longitude of the cochlear spiral has been related to a reduction of high frequency sensitivity limits (Kirk and Gosselin-Ildari 2009; Ekdale 2016). Also, relatively larger semicircular canals are more sensitive to rotations in space than relatively smaller ones, with the latter being more usually observed in slow-moving animals (Ekdale 2016). This suggests a functional link between relatively larger semicircular canals and faster and more agile movements (Spoor et al. 2007; Ekdale 2016). Additionally, previous work in primates also suggests that inner ear morphology, as well as vocalization frequency and locomotion, are related to changes in body size during evolutionary diversification (Spoor et al. 2007; Bowling et al. 2017).

In this context, the platyrrhines or New World monkeys make an ideal system in which to study in more detail the processes driving inner ear diversification. Platyrrhines constitute an old (ca. 25–35 Ma; Perez et al. 2013) monophyletic clade that diversified in Central and South America, generating a relatively large number of taxa that comprises ca. 130 extant species (Groves 2005; Fleagle 2013; Aristide et al. 2015a). The clade branched in six main subclades (denominated subfamilies in molecular studies; Perelman et al. 2011), where Pitheciinae plus Callicebinae represents the most ancient divergence, Atelinae is an intermediate subclade, and Cebinae plus Aotinae (i.e., *Aotus*) plus Callitrichinae are the last subclades to diverge (Fig. 1; Aristide et al. 2015a). Moreover, this diversification is considered a major primate adaptive radiation that unfolded along body size and locomotion axes, among others (Rosenberger 1992; Aristide et al. 2015a), while also presenting a large variation in vocalization characteristics (Bowling et al. 2017; Barbosa Caselli et al. 2018). Specifically, the species in the clade vary between ca. 0.1 and 10 kg in body mass; extremes of arboreal quadrupedal walk, clamber and bridge, and suspensory locomotion; as well as between medians of seven and 40 vocalization

repertoires with different values of mean dominant frequencies (Rosenberger 1992; Aristide et al. 2015a; Bowling et al. 2017; Barbosa Caselli et al. 2018). However, despite these peculiarities, no previous work has formally addressed the factors driving the diversification of the inner ear in platyrrhines in an integrated, quantitative comparative framework.

