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Size, not phylogeny, explains the morphology of the endosseous labyrinth in the crown clade Crocodylia

Yohan Pochat-Cottilloux^{1,2}  | Gwendal Perrichon¹  | Lionel Hautier^{3,4}  |
Nicolas Rinder¹  | Romain Amiot¹  | Irena Raselli^{5,6}  | Jérôme Adrien⁷  |
Joël Lachambre⁷  | Vincent Fernandez^{8,9}  | Jeremy E. Martin¹ 

¹Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, Villeurbanne, France

²Faculty of Biology, Institute of Evolutionary Biology, University of Warsaw, Warsaw, Poland

³Institut des Sciences de l'Evolution de Montpellier (ISEM), Univ. Montpellier, CNRS, IRD, Place E. Bataillon, Montpellier Cedex 05, France

⁴Natural History Museum of London, Mammal Section, Department of Life Sciences, London, UK

⁵Jurassica Museum, Porrentruy, Switzerland

⁶Geoscience Department, University of Fribourg, Fribourg, Switzerland

⁷INSA-Lyon, MATEIS UMR CNRS 5510, University of Lyon, Villeurbanne, France

⁸European Synchrotron Radiation Facility, Grenoble, France

⁹Imaging and Analysis Centre, The Natural History Museum, London, UK

Correspondence

Yohan Pochat-Cottilloux, Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, Villeurbanne, France & Faculty of Biology, Institute of Evolutionary Biology, University of Warsaw, Warsaw, Poland.
Email: yohan.pochat@orange.fr

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Abstract

The endosseous labyrinths are associated with several functions, including hearing and spatial orientation. Throughout their evolutionary history, crocodylomorphs have thrived in diverse environments, and the morphology of their endosseous labyrinths has been suggested as a proxy for inferring their lifestyle. However, the relationships between the shape of their endosseous labyrinths and ontogenetic and phylogenetic factors are difficult to interpret and have rarely been investigated in depth previously, particularly in terms of dataset size. Here, we present the most complete dataset to date on the endosseous labyrinths of extant crocodylians, including 111 specimens covering 22 species of different ontogenetic status (from hatchlings to adults). Using 3D geometric morphometrics, we show that allometry constitutes a major contributor of the shape variation of the crocodylian endosseous labyrinths and that the development of this structure is likely linked to the braincase conformation, in all extant genera. We also find a moderate phylogenetic signal, but only without considering the size effect, so it could not be translated into relevant discrete morphological characters. Based on these results, we discuss several remaining problems that prevent the inclusion of fossil forms with highly divergent lifestyles to study how ecological differences shaped the endosseous labyrinths of crocodylomorphs.

KEYWORDS

3D geometric morphometrics, Crocodylia, CT scan, endosseous labyrinths, ontogeny, phylogeny

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1 | INTRODUCTION

In most vertebrates, the endosseous labyrinth (Figure 1) consists of two main parts (Ekdale, 2016a): the vestibular apparatus, formed by three interconnected semicircular canals (Highstein et al., 2004) and a posteroventrally projecting and tubular lagena, or cochlear duct (Manley, 2017). The vestibular apparatus is involved in balance, spatial position, and linear and angular acceleration of the head, while the cochlear duct captures and transmits soundwaves (Georgi, 2008). The sensory epithelia of these structures detect linear (i.e., head orientation) and rotational motions, through the maculae and the cristae respectively. In both cases, the hair cells are deflected from the motion of the surrounding endolymphatic liquid (Georgi, 2008; Ifediba et al., 2007). Different morphologies of the endosseous labyrinth have been found to be associated with different behaviours and locomotions (Georgi, 2008; Hullar, 2006), in dinosaurs (Sipla, 2007; Hanson et al., 2021, 2022, but see David et al., 2022), mammals (Costeur et al., 2018; Grohé et al., 2016), sauropterygians (Neenan et al., 2017), and squamates (Palci et al., 2017), while also allowing the reconstruction of phylogenetic relationships in mammals (Alloing-Séguier et al., 2013; Billet et al., 2015; Costeur et al., 2018; Ekdale, 2016b; Fox & Meng, 1997; Geisler & Luo, 1996; Grohé et al., 2016; Ladevèze et al., 2020; Tambusso et al., 2021), reptiles (David, 2010; Palci et al., 2017), and lissamphibians (Maddin & Anderson, 2012).

However, this paradigm has recently begun to shift, as independent studies have failed to find associations between the endosseous labyrinth morphology and ecology or phylogeny (Benson et al., 2017, 2021; Evers et al., 2022; Latimer et al., 2023).

Crocodylomorpha Hay, 1930 is an ideal group to consider the evolution of these morphological sensory structures. Its members thrived and survived biological crises throughout the Mesozoic and Cenozoic (Nesbitt, 2011; Pol et al., 2012; Sellés et al., 2020), and include organisms that lived in diverse environments, ranging from fully pelagic to terrestrial (Wilberg et al., 2019). It is also one of the two extant lineages of archosaurs, along with Aves Linnaeus, 1758. As a result, they serve as a biological model for inferring the palaeobiology of extinct relatives within their phylogenetic bracket.

In crocodylomorphs, the relationship between the endosseous labyrinth shape and ecology has recently been investigated. A strong relationship between the endosseous labyrinth morphology and lifestyle was proposed, with significant differences between aquatic and terrestrial forms (Schwab et al., 2020). Another study, using a broader taxonomic sample (Aves, Phytosauria von Meyer, 1861 and Pterosauria Kaup, 1834), but a more limited sample of crocodylomorphs argued that variation in endosseous labyrinth morphology is mostly explained by spatial constraints within the skull (Bronzati et al., 2021). Surprisingly, none of these studies considered the effect of size on shape, although this has recently been shown to be important in a moderate sample of extant crocodylians (30 specimens, 8

