Inner ear sensory system changes as extinct crocodylomorphs transitioned from land to water

Julia A. Schwab[a,1], Mark T. Young[a], James M. Neenan[b], Stig A. Walsh[a,c], Lawrence M. Witmer[d], Yanina Herrera[e], Ronan Allain[f], Christopher A. Brochu[g], Jonah N. Choiniere[h], James M. Clark[i], Kathleen N. Dollman[h,j], Steve Etches[k], Guido Fritsch[l], Paul M. Gignac[m], Alexander Ruebenstahl[n], Sven Sachs[o], Alan H. Turner[p], Patrick Vignaud[q], Eric W. Wilberg[p], Xing Xu[r], Lindsay E. Zanno[s,t], and Stephen L. Brusatte[a,c]

[a]School of GeoSciences, Grant Institute, University of Edinburgh, EH9 3FE Edinburgh, United Kingdom; [b]Oxford University Museum of Natural History, OX1 3PW Oxford, United Kingdom; [c]Department of Natural Sciences, National Museum of Scotland, EH1 1JF Edinburgh, United Kingdom; [d]Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Ohio University, Athens, OH 45701; [e]Consejo Nacional de Investigaciones Científicas y Técnicas, División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, National University of La Plata, B1900 La Plata, Buenos Aires, Argentina; [f]Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements, Muséum National d'Histoire Naturelle, 75005 Paris, France; [g]Department of Earth and Environmental Sciences, University of Iowa, Iowa City, IA 52242; [h]Evolutionary Studies Institute, University of the Witwatersrand, 2000 Johannesburg, South Africa; [i]Department of Biological Sciences, George Washington University, Washington, DC 20052; [j]School of Geosciences, University of the Witwatersrand, 2000 Johannesburg, South Africa; [k]Museum of Jurassic Marine Life, BH20 5PE Kimmeridge, United Kingdom; [l]Department of Reproduction Management, Leibniz Institute for Zoo and Wildlife Research, 10315 Berlin, Germany; [m]Department of Anatomy and Cell Biology, Oklahoma State University Center for Health Sciences, Tulsa, OK 74107; [n]Department of Geology and Geophysics, Yale University, New Haven, CT 06511; [o]Abteilung Geowissenschaften, Naturkunde-Museum Bielefeld, Abteilung Geowissenschaften, 33602 Bielefeld, Germany; [p]Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794; [q]Laboratoire de Paléontologie, Evolution, Paléoécosystèmes et Paléoprimatologie, CNRS UMR 7262, Department of Geosciences, University of Poitiers, 86073 Poitiers Cedex 9, France; [r]Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 100044 Beijing, China; [s]Paleontology, North Carolina Museum of Natural Sciences, Raleigh, NC 27601; and [t]Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695

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Major evolutionary transitions, in which animals develop new body plans and adapt to dramatically new habitats and lifestyles, have punctuated the history of life. The origin of cetaceans from land-living mammals is among the most famous of these events. Much earlier, during the Mesozoic Era, many reptile groups also moved from land to water, but these transitions are more poorly understood. We use computed tomography to study changes in the inner ear vestibular system, involved in sensing balance and equilibrium, as one of these groups, extinct crocodile relatives called thalattosuchians, transitioned from terrestrial ancestors into pelagic (open ocean) swimmers. We find that the morphology of the vestibular system corresponds to habitat, with pelagic thalattosuchians exhibiting a more compact labyrinth with wider semicircular canal diameters and an enlarged vestibule, reminiscent of modified and miniaturized labyrinths of other marine reptiles and cetaceans. Pelagic thalattosuchians with modified inner ears were the culmination of an evolutionary trend with a long semiaquatic phase, and their pelagic vestibular systems appeared after the first changes to the postcranial skeleton that enhanced their ability to swim. This is strikingly different from cetaceans, which miniaturized their labyrinths soon after entering the water, without a prolonged semiaquatic stage. Thus, thalattosuchians and cetaceans became secondarily aquatic in different ways and at different paces, showing that there are different routes for the same type of transition.

bony labyrinth | vestibular system | morphology | thalattosuchia | CT scanning

Throughout the history of life, there have been occasional major evolutionary transitions, in which animals developed a restyled body capable of new behaviors and adapted to new habitats. A classic example is cetaceans (whales and dolphins), which evolved from land-living mammalian ancestors into pelagic (open-ocean, sea, or shelf environment) swimmers (1). In making this shift, cetaceans followed several groups of reptiles that became secondarily aquatic much earlier, during the Mesozoic Era (2). These marine reptiles—which include plesiosauroids, pliosaurids, ichthyosaurs, mosasaurs, and extinct relatives of crocodiles and turtles—filled many of the same niches cetaceans do today (3). While the land-to-sea transition in cetaceans is captured by a sequence of fossils, whose skeletal features (4, 5) and biological and sensory abilities (6–8) have been studied in detail, far less is known about how Mesozoic reptiles moved into the water (9). This makes it difficult to address a key question: did evolution follow a similar path in modifying different groups of secondarily aquatic tetrapods for life in the open oceans?

Thalattosuchians, ancient relatives of modern crocodylians, lived during the Jurassic and Cretaceous (ca. 182–125 Ma). They are the only members of the archosaur clade—the hyperdiverse group that originated ca. 250 mya and includes birds, dinosaurs, and crocodiles—to develop fully pelagic swimming lifestyles.

Significance

During major evolutionary transitions, groups acquire a new body plan that allows them to colonize new habitats and behave in new ways. The evolution of swimming cetaceans from land-living mammals is a prime example. We document changes to the inner ear sensory system, involved in balance and equilibrium, as extinct crocodile relatives called thalattosuchians underwent a similar transition in the Mesozoic (ca. 182–125 mya). We find that open-ocean thalattosuchians developed strikingly compact and thickened bony labyrinth after a long semiaquatic phase and after modifying their skeleton to become better swimmers. This differs from cetaceans, which miniaturized their bony labyrinths soon after entering the water. Therefore, thalattosuchians and cetaceans took different evolutionary paths from land to water.

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Data deposition: The data for all 32 endosseous labyrinth models has been uploaded to Morphosource and can be accessed at https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/952.

[1]To whom correspondence may be addressed. Email: julia.schwab@ed.ac.uk.