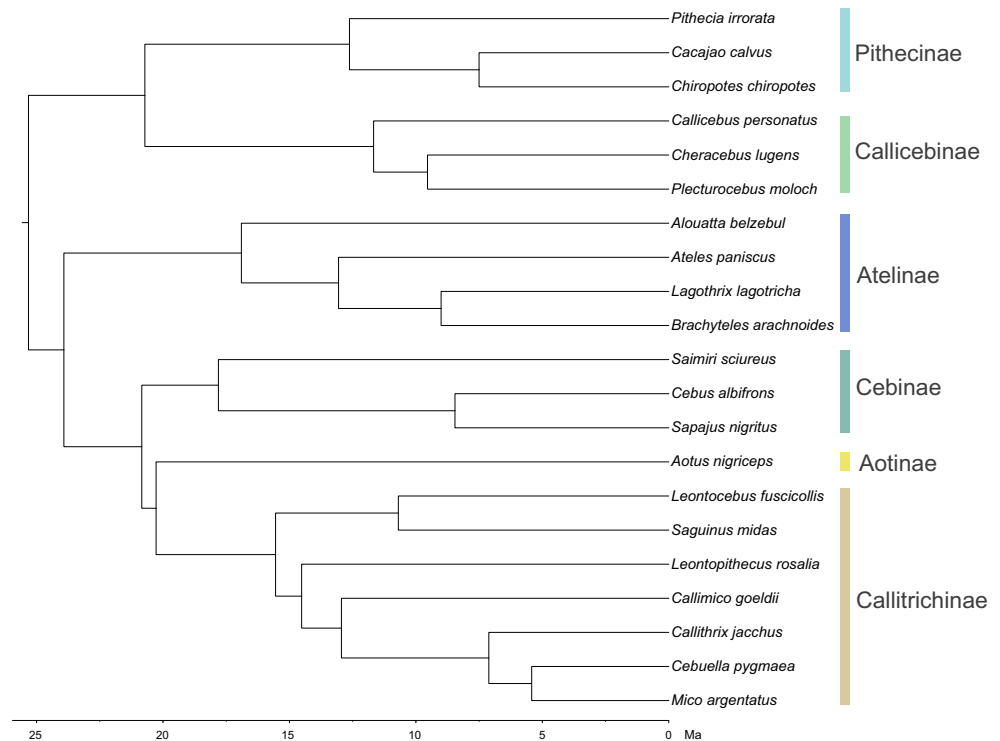
In this work, we first use μ CT and 3D geometric morphometrics (3D-GM; Mitteroecker and Gunz 2009) to explore the pattern of shape variation in the overall inner ear, as well as in the cochlea and the semicircular canals of platyrrhine primates. We then assess, using phylogenetic comparative methods (PCM; Martins and Hansen 1997; Blomberg et al. 2003; Harmon et al. 2003), whether this variation is related to body size, vocalization frequencies and repertoires, and/or locomotion behaviors (Aristide et al. 2015a; Bowling et al. 2017; Barbosa Caselli et al. 2018). If locomotion and communication demands are important factors driving inner ear shape diversification independent of size changes, we expect to find a strong evolutionary association between these ecological variables and inner ear shape variation. Particularly, although previous studies reported disparate results, we expect that species with a higher frequency of clamber and quadrupedal walk to display relatively larger semicircular canals than species with a major proportion of bridge and suspensory locomotion. Additionally, we expect species with higher dominant vocalization frequencies to have a smaller cochlea than species with lower dominant frequencies.

Material and Methods

Sample

In this study we analyzed 78 skulls of both sexes belonging to adult specimens of the 21 currently recognized platyrrhine genera (IUCN 2018; Fig. 1; Table S1), which are deposited in the Museu Nacional (MNRJ, Rio de Janeiro, Brazil) and the Museu de Zoologia (MZUSP, Universidade de São Paulo, Brazil). Each genus was represented by one species. Although this approach excludes intra-generic variation, which could be relatively large in genera with wide geographic variation such as *Alouatta*, it assured the representativeness of taxa across the phylogeny. Moreover, each species was represented by one to five individuals (median = 4; mode = 5). *Callimico goeldi* is the only taxa with only one representative specimen, given its paucity in the two visited scientific collections. Previous studies show that this sample size is adequate for morphological studies when variation among taxa is relatively large (Polly 2003; Perez et al. 2011; Aristide et al. 2015b; but see Cardini and Elton 2007). We included skulls belonging only to adult specimens defined as having a completely erupted dentition. Both sexes were indistinctly included as there is no described sexual dimorphism in

Fig. 1 Chrono-phylogenetic relationships among the species used in this study. The tree was estimated by Aristide et al. (2015a)



inner ear shape. However, the sampled species are generally balanced with respect to sex (Table S1).

Morphometric Analyses

We obtained μ CT scans of the skulls using a table top scanner (SkyScan/Bruker, model 1173), with a 55 kV, 8 W X-ray source. Pixel size and slice thickness were between 45 and 67 μ m. We generated 3D-surfaces from the μ CT slices of each right inner ear using a threshold-based 2D segmentation procedure in ITK-SNAP 3.6 (www.itksnap.org; Yushkevich et al. 2006; Neubauer et al. 2009; Aristide et al. 2015b). During this procedure a threshold gray value was standardized to separated bone from air and guarantee comparable 3D-surface reconstructions. The 3D-surfaces were saved in the PLY format.