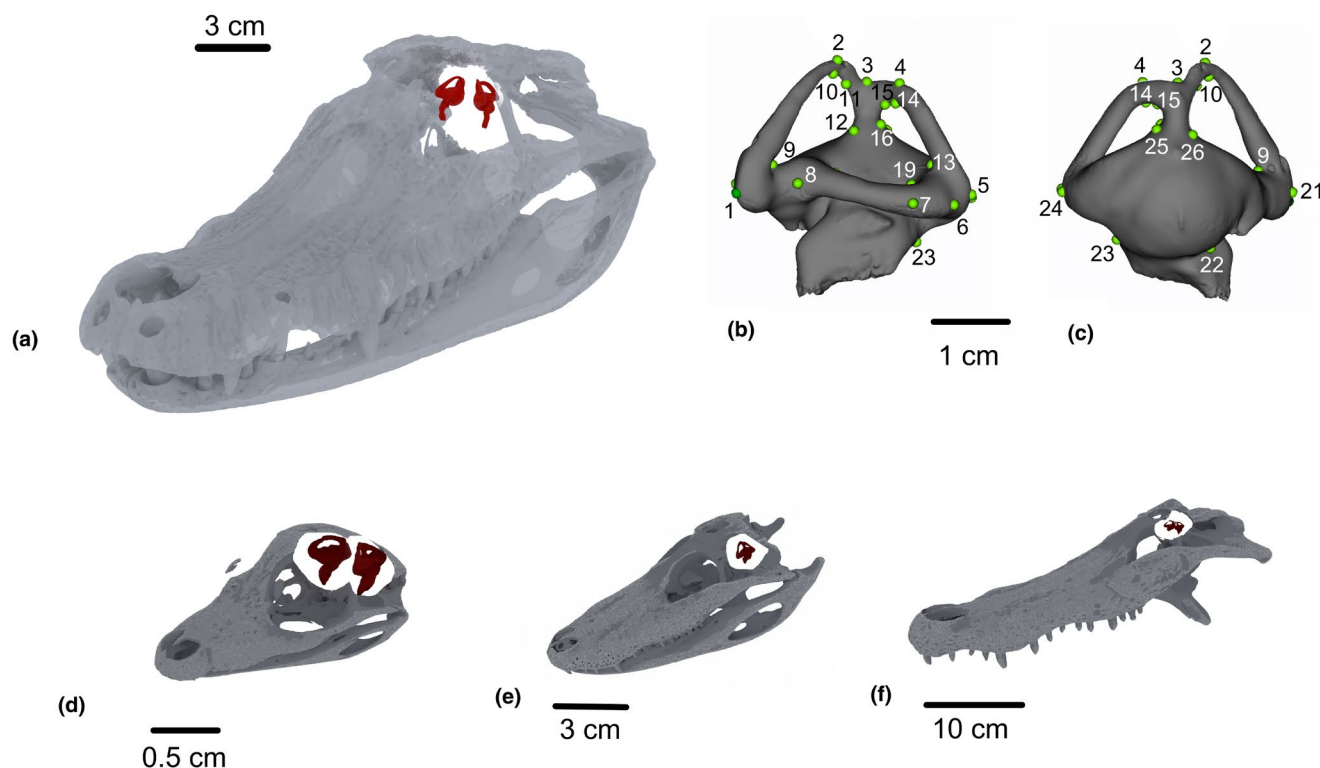


FIGURE 1 (a) 3D reconstruction of the endosseous labyrinths of *Caiman yacare* (IRSNB 13521) in red with the skull in semi-transparency. Position of the 26 landmarks mainly used in this study illustrated on the left endosseous labyrinth of *Caiman yacare* (IRSNB 13521) in lateral (b) and medial (c) views. Ontogenetic series of *Alligator mississippiensis* with skull in grey and endosseous labyrinths in red. (d) Hatchling (OUVC 10606), (e) Juvenile (MHNL 50002667), (f) Adult (MHNL 50001401).

genera and 15 species), with two major shifts occurring: an increase in size throughout ontogeny, and semicircular canals that are smaller in juveniles than in adults (Schwab et al., 2022; Figure 1d–f). If the endosseous labyrinth is constrained by the cranial morphology, its shape may indeed primarily reflect pervasive allometric changes rather than any ecological or phylogenetic signal. Indeed, although extant crocodylians are semi-aquatic, which limits their ecological disparity and diversity, they display a huge variation in snout shape, and hence in braincase conformation and feeding strategies (Grigg & Kirshner, 2015). As a matter of fact, allometric trends have been discussed in other groups, with contrasting results regarding the influence of size: in mammals, for example, this contribution has been shown to be rather small in primates and in xenarthrans (Alloing-Séguier et al., 2013; Billet et al., 2015; Lebrun et al., 2010) and larger in rodents (Da Cunha et al., 2023). Furthermore, the phylogenetic signal of the endosseous labyrinth morphology in extant crocodylians has never been assessed, although phylogeny was included in statistical tests in Bronzati et al. (2021).

Here, using the largest sample of extant crocodylian specimens to date (111 specimens, 10 genera and 22 species), with several ontogenetic series at the species level, we propose to explore the diversity of their endosseous labyrinth shape, allometrically at different levels for the first time (ontogenetic, static, and evolutionary), and to characterise both the effects of size and phylogeny on the evolution of these morphological structures using geometric morphometric analyses as a way to capture shape data and variation.

2 | METHODS

2.1 | Dataset

It is particularly difficult to identify clear boundaries between the different ontogenetic stages in crocodylians, due to their continuous growth and a lack of data (Morris et al., 2019; Schwab et al., 2022). Therefore, the specimens studied here were classified into three different size classes: hatchlings, juveniles and adults, according to skull length and genus, following Perrichon et al. (2023a), but with subadults regrouped with adults. For the purpose of this study, we considered *Alligator sinensis* Fauvel, 1879, all species of *Caiman* Spix, 1825, *Osteolaemus* Cope, 1860 and *Paleosuchus* Gray, 1862 as brevirostrine taxa; *Alligator mississippiensis* Daudin, 1802, *Crocodylus acutus* Cuvier, 1807; *Crocodylus halli* Murray et al., 2019; *Crocodylus intermedius* Graves, 1819; *Crocodylus johnstoni* Krefft, 1873; *Crocodylus moreletii* Duméril & Bibron, 1851, *Crocodylus niloticus* Laurenti, 1768, *Crocodylus novaeguineae* Schmidt, 1928, *Crocodylus palustris* Lesson, 1831, *Crocodylus porosus* Schneider, 1801, *Crocodylus siamensis* Schneider, 1801, *Melanosuchus* Gray, 1862 and *Voay Brochu*, 2007 as mesorostrine taxa; and *Gavialis* Oppel, 1811, *Mecistops* Gray, 1844 and *Tomistoma* Müller, 1846 as longirostrine taxa. This was done according to the overall shape of the rostrum of those taxa. Although there was a previous attempt to classify the species in those three categories using linear measurements

(Erickson et al., 2012; Grigg & Kirshner, 2015), the relatively low number of specimens used and the random cutoff values between categories prevent its use in our opinion. Some taxonomic uncertainties remain in the dataset, such as the delimitation between *Crocodylus porosus* and *Crocodylus siamensis* (Hekkala et al., 2011a) or the taxonomic content of *Crocodylus niloticus* and *Crocodylus suchus* Geoffroy Saint-Hilaire, 1807 (Hekkala et al., 2011; Meredith et al., 2011; Nicolai & Matzke, 2019; Pan et al., 2021). Here, all specimens of *C. suchus* are assigned to *C. niloticus*, pending further studies. At present, although morphometric data can help to distinguish *Mecistops cataphractus* Cuvier, 1825 from *Mecistops leptorhynchus* Bennett, 1835 (Carr et al., 2021), there are no true discrete morphological differences between them, so the specimens in this study are referred to as *Mecistops* sp. In fact, detecting the subtle morphological differences between these two species would require separate geometric morphometric analyses of the specimens studied (Carr et al., 2021), which is beyond the scope of this study.

2.2 | Surface scanning, X-ray CT, and production of 3D models

All specimens in the dataset were CT scanned at different facilities to reconstruct the 3D volumes of their endosseous labyrinths (see Electronic Table S1 for more details). Volume segmentation was performed in Avizo 8.1. The external surfaces of the skulls were digitised either using 3D surface scanners (Artec Space Spider 3D or Artec Eva 3D, reconstructed with Artec Studio 17) or by segmenting the bones from the CT data to measure their length, if available. Asymmetry between the left and right bony labyrinths of crocodylomorphs has been shown to be minimal (Schwab et al., 2020), so the left bony labyrinth was randomly considered here. When missing, the right bony labyrinth was mirrored using Blender 4.0 prior to landmark placement. All 3D data used in this study are available in online, see Data Availability Statement.

2.3 | Geometric morphometric analyses

3D geometric morphometric analyses were used to infer the shape variation of the studied endosseous labyrinth dataset. First, 26 type I (well-defined) and type II (maximum curvatures; Bookstein, 1997) fixed landmarks were placed using the MorphoDig 1.6.7 software (Lebrun, 2018) and chosen to reflect the shape and extent of the structures (Figure 1b,c), except for the lagenar region, which is a source of segmentation problems (Pochat-Cottilloux et al., 2022). The same 26 landmarks were then used as the basis for building landmark curves corresponding to the outline of the semicircular canals and the vestibula. Twenty sliding semi-landmarks (Bardua et al., 2019; Gunz & Mitteroecker, 2013) were then evenly distributed (i.e., 100 sliding semi-landmarks in total) over the five landmark curves to assess whether a different number of landmarks used to characterize the

same shape affected the statistical interpretations (Figure S1). To assess potential differences between the two landmarking protocols, a correlation test was performed only on extant adults for each protocol ($n = 73$), to eliminate any ontogenetic bias. This correlation test was performed using the function *integration.test*, which quantifies the degree of morphological integration between modules of Procrustes shape variables. In addition, the landmark placement protocol was also tested for any placement bias (i.e., significant errors in landmark placement due to unclear definitions or difficult structures), by placing the landmarks 10 times on the same set of three specimens and comparing them statistically.