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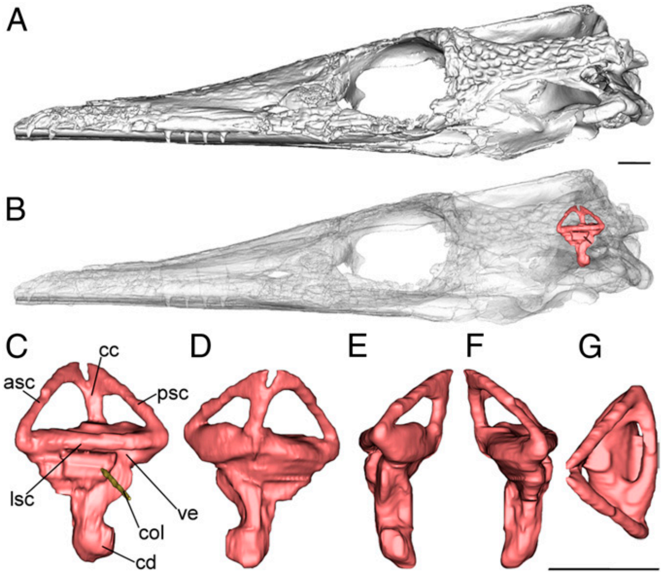

Fig. 1. Left bony labyrinth of the extinct thalattosuchian crocodylomorph *Pelagosaurus typus* (NHMUK PV OR 32599) based on CT data; (*A*) lateral view of the skull. (*B*) Transparent skull showing the position of the endosseous (bony) labyrinth; (*C*) lateral view; (*D*) medial view; (*E*) posterior view; (*F*) anterior view; and (*G*) dorsal view of the bony labyrinth. Abbreviations: asc, anterior semicircular canal; cc, crus commune; cd, cochlear duct; col, columella; lsc, lateral semicircular canal; psc, posterior semicircular canal; ve, vestibule. (Scale bars equal 1 cm.)

Thalattosuchians evolved from terrestrial ancestors (10), and include two main subgroups whose habitats are known from anatomical and geological evidence: semiaquatic nearshore teleosauroids, which resembled extant gharials (11), and fast-swimming open-ocean metriorhynchids, whose flippers, tail flukes, and streamlined bodies are often compared to cetaceans (3, 12, 13). Thalattosuchians are unique among marine reptiles in having their evolutionary transition documented by a series of well-preserved fossils with well-understood phylogenetic relationships, and having close living relatives (crocodylians) whose anatomy and biology can be directly observed. Thus, thalattosuchians can give critical insight into how reptiles became pelagic, and whether they underwent a similar evolutionary transformation as cetaceans.

We here study evolutionary trends in one of the most important vertebrate sensory systems—the inner ear—as thalattosuchians relocated from land to water, using high-resolution computed tomography (CT) scanning of 18 extinct species and 14 modern relatives for comparison. We focus on the endosseous labyrinth of the inner ear (Fig. 1), the bony cavity that housed the membranous sensory system. It is comprised of the vestibular system including the three semicircular ducts that detect angular acceleration and the vestibule (containing the saccule, utricle, and otolith organs) that detects linear acceleration and gravity (14). As a crucial component of the system of balance and equilibrium, bony labyrinth morphology is regularly used to reveal insights into ancient animal behavior and lifestyles (e.g., refs. 15–17). Because of the physical differences between air and water, this system should—and does—differ in terrestrial and aquatic species (18). In cetaceans, the labyrinth became highly reduced soon after they entered the water, without a long intermediate semiaquatic phase (6). One marine reptile group, pliosaurids, developed slightly smaller but more bulbous labyrinths as they changed from nearshore bottom walkers to pelagic swimmers (9). It is unclear whether other marine reptiles followed these or other evolutionary routes, which if so might speak to more general "rules" of how tetrapods become secondarily aquatic. Thalattosuchians provide a test.

Results

Crocodylomorph semicircular canal and vestibular shape reflects ecomorphology and habitat, which are independently known for all species based on osteological and environmental evidence (Fig. 2 and *SI Appendix*, Table S2). Terrestrial species have a dorsoventrally tall labyrinth, with a particularly high anterior semicircular canal. The canal cross-sections are slender, the crus commune is narrow, and the vestibule is elongate mediolaterally. In contrast, pelagic metriorhynchids have a dorsoventrally short (compact) labyrinth. The anterior canal is only slightly higher than the posterior one, and both the crus commune and the canals have thick cross-sectional diameters. Semiaquatic teleosauroids and extant crocodylians have an intermediate labyrinth morphology, with dorsoventrally taller semicircular canals than the pelagic forms but a more compact labyrinth than the terrestrial species. These bony labyrinth shape differences between habitat groups are corroborated by numerical analyses.

Principal component analysis (PCA) of three-dimensional (3D) geometric morphometric landmarks on the semicircular canals ordinates species into a morphospace in which the first three axes describe 53.50% of overall variance (Fig. 3). The first principal component axis (PC1), explaining 22.67% of variance, represents the dorsoventral depth of the labyrinth and canal cross-sectional thickness, and segregates species by habitat. The three derived pelagic metriorhynchids (*Cricosaurus araucanensis*, *C. schroederi*, and *Torvoneustes coryphaeus*) have the most positive PC1 scores, due to their dorsoventrally compressed labyrinths and thick canals. The three terrestrial taxa (*Junggarsuchus sloani*, *Protosuchus haughtoni*, and a "sphenosuchian") have the most negative PC1 scores, because of their tall labyrinths and thin canals. Various semiaquatic taxa, including extinct teleosauroids and extant crocodylians, occupy an intermediate region between these extremes. Habitat differences are reflected to a lesser extent on PCs 2 and 3 (18.44% and 12.39% of variance, respectively).

A statistical test of morphospace occupation (PERMANOVA) upholds the observation that habitat groups form clusters, in which terrestrial, semiaquatic, and pelagic species are each significantly

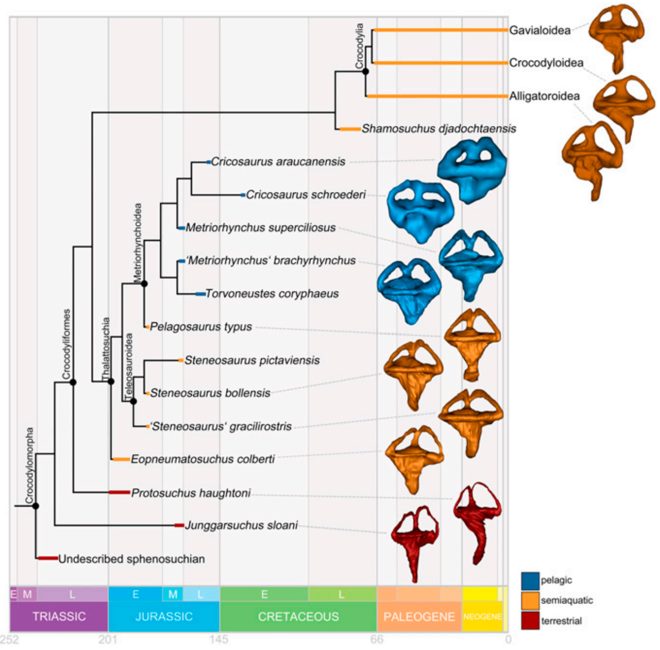

Fig. 2. Simplified time-scaled phylogeny showing right bony labyrinth shapes of key extinct and extant crocodylomorphs of different habitats. Labyrinths are not to scale.