A single researcher (JdR) digitized a total of nine landmarks and 115 curve semilandmarks onto the 3D surfaces (Fig. 2; Fig. S1; Table S2) using IDAV-Landmark software (www.idav.ucdavis.edu/research/EvoMorph; Wiley et al. 2005). Landmarks allowed us to describe the relative position of identifiable anatomical points in the structure (Bookstein 1991), whereas by using semilandmarks we were able to characterize anatomical regions where landmarks are absent or scarce (Bookstein 1997; Gunz and Mitteroecker 2013).

Morphometric variation among species in total inner ear, cochlea, and semicircular canals was explored using 3D-GM analyses (Mitteroecker and Gunz 2009). We described the size

of the inner ear for each species by estimating its centroid size (CS), which is defined as the square root of the squared sum of the distances of each landmark and semilandmark to the geometric center of the configuration. We calculated shape variables using a Generalized Procrustes Analysis (GPA), which removes non-shape differences (scale, original location, and orientation) in the landmark and semilandmark configurations by using a least squares criterion (Rohlf and Slice 1990). Additionally, to reduce non-shape variation along the tangent direction in curve and surface semilandmarks, we allowed the points to slide in order to reduce the Procrustes (d2) distance between each configuration and the consensus configuration (Gunz et al. 2005; Perez et al. 2006). We explored shape differences among species by calculating the Principal Components (PCs) of the covariance matrix of the Procrustes shape coordinates. The PC analysis generates new geometrically uncorrelated variables, or axes, that account for decreasing amounts of variance (Manly 1986; Mitteroecker and Gunz 2009). By retaining the first PCs, which describe the major trends in shape among species and can also be interpreted as the dimensions that best reproduce Euclidian distances among them, dimensionality of the dataset can be reduced.

Phylogenetic Comparative Analyses

A time calibrated phylogeny previously published (Aristide et al. 2015a) and then adapted for the studied species was used in the phylogenetic comparative analyses (Fig. 1). To examine

the relationship between phylogenetic structure and variation in the inner ear, we measured the phylogenetic signal of inner ear morphology among the studied platyrrhine species. Phylogenetic signal for a trait is the tendency of related species to be more similar than less related species (Blomberg et al. 2003). To measure the strength of phylogenetic signal on size (mean logCS and log Body Mass [logBM] for each species; Aristide et al. 2015a) and shape data (the first seven PCs explaining 90% of total variation), we calculated the univariate K-statistic proposed by Blomberg et al. (2003) and its multivariate version K-mult (Adams 2014). K values close to 0 represent a scenario with a lack of phylogenetic signal,

values close to 1 are expected under a purely stochastic model of trait evolution (Brownian motion) where differences are expected to be proportional to divergence times, and values exceeding 1 are indicative of trait values that tend to be more similar among closely related species than expected under Brownian motion. Significance values for K and K-mult were obtained via permutations of size and shape data among the tree tips (Blomberg et al. 2003; Adams 2014).

Additionally, the phylogenetic pattern of size (log CS) and shape (PCs 1–7 explaining 90% of variance) variation distribution through the evolutionary history of the clade was analyzed using Disparity Through Time (DTT) plots (Harmon