Geometric morphometric analyses were performed in R4.3.0 (R Core Team, 2023) using the geomorph 4.0.5 package (Adams & Otárola-Castillo, 2013). For each sub-analysis run, the first step was to correct the differences in size and alignment of the different specimens through a generalized least-squares Procrustes Analysis (GPA) superimposition using the *gpagen* function (Baken et al., 2021). Principal component analyses (PCA) were then applied on the Procrustes shape coordinates (function *gm.prcomp*) to find the major axes of variation of each sub-dataset. Factors such as size (centroid size or skull length) or skull shape (brevirostrine, meso-rostrine, longirostrine), can be statistically correlated with the shape information using phylogenetically informed Procrustes ANOVA on Procrustes shape variables (function *procD.pgls*), and factors such as genus and family level can be statistically correlated with the shape information using Procrustes ANOVA for Procrustes shape variable (function *procD.lm*), both of which correspond to a non-parametric Permutational Multivariate Analysis of Variance (Anderson, 2001). A broken stick model was used to determine how many principal components were significantly different from a random distribution (Guenser et al., 2022).

Results were visualized using the packages *rgl* 1.1.3 (R Core Team, 2023), *ggrepel* 0.9.3 (Slowikowski et al., 2018), *RColorBrewer* 1.1-3 (Neuwirth & Neuwirth, 2014), and *ggplot2* 3.4.2 (Wickham, 2011). Phylogenetic time-calibrations were performed using the packages *ape* 5.7-1 (Paradis et al., 2004), *paleotree* 3.4.5 (Bapst, 2012) and *phytools* 2.1-1 (Revell, 2024). The phylogenetic relationships of extant crocodylians are still debated (Brochu, 2003, 2007; Gatesy et al., 2003; Groh et al., 2020; Lee & Yates, 2018; McAliley et al., 2006; Murray et al., 2019; Oaks, 2011; Rio & Mannion, 2021; Shirley et al., 2014; Willis et al., 2007). In this study, we chose to use the results of the most recent and complete molecular study (Pan et al., 2021), as well as Perrichon et al. (2023b) for the position of *Voay robustus* Grandidier & Vaillant, 1872 and Murray et al. (2019) for the position of *Crocodylus halli* (Figure 2). Phylogenies were time scaled using the function *timePaleoPhy*. We used the “mbi” method (Laurin, 2004), which dates internal nodes by the oldest species they contain, with a minimum branch length of one million years to avoid zero-length branches. The stratigraphic ranges of the different species used here were obtained and checked from the Paleobiology Database (see also Electronic Data S1). The phylogenetic signal can be assessed using the multivariate version

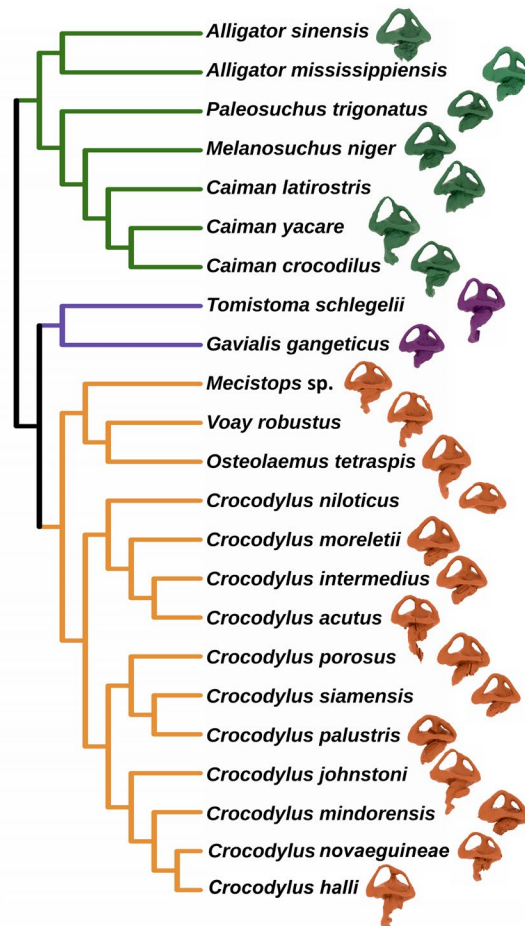


FIGURE 2 Phylogenetic framework used in this study. Dark green: Alligatoridae, purple: Gavialidae, orange: Crocodylidae. The left endosseous labyrinths illustrated are those highlighted in red in Table S1.

of the K-statistic (K_{mult} ; Adams, 2014). This value varies between 0 and 1 and assesses the degree of phylogenetic signal in a dataset compared to what would be expected under a Brownian model of evolution: the higher the phylogenetic signal, the closer the value will be to 1.

Ontogenetic data were available for *Alligator* Daudin, 1809, *Caiman*, *Crocodylus* Laurenti, 1768, *Gavialis*, *Mecistops*, *Osteolaemus*, *Paleosuchus* and *Tomistoma*. Allometric trajectories were reconstructed using a linear regression between the Procrustes coordinates of the first axis of greatest variation and the log-transformed centroid size or log-transformed cranial length of the specimens. When necessary, these regressions were phylogenetically informed using the function *phylolm* (package *phylolm*; Ho et al., 2016), and the R^2 was recalculated using the function *R2_pred* (package *rr2*; Ives & Li, 2018) to account for possible covariation between shape data and phylogeny (Ives, 2019). To accurately compare allometric trajectories between genera, we used phylogenetically informed Procrustes ANOVA of PC1 (most correlated with size variables) against log-transformed centroid skull length and genus (as a factor). A homogeneity of slopes test was performed using the *anova* function on the unique allometry (size \times genus) and common

allometry (size+genus) models to assess whether genus-specific slopes were significantly different from one another and from a common allometric trajectory. The pairwise function was used to make pairwise comparisons of the means and variances of groups and allometric trajectories. To remove the effect of size on shape, the residual shape components (RSC) of a regression between the common allometric component (CAC; Mitteroecker et al., 2004) of the sample and the centroid size were calculated using the *plotAllometry* function. Another PCA was then performed on these residual components, which are effectively Procrustes coordinates corrected for the effect of allometry. Here, ontogenetic allometry is understood as a measure of how the shape of a structure changes over the course of the development of specimens belonging to the same species. Static allometry will be considered as the influence of size on shape among individuals belonging to the same taxon and at the same ontogenetic stage and evolutionary allometry will be referred to as the influence of size on shape among different species (Hallgrímsson et al., 2015; Pélabon et al., 2013).

All data files, additional methods and the R script used for this study are available in the Supporting Information and online (see [Data Availability Statement](#)).