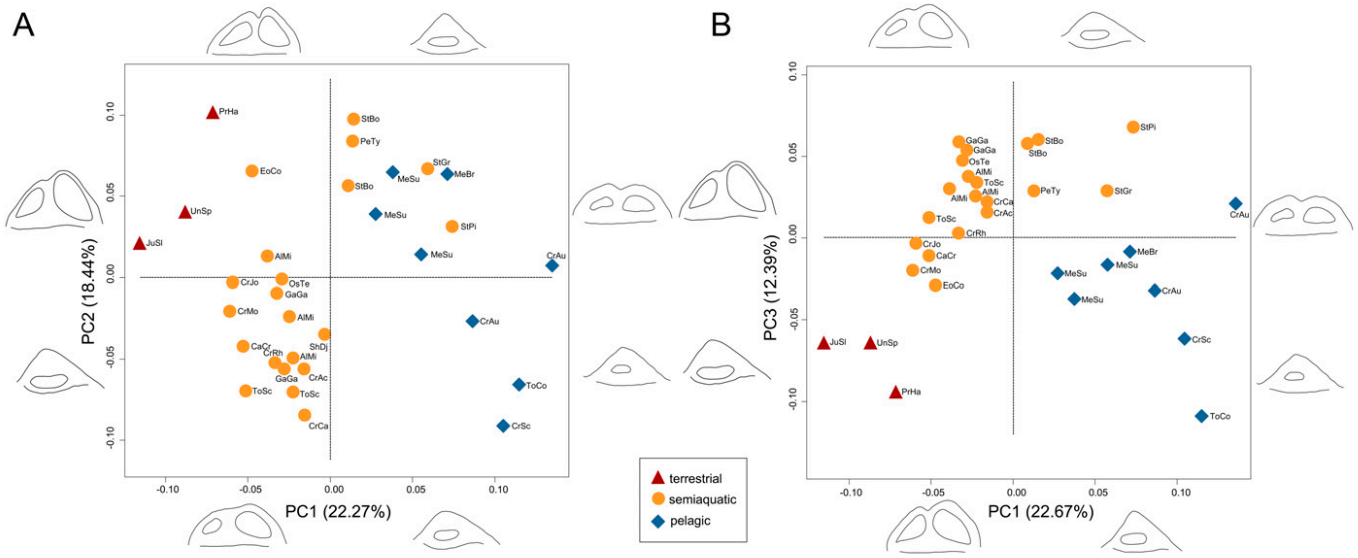

Fig. 3. Bony labyrinth shape morphospaces, showing the distribution of extinct and extant crocodylomorphs of different habitats, based on principal component analysis of 3D landmarks. (*A*) PC1 vs. PC2; (*B*) PC1 vs. PC3. Labyrinth outline diagrams correspond to morphological extremes at the ends of PC axes, in lateral and dorsal views. For taxa abbreviations see *SI Appendix*, Table S1.

separated from one another (P value < 0.005; *SI Appendix*, Table S5).

A canonical variate analysis (CVA) of the PC scores demonstrates that bony labyrinth shape predicts habitat. When all crocodylomorphs are placed into habitat groupings predetermined from osteological and environmental evidence, and individual taxa are then iteratively treated as having an unknown habitat, the CVA classifies them into the correct habitat 100% of the time (Fig. 4 and *SI Appendix*, Table S6).

Because the relationship between bony labyrinth shape and habitat may be confounded by phylogeny and labyrinth size, we further explored the relationships between these variables using phylogenetic comparative methods. Pagel's lambda shows that there is a strong and significant phylogenetic signal on PC1 and PC3, whereas PC2 has a weaker but still significant signal (*SI Appendix*, Table S7). Thus, we employed phylogenetic regressions (pGLS), which found that PC1 is significantly correlated with habitat even when phylogeny is accounted for, whereas PC2 and 3 are not. PC1 remains significantly correlated with habitat in a second phylogenetic regression on size-corrected residuals, necessitated because of the significant relationship between PC1 and labyrinth size (centroid size). This is strong evidence that, regardless of phylogeny and size, the shape of the bony labyrinth is strongly correlated with habitat.

A trend is apparent when PC1—the axis most strongly correlated with habitat—is optimized onto crocodylomorph phylogeny (Fig. 5). Terrestrial species with negative PC1 scores occupy basal positions, as outgroups to the clade of thalattosuchians and extant crocodylians. On the thalattosuchian line toward pelagic metriorhynchids, the early-diverging *Eopneumatosuchus colberti*,

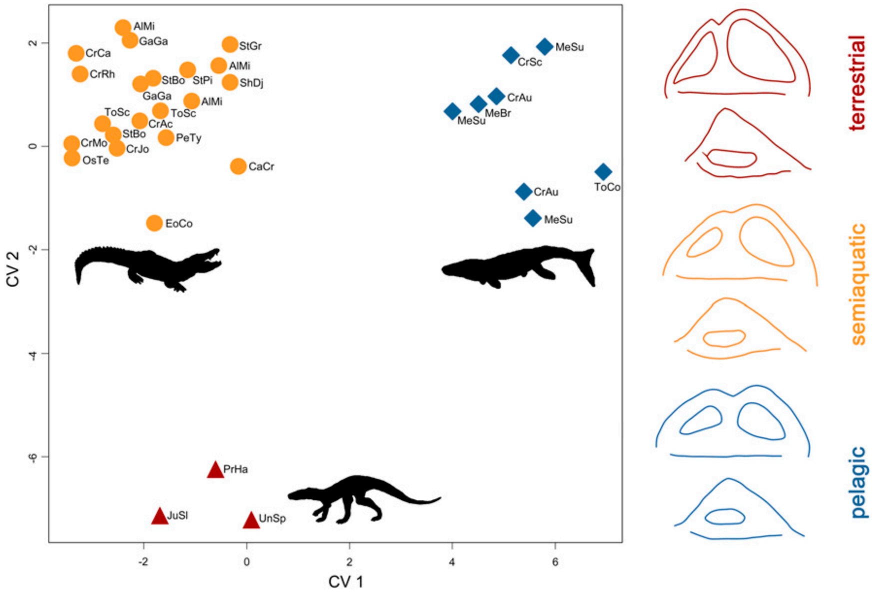

Fig. 4. Bony labyrinth shape morphospace, showing the distribution of extinct and extant crocodylomorphs of different habitats, based on canonical variate analysis of PC scores (Fig. 3), with mean labyrinth shapes for each habitat group, in lateral (*Top*) and dorsal (*Bottom*) views.