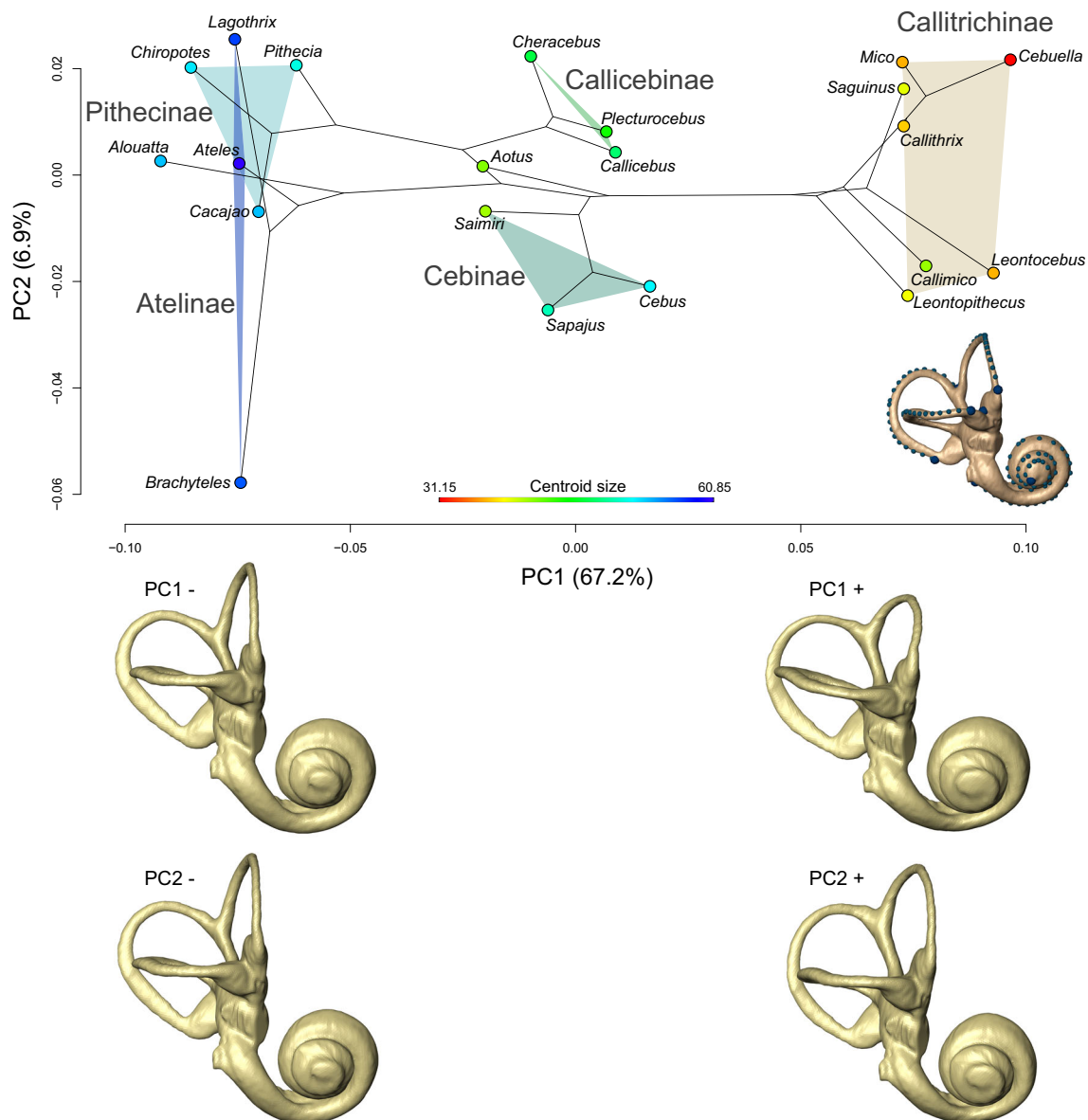


Fig. 2 Phylomorphospace of 21 platyrrhine species in the scatterplot defined by the first two PCs of inner ear shape variation. 3D surface reconstruction of inner ear at the right of phylomorphospace shows the digitalized landmarks (larger points) and curve semilandmarks (smaller points) on each specimen (see also Fig. S1 and Table S1 in electronic

supplementary material). Average centroid size values for each species are shown by the color of each data point. Five platyrrhine subfamilies are displayed as shadow colors. Inner ear shape changes along the two PC scores are displayed at the bottom of the figure

et al. 2003). Disparity was calculated using the mean Euclidean distances among extant species, both for the complete clade and for each subclade defined by a node in the phylogenetic tree. Then, the relative disparity was calculated as the proportion of subclade disparity relative to the complete clade disparity. Relative mean disparity was estimated for every cladogenetic event through the phylogenetic tree. Values near 0 suggest that subclades contain relatively less variation than the clade’s complete disparity; values near 1 indicate that subclades contain a considerable percentage of total variation of the clade (Harmon et al. 2003).