2.4 | Institutional abbreviations

- AMU: Université Aix-Marseille, Marseille, France.
- BMNH: British Museum of Natural History, London, United Kingdom.
- FMNH: Field Museum of Natural History, Chicago, United States.
- IRSNB: Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium.
- MHNH: Musée d'Histoire Naturelle de Lyon, Lyon, France.
- MHNH: Musée d'Histoire Naturelle de Marseille, Marseille, France.
- MNHN: Muséum National d'Histoire Naturelle, Paris, France.
- MZS: Musée Zoologique de Strasbourg, Strasbourg, France.
- NHMUK: Natural History Museum of the United Kingdom, London, United Kingdom.
- NHMW: Naturhistorisches Museum Wien, Vienna, Austria.
- OUV: Ohio University Vertebrate Collections, Athens, United States.
- SMNK: Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany.
- SVSTUA: Collections de l'Agrégation de l'ENS de Lyon, Lyon, France.
- TMM: Texas Memorial Museum, Austin, United States.
- UCBL: Université Claude Bernard Lyon 1, Lyon, France.
- UF: University of Florida, Gainesville, United States.
- UM: Université de Montpellier, Montpellier, France.
- Uma: University of Manchester, Manchester, United Kingdom.
- UMMZ: University of Michigan Museum of Zoology, Ann Arbor, United States.
- YPM: Yale Peabody Museum, New Haven, United States.

TABLE 1 Regression tests on the full extant sample ($n=111$).

Variable 1	Variable 2	p-value	R ²
Procrustes coordinates	Centroid size	0.001	0.12
Procrustes coordinates	Skull length	0.001	0.12
Procrustes coordinates	Genus	0.001	0.22
Procrustes coordinates	Family	0.001	0.08
Procrustes coordinates	Ontogenetic stage	0.001	0.16
Procrustes coordinates	Skull shape	0.97	0.009
PC1	Centroid size	0.001	0.55
PC1	Skull length	0.001	0.35
PC1	Genus	0.001	0.32
PC1	Family	0.001	0.23
PC1	Ontogenetic stage	0.001	0.40
PC1	Skull shape	0.91	0.001
PC2	Centroid size	0.001	0.26
PC2	Skull length	0.001	0.19
PC2	Genus	0.006	0.21
PC2	Family	0.006	0.10
PC2	Ontogenetic stage	0.001	0.46
PC2	Skull shape	0.61	0.009
PC3	Centroid size	0.18	0.01
PC3	Skull length	0.002	0.13
PC3	Genus	0.001	0.33
PC3	Family	0.90	<0.001
PC3	Ontogenetic stage	0.001	0.20
PC3	Skull shape	0.58	0.01

3 | RESULTS

The two landmarking protocols (26 landmarks vs. 100 semi-landmarks) yield similar results according to the integration test ($R^2=0.93$, p -value=0.001) on the extant adult specimens (Figure S2). As a result, the first landmarking protocol has been replicated on all specimens. The landmarking protocol is further validated for replicability (Figure S3) as the three selected specimens are significantly separated (the Procrustes coordinates are significantly correlated with the genus, $R^2=0.76$, p -value=0.001).

In the extant sample ($n=111$), the Procrustes ANOVA revealed a significant effect of centroid size, skull length, genus, family and ontogenetic stage ($p=0.001$), at different percentages on the shape of the endosseous labyrinths (Table 1). Furthermore, the first three principal components of the complete extant morphospace explain 40.5% of the total variance, with changes throughout ontogeny (Figure 3–7, S4 & S22; Table 1 & Data S2). The broken stick model approach on all extant specimens highlights that the first ten principal components are significantly different from a random distribution. However, as they represent a small percentage of the total shape variation, they are not considered here (Table S1). PC1 is related to the anteroposterior compression of the endosseous labyrinth with positive values associated with an anteroposterior

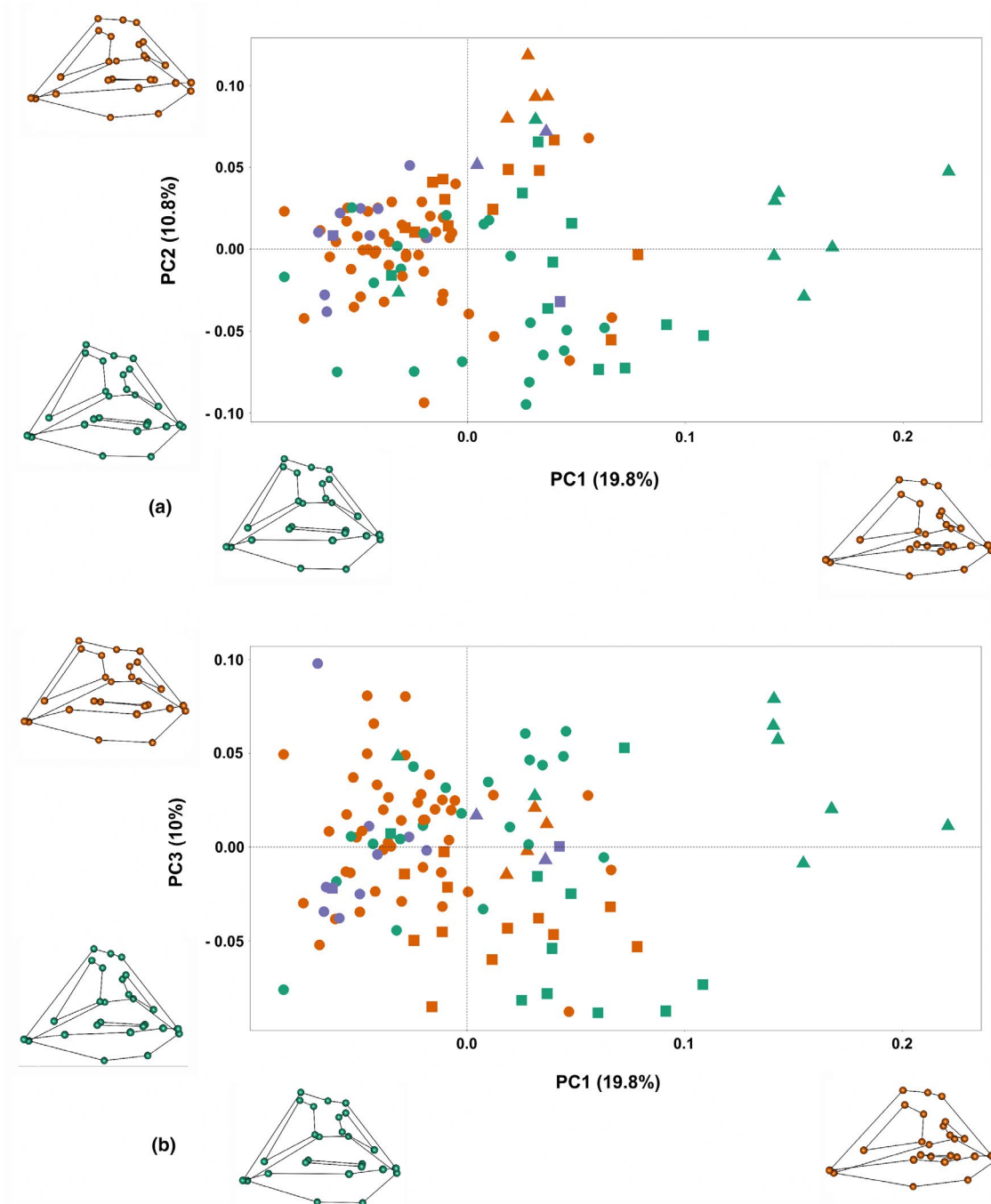


FIGURE 3 Principal Component Analysis results on the endosseous labyrinths shape in extant crocodylians showing the two major axes of variance ($n = 111$ specimens, spanning 22 species of the crown clade Crocodylia). Wireframes represent landmark coordinates for extreme PC values (dark green and orange points for minimum and maximum scores). (a) PC1 vs. PC2, (b) PC1 vs. PC3. Dark green: Alligatoridae, orange: Crocodylidae, purple: Gavialidae. Circles: Adults, squares: Juveniles, triangles: Hatchlings.