teleosauroids, and the basal metriorhynchoid *Pelagosaurus typus* form a grade of semiaquatic taxa with intermediate PC1 scores. PC1 scores become progressively more positive along this grade, culminating in the high PC1 scores of metriorhynchids. The most extreme labyrinth shapes, denoted by the highest PC1 scores, appear independently in two pelagic metriorhynchid subgroups: Geosaurinae (with *T. coryphaeus*) and Metriorhynchinae (with *C. schroederi* and *C. araucanensis*). Modern crocodylians exhibit a similar semiaquatic morphology as teleosauroids.

When we fit five standard models of trait evolution to PC1 scores across phylogeny, we found that an early burst model was best supported for the entire tree of extinct and extant crocodylomorphs, whereas a Brownian motion with directional trend model best fit the tree with extinct species only (*SI Appendix*, Table S10). Furthermore, when the phylogeny is plotted such that the *x* axis is scaled to time and the *y* axis to PC1 score, metriorhynchids/thalattosuchians are found to have higher rates of PC1 evolution than other crocodylomorphs (*SI Appendix*, Fig. S7). These results support the hypothesis that there was an evolutionary trend of increasingly specialized labyrinth shape in pelagic thalattosuchians, which involved relatively rapid rates of change compared to the background.

The cochlear duct is more challenging to characterize with landmarks than the semicircular canals, but a linear regression shows that minimum cochlear duct length correlates positively with labyrinth length. Pelagic metriorhynchids fall below the regression line, indicating that they had shorter cochlear ducts than other crocodylomorphs even when labyrinth length is held constant, which may indicate reduced hearing frequency ranges (ref. 19 and *SI Appendix*, Fig. S8).

Discussion

We find that the shape of the crocodylomorph vestibular system corresponds to habitat, in extinct and extant species spanning more than 200 million years of evolution. There are distinct terrestrial, semiaquatic, and pelagic clusters in endosseous labyrinth morphospace, and transitions between these labyrinth types on the phylogeny. Fully pelagic Mesozoic metriorhynchids have the most transformed vestibular systems, relative to their immediate extinct semiaquatic kin, extant semiaquatic crocodylians, and terrestrial antecedents near the base of the phylogeny. In particular, metriorhynchids have a reduced, dorsoventrally shortened labyrinth with thickened semicircular canal diameters and an enlarged vestibule.

The metriorhynchid condition is reminiscent of modifications to labyrinth size and shape in other aquatic tetrapods that evolved from terrestrial ancestors. Swimming sauropterygian reptiles have smaller labyrinths than their nearshore bottom-walking relatives, and the most pelagic, fastest-swimming species (such as plesiosaurs) have compact and bulbous labyrinths with wide semicircular canal diameters, comparable to metriorhynchids like *Cricosaurus* and *Torvoneustes* (9, 20) and also sea turtles (18, 21). Cetaceans have miniaturized labyrinths, approximately 3 times smaller than terrestrial mammals of equivalent body size, although not drastically different in shape (6, 22). Aquatic mammals, like sirenians and seals, also reduced