Finally, the association of the inner ear shape variation (PCs 1–7 explaining 90% of variance) with several explanatory variables was calculated using a Phylogenetic Generalized Least Squares (PGLS [Martins and Hansen 1997]) regression model. The explanatory variables used were size (logBM [Aristide et al. 2015a]), vocalization (log total repertoire, logRep [Barbosa Caselli et al. 2018]; and log mean dominant frequency, logDF10 [Bowling et al. 2017]) and locomotion (PC scores of locomotion data: percentages of arboreal quadrupedal walk, clamber and bridge plus suspensory locomotion; see [Youlatos and Meldrum 2011; Aristide et al. 2015a] for details). The PGLS regression takes into consideration the lack of independence among species arising from common phylogenetic history. Covariation in the regression error term structure is modeled by incorporating phylogenetic relationships as a covariance matrix derived from the

platyrrhine phylogenetic tree topology, its branch lengths, and a Brownian motion model of trait evolution. We also explored the association between logBM and logCS for overall inner ear, semicircular canals, and cochlea shape.

All morphometric and comparative analyses were performed using the Morpho, geomorph, picante, phytools, Caper, and geiger packages in the software R (R Development Core Team 2018). Additionally, the morphometric and ecological data, as well as the chronophylogenetic tree, used in these comparative analyses are available in electronic supplementary material, Datafiles S1 and S2.

Results

PC1 and PC2 (Fig. 2) explain 74% of the total inner ear shape variation, with PC1 showing the largest separation among platyrrhine subfamilies. Particularly, Cebinae is separated from Callitrichinae, and Callicebinae from Pitheciinae, whereas Callicebinae shows similarity to Cebinae plus *Aotus*, and Pitheciinae with Atelinae plus *Alouatta* (Atelidae; Fig. 2). Shape changes along PC1 involve variation in relative size and orientation of the semicircular canals, as well as the relative size of the cochlea, these structures being larger in Atelidae and Pitheciinae. Shape variation along PC2 is small. Centroid size is larger in the Atelinae clade and gradually