elongation (Figure 3a & S4a). PC2 characterizes the extension of the semicircular canals, with positive values associated with a minimal extension (Figure 3a & S4a). PC3 is associated with the dorsoventral extension of the endosseous labyrinth with negative values corresponding to a maximal dorsoventral extension (Figure 3b & S4b). PC1 scores are significantly correlated with centroid size,

skull length, genus, family, and ontogenetic stage, PC2 scores are significantly correlated with centroid size, genus, family, and ontogenetic stage, while PC3 scores are only significantly correlated with skull length, genus, and ontogenetic stage (Table 1). As a result, adult specimens are located towards negative PC1 and PC2 values, juveniles towards null values and hatchlings specimens

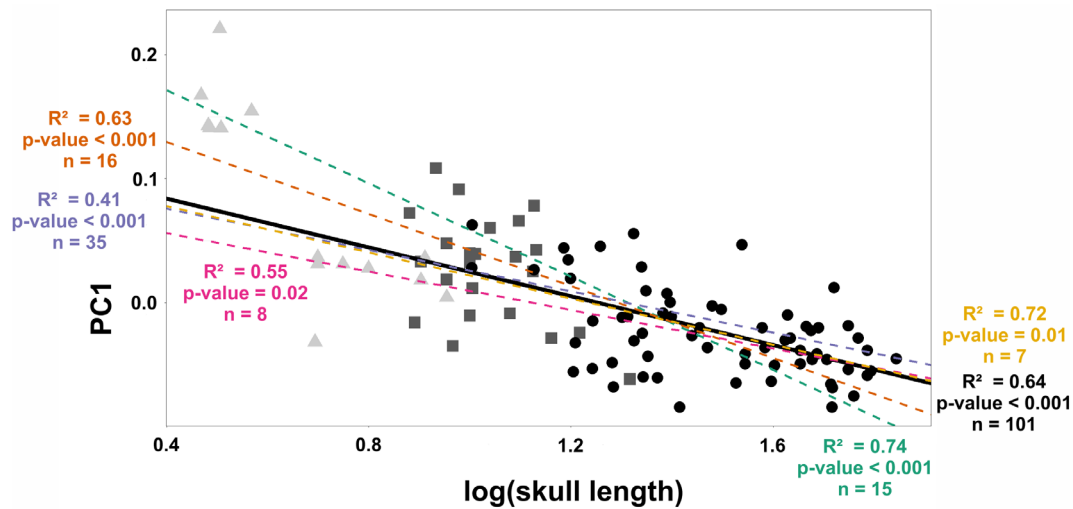


FIGURE 4 Allometric trajectories in extant crocodylians, all specimens (PC1 vs. log-transformed skull length). Plain black line represents the trajectory for the whole dataset, dark green dashed line represents the trajectory for *Alligator*, orange dashed line represent the trajectory for *Caiman*, purple dashed line represents the trajectory for *Crocodylus*, pink dashed line represents the trajectory for *Mecistops*, and dark yellow dashed line represents the trajectory for *Gavialis*. Triangles are hatchlings, squares are juveniles and circles are adults.

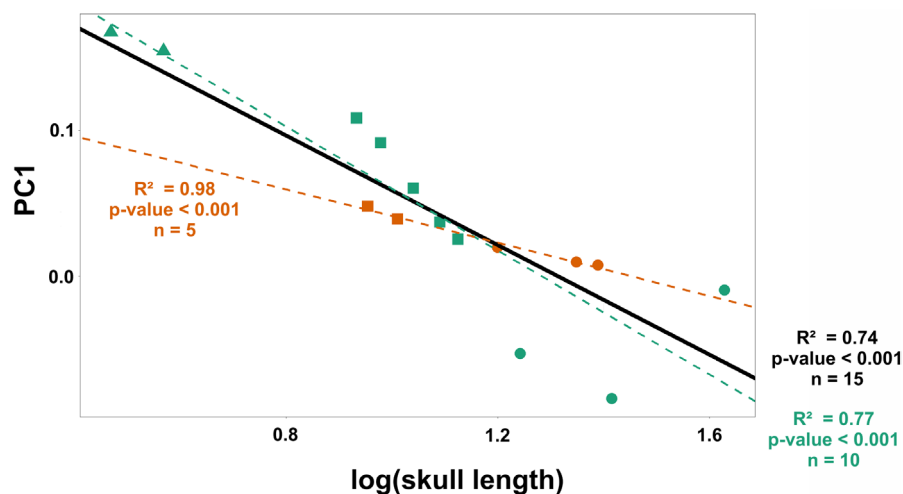


FIGURE 5 Allometric trajectories in *Alligator*, all specimens (PC1 vs. log-transformed skull length). Plain black line represents the trajectory for *Alligator*, dark green dashed line is for *Alligator mississippiensis*, and orange one is for *Alligator sinensis*. Triangles are hatchlings, squares are juveniles and circles are adults.

towards positive PC1 and PC2 values (Figure 3a & S4a). However, there is no clear visual delimitation between families on the PC1 and PC2 axes (Figure 3a & S4a).

A strong allometric signal is detected in the endosseous labyrinth of extant crocodylians (70% of common allometric component when regressed against centroid size and 50% of common allometric component when regressed against skull length), with significant correlations between PC1 scores, which are the most highly correlated with size variables, and log (skull length) across the whole sample, and in *Alligator*, *Caiman*, *Crocodylus*, *Gavialis*, and *Mecistops* (Figures 4–7, S6, S8, S10, S12, S14 & S22). During ontogeny, the endosseous labyrinth becomes compressed anteroposteriorly (as seen on PC1, Figure 3a

& S4a) with thinner semicircular canals (as seen on PC2, Figure 3a & S4a).

For all extant specimens, the ANOVA of unique allometries vs. common allometry is not significant (p -value = 0.91), as is the ANOVA of common allometry vs. unique allometries (p -value = 0.34). Thus, the allometric trajectories in Figure 4 cannot be considered significantly different from one another and from the common allometry model, and a common allometry model can be considered (Morris et al., 2019; Perrichon et al., 2023a). Negative ontogenetic allometries are retrieved, meaning that the development of the endosseous labyrinth is slower than that of the skull, in all species. Therefore, to assess the phylogenetic implications of the endosseous labyrinth,

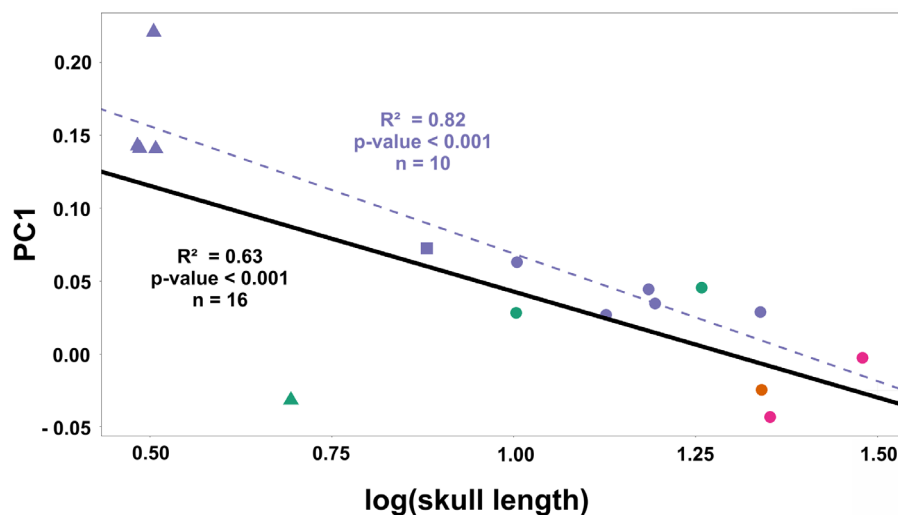


FIGURE 6 Allometric trajectories in *Caiman*, all specimens (PC1 vs. log-transformed skull length). Plain black line represents the trajectory for *Caiman* and purple dashed line is for *Caiman latirostris*. Dark green points are *Caiman crocodilus* and pink ones are *Caiman yacare*. Triangles are hatchlings, squares are juveniles and circles are adults.