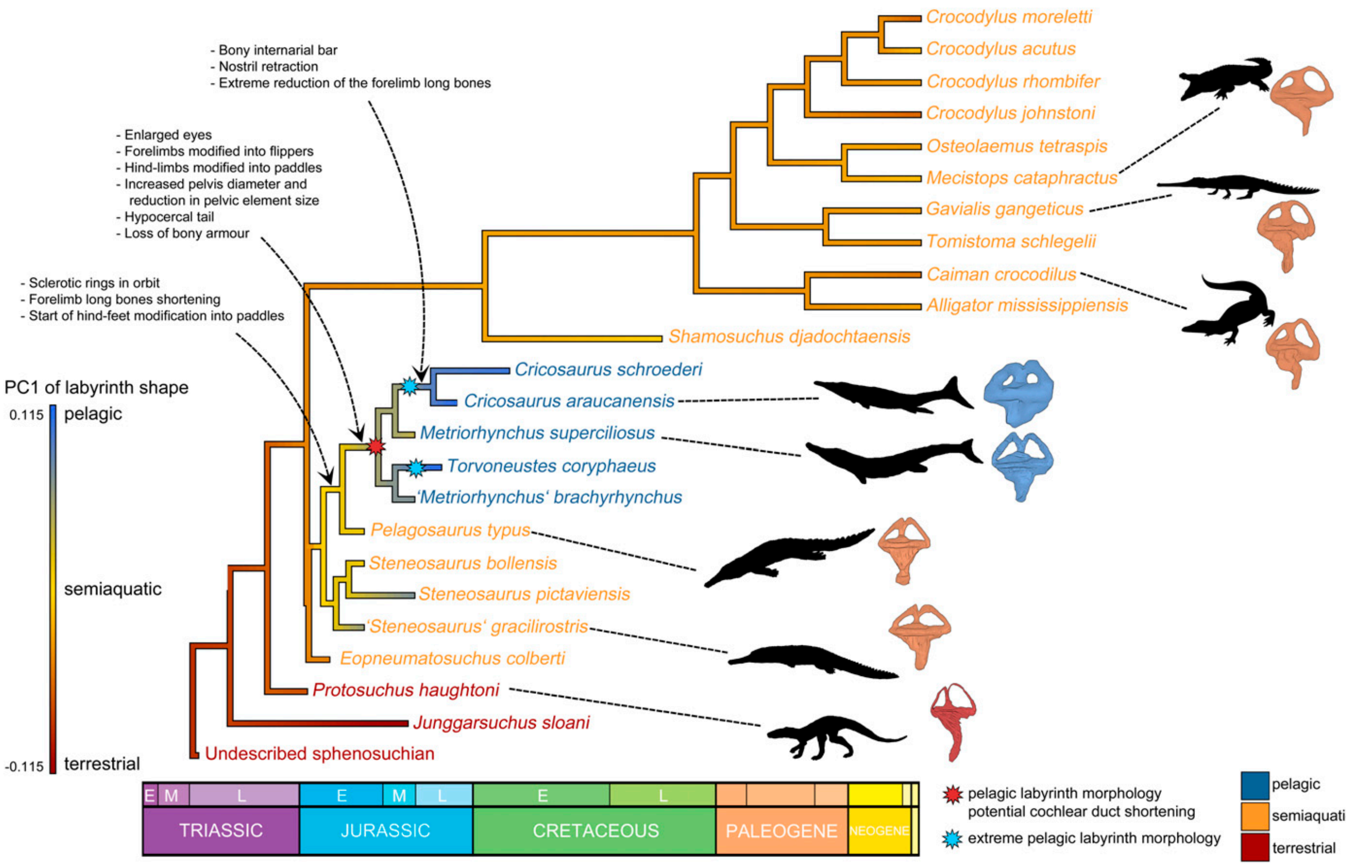

Fig. 5. Pelagic adaptions plotted on a time-scaled crocodylomorph phylogeny. PC1 scores of labyrinth shape, which are correlated with habitat (Figs. 3 and 4), are optimized on the phylogeny to predict ancestral states for the major clades, demonstrating a trend of increasing PC1 scores (increasingly pelagic-shaped ears) in thalattosuchians. Key cranial and postcranial features related to aquatic lifestyles are listed next to the nodes at which they appeared, based on optimizations (43). This demonstrates that thalattosuchians first developed features permitting aquatic locomotion before they developed a modified pelagic labyrinth morphology.

their canals to a lesser degree (22–24). Thus, distantly related radiations of marine reptiles independently evolved similar compact, robust, but not extremely atrophied cetaceanlike labyrinths, suggesting a general manner in which reptile vestibular sensory systems are altered for a pelagic lifestyle. More broadly, despite differences between labyrinths of pelagic reptiles and cetaceans, both exhibit labyrinth size reductions and shape modifications. This appears to be a common theme for secondarily aquatic tetrapods, transcending phylogenetic distance, tens of millions of years of time, and vastly different swimming styles (slower lateral tail undulation of reptiles vs. faster dorsoventral movements of cetaceans; ref. 25).

Similarities in labyrinth morphology indicate common physical constraints acting on agile, swimming tetrapods in the open water, but interpreting the functional significance of labyrinth size and shape changes is challenging. Longer and more arching semicircular canals are more sensitive to rotations in space (6, 26). The reduced canals of cetaceans may prevent overstimulation during exaggerated head movements associated with swimming and diving, which cannot easily be stabilized by their shortened necks (6). However, experimental evidence that extant cetaceans experience similar head accelerations as terrestrial mammals is inconsistent with this hypothesis (27). That said, it is notable that metriorhynchids, like some sauropterygians and cetaceans, have shorter necks than their close relatives (five instead of seven postaxial cervical vertebrae; refs. 11, 28), hinting that neck length may be a factor in labyrinth modifications. Perhaps the shorter neck made the head more integrated with the torso, resulting in a larger and more drag-prone head–body unit that made vestibular sensitivity less important. Alternatively, because the vestibular system is also involved in head and gaze stabilization, its reduction may reflect lesser reliance on terrestrial-style vision (compared to other senses) in pelagic species (29). Less clear is why the semicircular canals and vestibule are expanded in cross-section in metriorhynchids and other pelagic marine reptiles (9). The expansive vestibule may have housed a larger otolith, a calcium carbonate structure that is involved in perceiving linear acceleration and gravity. Large otoliths are seen in aquatic mammals such as cetaceans, sirenians, and pinnipeds (7, 22, 30), but otoliths are not visible in any of our fossil CT scans. Future work is needed to understand how bony labyrinth shape corresponds to the enclosed structures involved in sensory processing (membranous labyrinth and otoliths), and engineering techniques like computational fluid dynamics may be particularly fruitful for testing functional hypotheses (31).

The rich record of thalattosuchian fossils spanning the land-to-sea transition makes them an exemplar for illuminating evolutionary trends in secondarily aquatic reptiles, and for comparing to the well-known transitional sequence of early cetaceans. Thalattosuchians developed fully pelagic species after a long semiaquatic phase on the phylogeny, represented by the grade of close thalattosuchian outgroups, teleosauroids, and basal metriorhynchoids on the line to pelagic metriorhynchids like *Cricosaurus* and *Torvoneustes* (Fig. 5). Ancestral character state reconstructions demonstrate that this grade maintained semiaquatic labyrinth shapes along a lengthy series of internal branches, before the signature compact and bulbous pelagic labyrinths evolved in derived metriorhynchids. Pelagic labyrinths appeared after the first changes to the postcranial skeleton that allowed thalattosuchians to locomote in the water, such as shortening of the forelimbs and the modification of hindlimbs into paddles. Thus, changes to the vestibular system apparently did not lead the transition, but likely were a response to changing sensory requirements as metriorhynchids moved into deeper, more open waters. Furthermore, after the transition occurred, semiaquatic teleosauroids persisted alongside pelagic metriorhynchids for tens of millions of years (32).

Cetaceans, on the other hand, did not have such a prolonged semiaquatic phase, and the labyrinth became miniaturized rapidly as early cetaceans entered marine environments, followed by gradual changes to the postcranial skeleton associated with powerful swimming (6). The basal cetaceans that we consider most skeletally analogous to semiaquatic thalattosuchians—the nearshore remingtonocetids, which had teleosauroidlike elongate snouts, comparatively long necks, forelimbs and hindlimbs used in swimming, and robust pelves (1, 33)—had miniaturized pelagic-style labyrinths, and flourished for only a few million years. It may be that cetaceans were able to adapt more quickly to fully pelagic lifestyles, because they evolved from terrestrial ancestors that were already endothermic and gave live birth, whereas metriorhynchids had to develop these attributes after entering the water (34, 35).