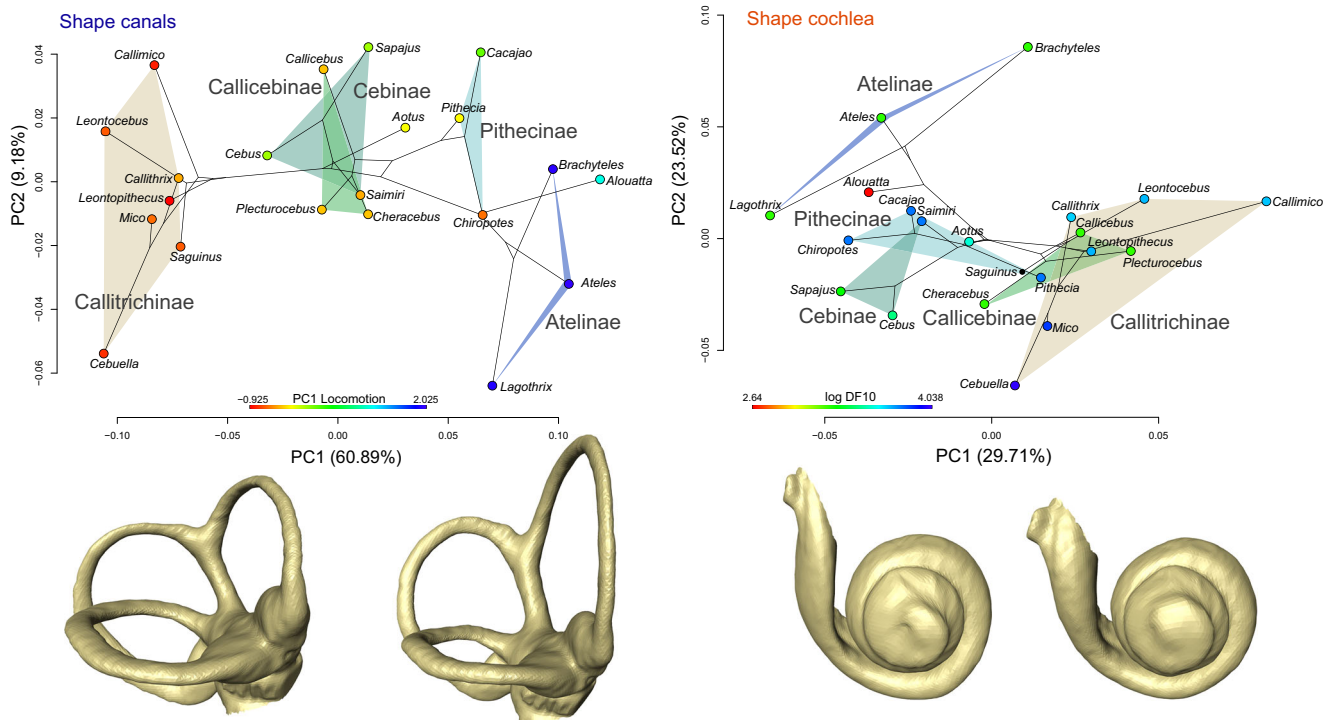


Fig. 3 Phylomorphospace of 21 platyrrhine species in the scatterplot defined by the first two PCs of semicircular canals (left panel) and cochlea (right panel) shape variation. Locomotion (left panel) and vocalization repertoire (right panel) values for each species are shown

by the color of each data point. Five platyrrhine subfamilies are displayed as shadow colors. Shape changes along the PC1 scores for semicircular canals and cochlea are displayed at the bottom of the figure

decreases along PC1, being the smallest in the Callitrichinae (Fig. 2). Shape variation among species in the cochlea and semicircular canals differs slightly from the total shape pattern (Fig. 3); variation in semicircular canals is more phylogenetically structured than variation in the cochlea.

Size and shape data (except for cochlear shape) showed phylogenetic signal values slightly higher than one, indicating that closely related species tend to be somewhat more similar than expected under Brownian motion (Total shape, $K = 1.349$; semicircular canals shape, $K = 1.197$; cochlear shape, $K = 0.757$; log-CS, $K = 2.175$; log-BM, $K = 2.209$; all $p < 0.001$).

Changes in size and shape disparity through their evolutionary history are shown in the DTT-plots of Fig. 4. Size, total inner ear shape, and semicircular canals shape show similar temporal patterns, with an early increase of among-clade variation, departing from the Brownian motion expectation along most of the evolutionary history of the clade. On the other hand, cochlear shape initially follows the Brownian

expectation, later displaying an increase of within-clade variation towards more recent times (Fig. 4).

PGLS regressions indicate that inner ear shape is strongly and significantly associated with body size (ca. 80% of fit; Table 1, Table S3), whereas no significant association was recovered with vocalization or locomotion variables. When cochlear and semicircular canals shape are analyzed separately, the latter shows a low but significant association with locomotion independently of size, while no significant association with any of the explored variables (size or vocalization) was recovered for the former (Fig. 3; Table 1, Table S3). However, we did not observe the expected pattern of shape change. On the contrary, we observed relatively smaller semicircular canals in the Callitrichinae subclade, which are the species with proportionally more clamber and quadrupedal walk. Finally, the association between logCS and logBM was significant for all datasets, being higher for overall inner ear and semicircular canals, than for the cochlea (Table S4).