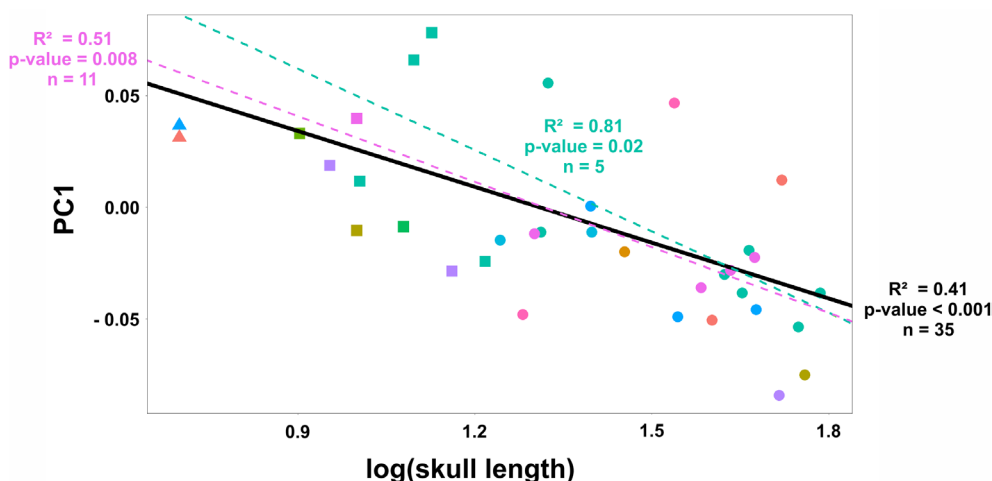


FIGURE 7 Allometric trajectories in *Crocodylus*, all specimens (PC1 vs. log-transformed skull length). Plain black line represents the trajectory for *Crocodylus*, turquoise dashed line is for *Crocodylus niloticus*, and light pink one is for *Crocodylus siamensis*. Light red points are *Crocodylus acutus*, dark brown one is *Crocodylus halli*, kaki ones are *Crocodylus intermedius*, light green one is *Crocodylus mindorensis*, dark green one is *Crocodylus moreletii*, light blue one is *Crocodylus novaeguineae*, dark blue one is *Crocodylus palustris*, purple ones are *Crocodylus porosus* and dark pink ones are *Crocodylus* sp. Triangles are hatchlings, squares are juveniles and circles are adults.

the dataset was restricted to adult specimens, to remove any ontogenetic bias.

In the sample consisting only of extant adult specimens ($n = 73$), the Procrustes ANOVA revealed a significant effect of centroid size, skull length, genus and family ($p < 0.05$), at different percentages on the shape of the endosseous labyrinths (Table 2). Furthermore, the first two principal components of the complete adult morphospace explain 23.9% of the total variance, highlighting changes between taxa (Figure 8a & S23). For all adult specimens, the broken stick model approach highlights that the first 13 principal components are significantly different from a random distribution. However, as they represent a small percentage of the total shape variation, they

are not considered (Data S2). PC1 is associated with the dorsoventral extension of the endosseous labyrinth with negative values corresponding to a minimal dorsoventral extension. PC2 is associated with the anteroposterior compression of the endosseous labyrinth with negative values corresponding to an anteroposterior compression. PC1 scores are significantly correlated with centroid size, skull length, genus and family, while PC2 scores are only significantly correlated with skull length and genus. However, there is no clear visual phylogenetic or morphological delimitation on the PCA graph (Figure 8a & S23).

A significant allometric signal is retrieved in the endosseous labyrinth of extant adult crocodylians (40% of common allometric

TABLE 2 Regression tests on the adult extant sample ($n = 73$).

Variable 1	Variable 2	p-value	R ²
Procrustes coordinates	Centroid size	0.04	0.04
Procrustes coordinates	Skull length	0.01	0.04
Procrustes coordinates	Genus	0.001	0.27
Procrustes coordinates	Family	0.001	0.12
Procrustes coordinates	Skull shape	0.99	0.009
PC1	Centroid size	0.001	0.29
PC1	Skull length	0.01	0.04
PC1	Genus	0.001	0.68
PC1	Family	0.001	0.44
PC1	Skull shape	0.19	0.05
PC2	Centroid size	0.36	0.01
PC2	Skull length	0.01	0.04
PC2	Genus	0.006	0.30
PC2	Family	0.45	0.04
PC2	Skull shape	0.82	0.005
Procrustes coordinates corrected for allometry	Centroid size	0.06	0.02
Procrustes coordinates corrected for allometry	Skull length	0.001	0.06
Procrustes coordinates corrected for allometry	Genus	0.001	0.21
Procrustes coordinates corrected for allometry	Family	0.007	0.04
Procrustes coordinates corrected for allometry	Skull shape	1	0.004
RSC1	Centroid size	0.73	0.002
RSC1	Skull length	0.001	0.20
RSC1	Genus	0.03	0.25
RSC1	Family	0.56	0.02
RSC1	Skull shape	0.95	0.001
RSC2	Centroid size	0.18	0.02
RSC2	Skull length	0.12	0.04
RSC2	Genus	0.001	0.41
RSC2	Family	0.41	0.02
RSC2	Skull shape	0.83	0.005

component when regressed against centroid size and 45% when regressed against skull length), with significant correlations between PC1 scores, which are the most highly correlated with size variables, and log (skull length) in the whole sample, as well as in *Mecistops* (Figure 9, S34 & S40). However, these changes appear to be linked with very subtle morphological changes in the endosseous labyrinths (Figure 8a & S23). A negative static allometry is observed in the adult series, meaning that the more the adult skull grows, the less the endosseous labyrinths consequently extend.

For adult extant specimens, the ANOVA of unique allometries vs. common allometry is not significant (p -value=0.97), as is the ANOVA of common allometry vs. unique allometries (p -value=0.87). Thus, the allometric evolutionary trajectory of *Mecistops* in Figure 9

cannot be considered significantly different from the common static allometry model. Therefore, in order to assess the phylogenetic implications of the endosseous labyrinth, the dataset needs to consist only of adult specimens and to also be corrected for this residual allometry.

In the sample consisting only of extant adult specimens corrected for allometry ($n = 73$), the Procrustes ANOVA still revealed a significant effect of skull length, but at a low percentage ($R^2 < 0.06$) and of genus and family ($p \leq 0.01$), at different percentages (Table 2). The first two residual shape components explain 22% of the total shape variation of the complete adult morphospace corrected for allometry and are not clearly associated with changes between different taxa (Figure 8b & S24). RSC1 is related to the dorsoventral extension of the endosseous labyrinth, with positive RSC1 values corresponding to a maximum dorsoventral extension. RSC2 is related to the size of the anterior semicircular canal, with positive RSC2 values corresponding to a larger posterior semicircular canal. RSC1 scores are significantly correlated with skull length and genus, while RSC2 scores are significantly correlated with genus only, there is a moderate effect of phylogeny, but only in the sample of all extant specimens and the sample of extant adults not corrected for allometry: $K_{mult}=0.27$ (p -value=0.001) and $K_{mult}=0.34$ (p -value=0.001), respectively.