Thalattosuchian crocodylomorphs are a prime example of a major evolutionary transition, and their vestibular sensory systems changed as they left the land and adapted to the water. It was a phylogenetically lengthy transition with a long semiaquatic stage, seemingly led by changes in the skeleton, related to locomotion, that allowed thalattosuchians to move in the water, followed by modifications to at least one sensory system. Key open questions, to test with future fossil discoveries and CT analyses, are how fast (in temporal terms) metriorhynchids developed a pelagic labyrinth after splitting from their semiaquatic ancestors, and how other sensory systems changed during this transition. Thalattosuchians (and other marine reptiles), like cetaceans, dramatically altered their labyrinths when becoming secondarily aquatic, but they did so in different ways and at different paces. Evolutionary transitions can start and finish in the same places, but take different routes depending on the organisms involved.

Methods

Dataset. We compiled a dataset of extinct and extant crocodylomorph endosseous labyrinths, using computed-tomography scanning. Our extinct (fossil) sample (18 specimens) includes all thalattosuchians with well-preserved skulls that were accessible to us (13 specimens, including 4 teleosauroids, the basal metriorhynchoid *Pelagosaurus typus*, and 8 metriorhynchids), two basal "sphenosuchian"-grade taxa, *Protosuchus haughtoni*, *Eopneumatosuchus colberti,* and the neosuchian *Shamosuchus djadochtaensis*. These taxa span much of the evolutionary history of crocodylomorphs, from the Late Triassic to Early Cretaceous, and include a series of fossil outgroups that polarize the primitive conditions for Thalattosuchia, our main clade of interest (Fig. 2). To this dataset, we added 14 extant crocodylians for comparative purposes, including members of the 3 major extant lineages (Alligatoroidea, Crocodyloidea, and Gavialoidea) (*SI Appendix*, Table S1). Our dataset includes only adult and subadult specimens. For specimen details, see *SI Appendix*.

Ecological Categories. Our dataset includes species belonging to three ecomorphological or habitat groups: terrestrial, semiaquatic, and pelagic (i.e., fully aquatic). All extant crocodylians are semiaquatic, as extensive observational data show that they move between the land and nearshore aquatic habitats (36). The habitats of extinct species were assigned based on a combination of osteological and geological (environmental) data (*SI Appendix*, Table S2).

Data Assembly. Skulls were CT scanned at various facilities, so the scanners and scanning parameters vary (*SI Appendix*, Table S1). Some scans were sourced from the online databases Morphosource (https://www.morphosource.org/) and Digimorph (http://digimorph.org/). Bony labyrinths were segmented from the scans using Materialise Mimics 19.0 and 20.0, using the livewire and lasso tools. We segmented right labyrinths and retained them for the numerical analyses (see below); if these were not preserved, then the left labyrinth was segmented and mirrored. A recent study found no significant bilateral variation in the inner ears of wild turkeys (37), justifying this procedure. We also show that left–right asymmetry is minimal in extant crocodylians (*SI Appendix*, Figs. S9 and S10).

Geometric Morphometric Analysis. For each 3D rendered endosseous labyrinth model, we placed two series of semilandmarks along each of the semicircular canals, one on the internal surface and one on the external surface (*SI Appendix*, Fig. S1), using the IDAV Landmark software (38). The landmarks were digitalized using the digit.curves() function in the geomorph 3.1.2 package (39) in RStudio (40) to evenly spaced semilandmarks, 11 on the internal surface and 12 on the external surface. Landmarks on the internal surface of the canals were treated as closed structures, and those on the external surface as open structures. Subsequently, we applied Procrustes superimposition to minimize the effects of size and orientation.

Multivariate Analyses. We subjected the Procrustes-corrected geometric morphometric landmark dataset to principal component analysis in geomorph 3.1.2, which assimilates data from all landmarks and reduces them to a set of PC scores that summarize the labyrinth shape of each species, and allow the species to be plotted in a morphospace. We used PERMANOVA to test whether different habitat groups (terrestrial, semiaquatic, pelagic) are significantly separated from each other in the PCA morphospace using the pairwiseAdonis() function in vegan 2.5–3 (41). We calculated the mean shape for each habitat group in morphospace, along with the extreme shapes on the ends of each PC axis. We also performed a canonical variate analysis in Morpho 2.6 (42) to test the ability of the PC scores to assign individuals to known ecological categories.

Phylogenetic Comparative Methods. For the following phylogenetic methods, we utilized a consensus phylogeny of Crocodylomorpha based on the latest iteration of the Crocodylomorph SuperMatrix Project (43–45). The relationships of the species in our dataset are generally well resolved, but a few taxa are labile in recent phylogenetic analyses. Thus, as a sensitivity analysis, we repeated phylogenetic methods on a set of alternative phylogenies. The results were generally identical to the results gleaned from our consensus phylogeny, and we report the details in the *SI Appendix*. In all phylogenetic comparative analyses, the trees were time scaled using strap 1.4 (46) and zero-length branches were extended using the "equal" method (47).

We tested for phylogenetic signal in the PC scores with Pagel's lambda (λ), using phytools 0.6 in R (48). A λ value close to 1.0 indicates strong phylogenetic signal, with correlation between species equal to the Brownian motion expectation that phylogeny alone can explain trait changes (49), whereas values close to zero indicate no such phylogenetic correlation between species. The λ values are associated with a P value, denoting significance or nonsignificance.

We tested the correlations of labyrinth shape, labyrinth size, and habitat, using phylogenetic generalized least square regression in the R package nlme 3.1 (50), which accounts for the nonindependence of species due to phylogenetic relationships (51, 52). We performed three series of pGLS. First, we tested for correlations between raw PC scores and labyrinth size, as denoted by centroid size. Second, we tested for correlations between raw PC scores and habitat. Third, because the first pGLS found a significant relationship between labyrinth shape and size, we calculated residuals of raw PC scores vs. size, and then used the residuals in a further pGLS to test the relationship between size-corrected PC scores and habitat. We experimented with allowing the strength of phylogenetic signal (λ) to vary as a free parameter, but set $\lambda = 1.0$ (equivalent to pGLS assuming Brownian motion) because Pagel's lambda indicated a strong phylogenetic signal (see above and *SI Appendix*, Table S7).

We optimized PC scores as a continuous variable onto the phylogeny, in order to predict ancestral states for major clades and assess evolutionary trends (Fig. 5). Optimizations were performed using maximum likelihood using the fastAnc() function in phytools 0.6 (*SI Appendix*, Figs. S2–S4).