Discussion

In this work we employed a quantitative and comparative phylogenetic approach to explore functional and ecological factors driving the diversification of an ecologically relevant morphological structure in the continental radiation of New World monkeys. The morphometric and comparative results obtained in this study demonstrate that inner ear shape differs considerably among the main platyrrhine clades (i.e., subfamilies; Figs. 2 and 3), where Atelidae plus Pitheciidae are separated from Cebinae plus *Aotus* and Callitrichinae, with the latter as the most distant subclade. This result is concordant with the relationships among the main platyrrhine subclades observed in previous phylogenies based on morphological data, but differs from the phylogenies based on molecular data (Fig. 1; Perez and Rosenberger 2014).

Our results also show that inner ear shape diversification was not independent from size diversification (Fig. 2). Additionally, phylogenetic signal and DTT analyses suggested that size and shape differences between closely related species tend to be smaller than expected, with exception of cochlear shape variation, and that deterministic factors seem to be responsible for the morphological diversification of the clade (Fig. 4). All these results support previous studies that have suggested that platyrrhine morphological diversity was mostly achieved during the early stages in its evolutionary history and was related to the ecological diversification of the clade, conforming to an adaptive radiation scenario (Rosenberger et al. 2009; Aristide et al. 2015a, 2018).

In this context, we ask what ecological factors were responsible for the inner ear shape diversification in platyrrhines. The main shape changes among species observed in our results comprise the relative size of the cochlea and the shape of the

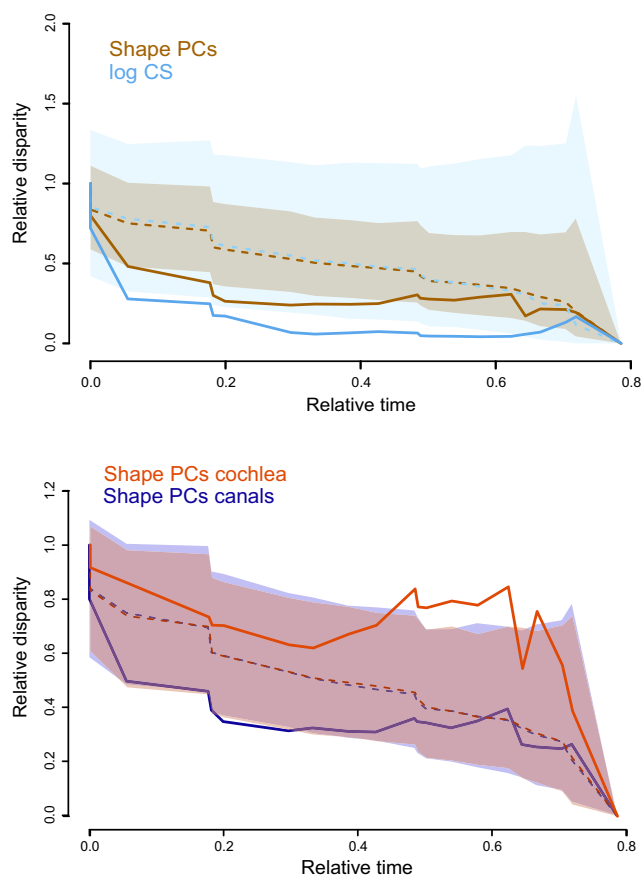


Fig. 4 Disparity-through-time (DTT) plots for inner ear shape (PC-90%) and log-CS (BM) at the top of the figure and for semicircular canals and cochlea shape (PC-90%) at the bottom of the figure. Disparity values at each time point represent the average disparity of the subclades with an ancestor at that time related to the total clade disparity. The expectation under a Brownian motion model and its 95% confidence interval are displayed by a dashed line and shadow area, respectively

Table 1 PGLS regression of shape variation (PC-90%) against log-BM plus locomotion and vocalization variables