4 | DISCUSSION

As noted by Schwab et al. (2022), there is a strong influence of allometry in the endosseous labyrinth of extant crocodylians. This allometry is both ontogenetic, with significant correlations in specimens of *Alligator*, *Caiman*, *Crocodylus*, *Gavialis*, *Mecistops* of different ontogenetic stages (Figure 4–7, S6, S8, S10, S12, S14 & S22), and static, with a significant correlation only in adult specimens (Figure 9, S34 & S40). With increasing skull length, the endosseous labyrinth becomes anteroposteriorly compressed (PC1) with thinner semicircular canals (PC2, Figure 3 & S4), both throughout the life of the organisms and during adulthood. This would be consistent with the hypothesis that braincase dimensions, and how they change throughout the life of the organism, have a direct effect on the size and shape of the endosseous labyrinths (Schwab et al., 2022). According to this hypothesis, the morphological changes of the endosseous labyrinth would be associated with the verticalization of the braincase during the first years of life in crocodylians (Tarsitano et al., 1989), resulting in a dorsoventral expansion of the braincase and a flattening of the cranial roof (Dufeu & Witmer, 2015; Gold et al., 2014; Morris et al., 2022; Witmer, 1995). Different skull lengths are associated with different constraints on the braincase dimensions expressed after the hatchling phase (Morris et al., 2022), and they have an influence on the morphology of the endosseous labyrinths. Indeed, brevirostrine taxa tend to have an enlarged braincase, whereas longirostrine taxa tend to have a reduced braincase (Morris et al., 2019). This developmental trajectory is particularly interesting because it is quite similar,

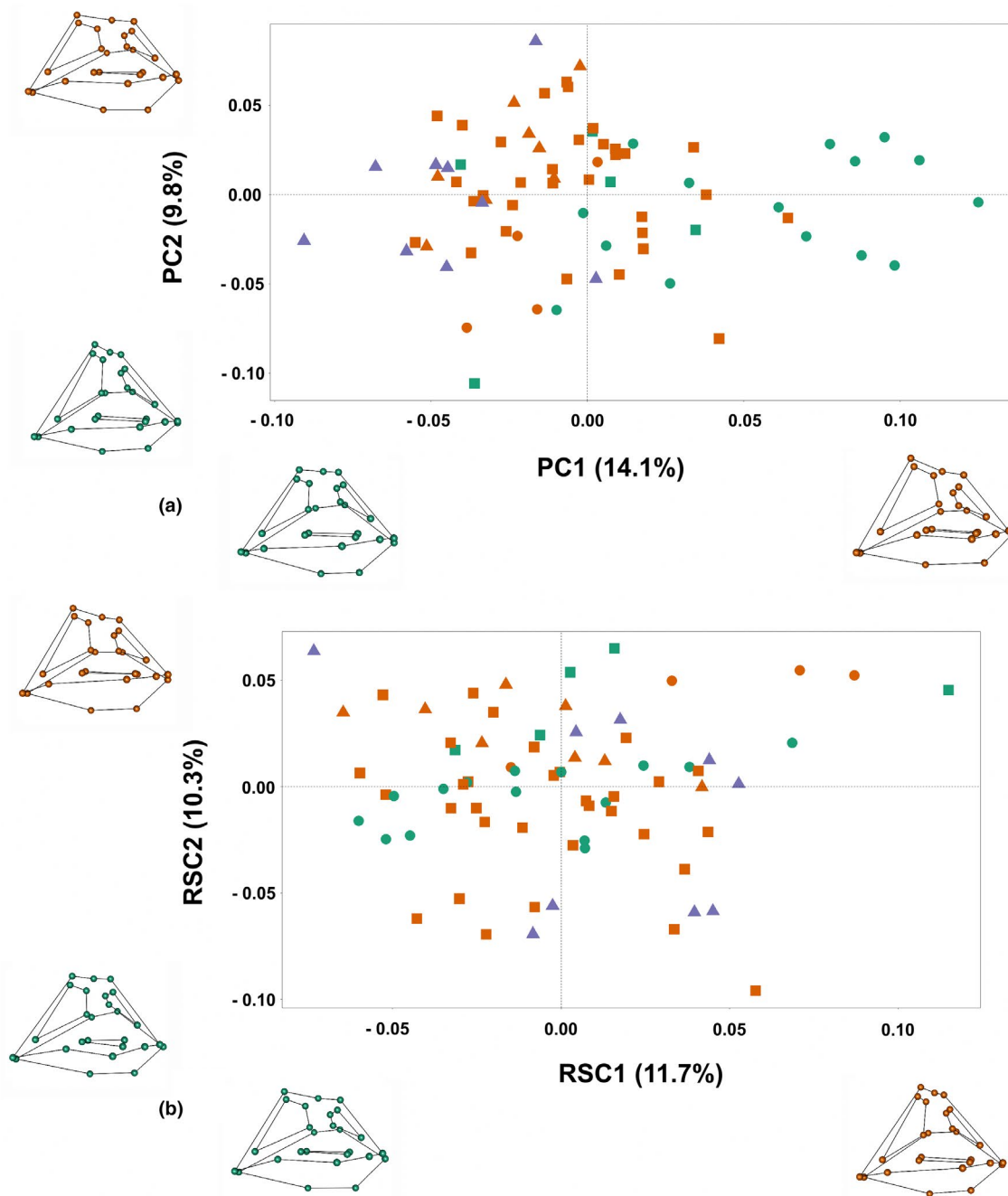


FIGURE 8 (a) Principal Component Analysis results (PC1 vs. PC2) on the endosseous labyrinths shape in adult extant crocodylians showing the two major axes of variance ($n = 73$ specimens, spanning 22 species of the crown clade Crocodylia). (b) Residual Shape Component Analysis results on the endosseous labyrinths shape variations in adult extant crocodylians showing the major axes of variance ($n = 73$ specimens, spanning 22 species of the crown clade Crocodylia). Wireframes represent landmark coordinates for extreme PC values (light green and orange points for minimum and maximum scores). Light green: Alligatoridae, orange: Crocodylidae, purple: Gavialidae. Circles: Brevirostrines, squares: mesorostrines, triangles: longirostrines.

in both morphology and trend, to what has been inferred for dinosaurs (Benson et al., 2017; Neenan et al., 2019), but different from that found in mammals, for example, where the development of the endosseous labyrinths has usually already reached adult size before birth (Berlioz et al., 2021; Ekdale, 2010; Hoyte, 1961; Jeffery & Spoor, 2004; Pujol & Marty, 1970; Richard et al., 2010; Sánchez-Villagra & Schmelzle, 2007; Thean et al., 2017).