We fitted five standard models of trait evolution to the PC scores on the phylogeny: Brownian motion, Ornstein–Uhlenbeck (OU), early burst, Brownian motion with directional trend, and Lambda (Pagel). The fit of each model was assessed with maximum likelihood and the best supported model was determined by the lowest AICc score, using the R package geiger 2.0.6.2 (53). Further information on the mathematical properties of each model can be found in refs. 54–59. We recognize that interpretation of OU models can be complex and sometimes mimic other models (60), but include them here for completeness.

Testing whether certain portions of the phylogeny have variable rates of labyrinth shape evolution is challenging, because PC scores and continuous data present problems compared to discrete characters (61). To visualize rates of evolution, we used phytools 0.6 to plot a phylogeny in which the x axis is scaled to time and the y axis to PC1 value. The slopes of individual branches give an indication of which parts of the tree underwent faster or slower rates of shape evolution. We emphasize that this is a visual method and not a statistical test.

Cochlear Duct Measurements. We did not use 3D landmarks to quantify the shape of the cochlear duct, because the distal end is difficult to discern in CT scans, as is often not enclosed by bone. This issue also characterizes other reptile groups (21). Given these uncertainties, we favored a straightforward approach of measuring minimum cochlear duct length and using pGLS to test for correlation with specimen size. Developing a proxy for specimen size is challenging. Most of the specimens we CT scanned are skulls (often partial skulls) not associated with the postcranial bones needed to robustly estimate body mass or length. Other authors (9) have used skull length as a proxy for head size (either as a proxy for body size or to directly examine the relationship between labyrinth shape and head size), but this too is difficult for crocodylomorphs because snout length and skull proportions vary drastically within the group (62). Thus, in our cochlear duct length regression, we used the distance between the vestibules of the right and left labyrinths as a measure of specimen size, as head width is highly correlated with measures of body size in extant species (63). We realize, however, that this is a nuanced measure of specimen size, which is why we did not use it more extensively to represent specimen/head/body size to test for relationships with labyrinth size, shape, and linear measurements, as other authors have done (e.g., refs. 6 and 9).

Data Availability. The data for all 32 endosseous labyrinth models has been uploaded to Morphosource (https://www.morphosource.org/) and can be accessed here: https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/952.

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Supplementary Information for:

Inner ear sensory system changes as extinct crocodylomorphs transitioned from land to water

Julia A. Schwab[a,*], Mark T. Young[a], James M. Neenan[b], Stig A. Walsh[a,c], Lawrence M. Witmer[d], Yanina Herrera[e], Ronan Allain[f], Christopher A. Brochu[g], Jonah N. Choiniere[h], James M. Clark[i], Kathleen N. Dollman[h,j], Steve Etches[k], Guido Fritsch[l], Paul M. Gignac[m], Alexander Ruebenstahl[n], Sven Sachs[o], Alan H. Turner[p], Patrick Vignaud[q], Eric W. Wilberg[p], Xu Xing[r], Lindsay E. Zanno[s,t] & Stephen L. Brusatte[a,c]

[a]School of GeoSciences, Grant Institute, James Hutton Road, The King's Buildings, University of Edinburgh, Edinburgh, EH9 3FE, UK; [b]Oxford University Museum of Natural History, Oxford, OX1 3PW, United Kingdom; [c] Department of Natural Sciences, National Museum of Scotland, National Museum of Scotland, Chambers Street, Edinburgh, EH 1 1JF, UK; [d]Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Ohio University, Athens, Ohio 45701, USA; [e]Consejo Nacional de Investigaciones Científicas y Técnicas, División Paleontología Vertebrados, Museo de La Plata, FCNyM, UNLPNational University of La Plata, La Plata, Argentina; [f] Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements, Muséum National d'Histoire Naturelle, CP 38, 8 rue Buffon, 75005 Paris, France; [g]Department of Earth and Environmental Sciences, University of Iowa, Iowa City, Iowa 52242, USA; [h]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg 2000, South Africa; [i]Department of Biological Sciences, George Washington University, Washington DC 20052, USA; [j]School of Geosciences, University of the Witwatersrand, Johannesburg 2000, South Africa;

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[k]Museum of Jurassic Marine Life, Kimmeridge, BH20 5PE, UK; [l]Department of Reproduction Management, Leibniz Institute for Zoo and Wildlife Research, 10315 Berlin, Germany; [m]Department of Anatomy and Cell Biology, Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma 74107, USA; [n]Department of Geology and Geophysics, Yale University, New Haven, CT 06511, USA; [o]Abteilung Geowissenschaften, Naturkunde-Museum Bielefeld, Naturkunde-Museum Bielefeld, Abteilung Geowissenschaften, Adenauerplatz 2, 33602 Bielefeld, Germany; [p]Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794, USA; [q] Laboratoire de Paléontologie, Evolution, Paléoécosystèmes et Paléoprimatologie, CNRS UMR 7262, Department of Geosciences, University of Poitiers, France; [r]Institute of Vertebrate Paleontology & Paleoanthropology, Chinese Academy of Sciences, Beijing, China; [s]Paleontology, North Carolina Museum of Natural Sciences, Raleigh, NC 27601, USA; [t]Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695, USA

* Correspondence: julia.schwab@ed.ac.uk

1. Specimens examined

2. Geometric morphometric analysis

3. Principal component analysis

4. Morphospace clustering analysis

5. Canonical variate analysis

6. Phylogenies used for phylogenetic comparative methods

7. Pagel's Lambda analysis

8. pGLS regressions

9. Labyrinth character optimization on phylogeny

10. Evolutionary model fitting

11. Evolutionary rates

12. Cochlear measurements

13. Inclusion of *Crocodylus porosus* juvenile

14. Left-right ear asymmetry

15. Supplementary References

1. Specimens Examined

Table S1. Detailed information on the specimens we scanned; their museum specimen numbers, ages, and CT scanning parameters. The abbreviations are the notions used in the Figures in the main text and the Supplementary Tables.