Structure	PGLS model	<i>F</i>	<i>P</i>	Adjusted <i>R</i> ²
Overall inner ear	PC90% ~ LogBM + logRep + logDF10 + PCs Loc	17.990	7.33E-06	0.809
	PC90% ~ LogBM	51.630	7.95E-07	0.717
Cochlea	PC90% ~ LogBM + logRep + logDF10	1.258	0.320	0.037
	PC90% ~ LogBM	0.030	8.63E-01	-0.051
Semicircular canals	PC90% ~ LogBM + PCs Loc	9.381	6.94E-04	0.557
	PC90% ~ LogBM	11.390	3.18E-03	0.342

semicircular canals (Fig. 2), traits that have been previously suggested to be related to hearing capabilities, head movements, and locomotion (Ekdale 2016). In this sense, it has been shown that some primates (e.g., tarsiers, Ramsier et al. 2012) and other animals (e.g., geckos, Manley and Kraus 2010; or cetaceans, Ritsche et al. 2018) have particular hearing capabilities that match features of their vocalizations (e.g., the dominant frequency), suggesting that inter-individual communication could be a main driver of cochlear shape evolution. However, our analyses failed to find any significant association between platyrrhine cochlear variation and vocalization variables (Fig. 3). Additionally, body size variation was also unrelated to cochlear shape. Together, these results suggest that alternative features of vocalizations or other factors additional to those explored here, might be responsible for driving cochlear shape evolution in the clade.

On the other hand, when considering the changes in the relative size of the semicircular canals, we found evidence of a weak relationship with locomotor modes. However, the pattern of shape change does not match our expectations and displays small values of association (Fig. 3). This result is consistent with previous studies that did not find any clear relationship between semicircular canals shape and specific locomotor behaviors (Rae et al. 2016). Nonetheless, our analyses revealed that body size has the strongest evolutionary association with both the semicircular canals and total inner ear shape variation. This suggests, contrary to our expectations, that size variation is potentially the main factor driving inner ear shape change in platyrrhines. Noticeably, this result contrasts with a recent study on platyrrhine cranial evolution that indicated that allometric effects explain only partially the diversification of cranial shape in the clade (Aristide et al. 2018).

Several relatively young and geographically restricted clades have shown evidence of a rapid diversification related to ecological factors (Gavrilets and Losos 2009), but platyrrhines constitute one of the few examples of an old continental clade studied in a formal comparative phylogenetic framework that displays evidence of an adaptive radiation process (Aristide et al. 2016, 2018). However, although all recent studies have suggested that the morphological diversification of this clade was related to ecological or functional factors,

supporting previous models of adaptive radiation (e.g., Rosenberger 1992; Rosenberger et al. 2009; Aristide et al. 2015a, 2016, 2018), these works also suggest that no single ecological or functional factor drove this diversification. Particularly, Aristide et al. (2018) suggested that diversification of different cranial anatomical structures was driven by different ecological or functional factors, such as diet and social group size, whereas allometry has a limited effect on few traits. In this sense, our results are in line with those obtained by Aristide et al. (2018), highlighting the complexity of the platyrrhine diversification process. At the same time, our results indicate that the variation in inner ear shape is mainly related to the changes in body size, a factor not pointed out as relevant by this previous study.

Our results suggest that further studies will be necessary to explain the particularities of the platyrrhine inner ear diversification beyond the strong allometric pattern. In this sense, and more generally, we will need additional macroevolutionary studies to understand the factors behind morphological diversification of specific anatomical structures in the platyrrhine skull. Finally, considering the importance of allometry for the inner ear evolution, further explicit tests of the existence of evolutionary constraints or covariation between inner ear and other skull structures will be needed.

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Authors' Contributions S.I.P., L.A. and S.F.d.R. conceived the study. J.d.R., T.M.P.d.S and R.T.L. collected image and morphometric data. J.d.R., L.A. and S.I.P. analysed morphometric data. J.d.R., L.A., S.F.d.R. and S.I.P. interpreted the data and wrote the manuscript. All authors approved the final version of the manuscript.

Data Availability The morphometric data and chrono-phylogenetic tree for the species are available in electronic supplementary material, Datafiles S1 and S2. No human skulls were used in this work.

Compliance with Ethical Standards

Conflict of Interest The authors declare no conflict of interest.

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