Previous studies (Bronzati et al., 2021; Schwab et al., 2020, 2022) have not investigated the relationship between phylogeny and the shape of crocodylian endosseous labyrinths. The present dataset shows a moderate phylogenetic signal (Kmult between 0.31 and 0.35), but only on the data not corrected for allometry, while the shape information corrected for allometry is much more correlated with the genera than with the families (Table 2). As a result, it would be quite

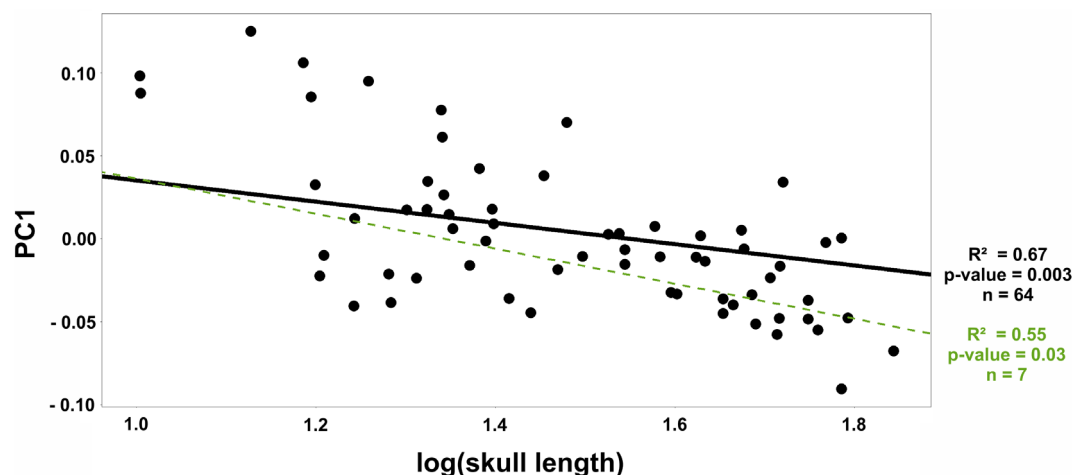


FIGURE 9 Allometric trajectories in adult extant crocodylians, all specimens (PC1 vs. log-transformed skull length). Plain black line represents the trajectory for the whole dataset, and green dashed line represents the trajectory for *Mecistops*.

difficult to identify relevant morphological characters that could be used in future phylogenetic analyses. For example, our analysis does not enable to distinguish *Voay robustus* from other crocodylid taxa, although its phylogenetic position is still under debate (Brochu, 2001, 2007; Hekkala et al., 2021; Perrichon et al., 2023b). This is also the case for taxa such as *Tomistoma schlegelii* Müller, 1846 in relation to *Gavialis gangeticus* Gmelin, 1789 or *Mecistops* compared to the rest of Crocodylidae (Brochu, 2001, 2003, 2007; Gatesy et al., 2003; Groh et al., 2020; Lee & Yates, 2018; McAliley et al., 2006; Oaks, 2011; Pan et al., 2021; Perrichon et al., 2023b; Shirley et al., 2014; Willis et al., 2007), which are indistinguishable using the shape data presented here.

Different specialised lifestyles (from fully terrestrial to fully aquatic) have repeatedly evolved throughout the history of Crocodylomorpha (Wilberg et al., 2019). Our dataset does not enable to test for the influence of ecology on the shape of the endosseous labyrinth, as all extant crocodylians sampled here have similar semi-aquatic lifestyles (Grigg & Kirshner, 2015). The morphology of the endosseous labyrinths in these fossil taxa has been described and tentatively used as a proxy for ecological differences (Bronzati et al., 2021; Brusatte et al., 2016; Conedera et al., 2023; David, 2010; Dumont et al., 2022; Erb & Turner, 2021; Fonseca et al., 2020; Herrera et al., 2018; Leardi et al., 2020; Melstrom et al., 2022; Pierce et al., 2017; Pochat-Cottilloux et al., 2022, 2023; Ristevski, 2022; Schwab et al., 2020, 2021; Wilberg et al., 2022a). However, in order to truly assess whether such particular lifestyles have a significant effect on the shape of their endosseous labyrinths, a number of caveats need to be addressed: first, the specimens sampled should be truly adult individuals, to rule out any ontogenetic effect (as confirmed here); second, the ontogenetic development of the endosseous labyrinths in such taxa should be the same as in the extant crocodylians studied here (i.e., potential heterochronic effects); third, these ecological types have most likely evolved convergently rather than from a single acquisition; and, fourth, the remaining shape information must also be corrected for any potential phylogenetic effects,

especially since some of these groups may be very distant phylogenetically. This last point can be addressed using phylogenetic comparative methods: phylogenetic PCA (Revell, 2009) or phylogenetically aligned component analysis (Collyer & Adams, 2020). However, such methods rely heavily on the chosen phylogenetic backbone, and, unfortunately, the phylogenetic relationships of early crocodylomorphs are still highly debated especially in sphenosuchians and protosuchians (Benton & Clark, 1988; Buscalioni, 2017; Clark et al., 2001; Clark & Sues, 2002; Dollman et al., 2021; Dollman & Choiniere, 2022; Nesbitt, 2009, 2011; Pol et al., 2004, 2013; Wu et al., 1994, 1997; Wu & Chatterjee, 1993; Wu & Li, 1994), notosuchians (Cunha et al., 2020; Dumont et al., 2020; Gasparini et al., 1993; Godoy et al., 2016; Leardi et al., 2015; Martin et al., 2022; Martinelli et al., 2018; Nascimento & Zaher, 2011; Pinheiro et al., 2018, 2021, 2023; Pol et al., 2014; Ruiz et al., 2021; Soto et al., 2011; Turner & Sertich, 2010) and thalattosuchians (Foffa et al., 2018; Johnson, 2019; Johnson et al., 2020, 2022; Jouve, 2009; Mueller-Töwe, 2005, 2006; Pol & Gasparini, 2009; Wilberg, 2015; Wilberg et al., 2022b; Young et al., 2024). Finally, there is a growing debate about the use of geometric morphometrics to assess links between shape and function, because shape analyses might cluster morphological signal in an incompatible way compared to biomechanical models, especially those of the inner ear (David, 2010; David et al., 2022, 2016; Hanson et al., 2021, 2022). This issue would also need to be addressed in the future.

5 | CONCLUSION

In conclusion, we show that the shape of the endosseous labyrinths in extant crocodylians is mainly related to size constraints, and hypothetically to braincase constraints, with a negative allometry, that is both ontogenetic and static. A moderate link with phylogeny is also found, but only without considering the effect of size, and it will be very difficult to translate this into relevant phylogenetic and taxonomically diagnostic characters. Further research on fossil forms may allow the

assessment of a potential link between endosseous labyrinths shape and lifestyle, but unresolved phylogenetic relationships between different groups of crocodylomorphs will need to be addressed first.

AUTHOR CONTRIBUTIONS

YP: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft, Writing – review & editing; **GP:** Formal Analysis, Investigation, Methodology, Software, Validation, Writing – review & editing; **LH:** Conceptualization, Formal Analysis, Investigation, Methodology, Resources, Software, Validation, Writing – review & editing; **NR:** Data curation, Resources, Software, Validation, Writing – review & editing; **RA:** Conceptualization, Project administration, Supervision, Validation, Writing – review & editing; **IR:** Data curation, Resources, Validation, Writing – review & editing; **JA:** Data curation, Resources, Software, Validation, Writing – review & editing; **JL:** Data curation, Resources, Software, Validation, Writing – review & editing; **VF:** Data curation, Resources, Software, Validation, Writing – review & editing; **JEM:** Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

OPEN RESEARCH BADGES



This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the

reported results. The data is available at <https://zenodo.org/records/13739699>.

DATA AVAILABILITY STATEMENT

The data supporting this article, and the R code used to analyse the data are available on this link: <https://zenodo.org/records/13739699>.

ORCID

Yohan Pochat-Cottilloux <https://orcid.org/0000-0002-6216-2721>

Gwendal Perrichon <https://orcid.org/0000-0001-5831-764X>

Lionel Hautier <https://orcid.org/0000-0001-8701-5421>

Romain Amiot <https://orcid.org/0000-0003-2779-9652>

Irena Raselli <https://orcid.org/0000-0002-8148-3256>

Jérôme Adrien <https://orcid.org/0000-0003-0341-3559>

Vincent Fernandez <https://orcid.org/0000-0002-8315-1458>

Jeremy E. Martin <https://orcid.org/0000-0001-9159-645X>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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