Taxa	ID	Abbr.	voxel size (mm)	facility
Junggarsuchus sloani	IVPP V14010	JuSl	0.13	Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) of the Chinese Academy of Sciences
Undescribed sphenosuchian	NCSM 21722	UnSp	0.039327	Nikon XTH 225 ST µCT scanner, Shared Materials Instrumentation Facility, Duke University, Durham, NC
Eopneumatosuchus colberti	MNA V2460	EoCo	0.092	General Electric eXplore Locus in vivo Small Animal µCT scanner, Ohio University µCT Scanning Facility
Protosuchus haughtoni	BP/1/4770	PrHa	0.0538	Nikon Metrology XTH 225/320 LC dual source industrial CT system, University of the Witwatersrand, Johannesburg
'Steneosaurus' cf. gracilirostris	NHMUK PV OR 33095	StGr	0.089	Nikon XT H 225S CTsystem, Natural History Museum, London
Steneosaurus bollensis	BSPG 1984 I258	StBo1	0.043	Nanotom Scan, Zoologische Staatsammlung München
Steneosaurus bollensis	MCZ 1063	StBo2	0.404297	micro CT scanner at the American Museum of Natural History
Steneosaurus pictaviensis	LPP.M.35	StPi	0.140036	RX-solutions EasyTom XL Duo, Plateforme de Microtomographie, University of Poitiers
Pelagosaurus typus	NHMUK PV OR 32599	PtTy	0.098627983	Nikon XT H 225S CTsystem, Natural History Museum, London
Metriorhynchus superciliosus	MNHN.F RJN 256	MeSu1	0.10358673X 0.265	Muséum national d'Histoire naturelle, Paris, France
Metriorhynchus superciliosus	NHMUK PV R11999	MeSu2	0.12	µ-VIS X-Ray Imaging Centre, University of Southampton
Metriorhynchus superciliosus	AMNH 997	MeSu3	0.14177665	micro CT scanner at the American Museum of Natural History
Cricosaurus araucanensis	MLP 72-IV-7-1	CrAu1	0.448X0.448	SNSB X-ray facility
Cricosaurus araucanensis	MLP 76-XI-19-1	CrAu2	0.39	SNSB X-ray facility
Cricosaurus schroederi	MMGLV #	CrSc	0.5	Leibniz Institute for Zoo and Wildlife Research, Berlin
'Metriorhynchus' brachyrhynchus	NHMUK PV OR 32618	MeBr	0.0546	µ-VIS X-Ray Imaging Centre, University of Southampton
Torvoneustes coryphaeus	MJML K1863	ToCo	0.2267	µ-VIS X-Ray Imaging Centre, University of Southampton
Shamosuchus djadochtaensis	IGM 100-1195	ShDj	0.011260684	micro CT scanner at the American Museum of Natural History
Alligator mississippiensis	USNM 211232	AlMi4	0.625	Ohio Health O'Bleness Hospital
Alligator mississippiensis	USNM 211233	AlMi5	0.625	Ohio Health O'Bleness Hospital
Alligator mississippiensis	OUVC 9761	AlMi6	0.5X1	Ohio Health O'Bleness Hospital
Caiman crocodilus	FMNH 73711	CaCr	0.065X0.142	University of Texas, Austin
Crocodylus acutus	FMNH 59071	CrAc	0.625	Ohio Health O'Bleness Hospital
Crocodylus johnstoni	TMM M-6807	CrJo	0.223	University of Texas High-Resolution X-ray CT Facility
Crocodylus moreletii	TMM M-4980	CrMo	0.1904X0.5	High-Resolution X-ray CT Facility, University of Texas
Crocodylus rhombifer	MNB AB50.0171	CrRh	0.1748X0.5	High-Resolution X-ray CT Facility, University of Texas
Mecistops cataphractus	TMM M-3529	CrCa	0.165X0.5	High-Resolution X-ray CT Facility, University of Texas
Gavialis gangeticus	UF-herp-118998	GaGa2	0.14654672	Florida Museum of Natural History Herpetology
Gavialis gangeticus	TMM M-5490	GaGa1	0.228	High-Resolution X-ray CT Facility, University of Texas
Osteolaemus tetraspis	FMNH 98936	OsTe	0.0546875X0 .1108	High-Resolution X-ray CT Facility, University of Texas
Tomistoma schlegelii	TMM M-6342	ToSc1	0.165X0.46	High-Resolution X-ray CT Facility, University of Texas
Tomistoma schlegelii	USNM 211322	ToSc2	0.625	Ohio Health O'Bleness Hospital

Table S2. Information of the habitat (ecomorphology) and age of each species used in our sample.

Taxa	habitat	Age	Reason	Reference
Junggarsuchus sloani	terrestrial	M. Jurassic	Inferred, from deposit, and limb-dimensions and cranial shape	1
Undescribed sphenosuchian	terrestrial	Carnian	Inferred, from deposit, and limb-dimensions and cranial shape	NCSM 21722
Eopneumatosuchus colberti	semiaquatic	Sinemurian*	Inferred, from deposit and cranial shape	2
Protosuchus haughtoni	terrestrial	Hettangian	Inferred, from post-cranial skeleton	3
'Steneosaurus' gracilirostris	semiaquatic	Toarcian	Inferred, from a marine deposit, but has extant-like limbs, and has osteoderms	4
Steneosaurus bollensis	semiaquatic	Toarcian	Inferred, from a marine deposit, but has extant-like limbs, and has osteoderms	4
Steneosaurus pictaviensis	semiaquatic	Toarcian	Inferred, from a marine deposit and is a teleosaurid	5
Pelagosaurus typus	semiaquatic	Toarcian	Inferred, from a marine deposit, but has extant-like limbs, and has osteoderms	4
Metriorhynchus superciliosus	pelagic	Callovian	Inferred, marine deposit, has flippers and a tail-fin	5
Cricosaurus araucanensis	pelagic	Tithonian	Inferred, marine deposit, has flippers and a tail-fin	6, 7
Cricosaurus schroederi	pelagic	Valanginian	Inferred, marine deposit and is a metriorhynchid	8
'Metriorhynchus' brachyrhynchus	pelagic	Callovian	Inferred, marine deposit and has a tail-fin	5
Torvoneustes coryphaeus	pelagic	Kimmeridgian	Inferred, marine deposit and is a metriorhynchid	9
Shamosuchus djadochtaensis	semiaquatic	L. Cretaceous	Inferred, based on post-cranial anatomy	10
Alligator mississippiensis	semiaquatic	Recent	extant, observed	e.g. 11
Caiman crocodilus	semiaquatic	Recent	extant, observed	e.g. 11
Crocodylus acutus	semiaquatic	Recent	extant, observed	e.g. 11
Crocodylus johnstoni	semiaquatic	Recent	extant, observed	e.g. 11
Crocodylus moreletii	semiaquatic	Recent	extant, observed	e.g. 11
Crocodylus rhombifer	semiaquatic	Recent	extant, observed	e.g. 11
Mecistops cataphractus	semiaquatic	Recent	extant, observed	e.g. 11
Gavialis gangeticus	semiaquatic	Recent	extant, observed	e.g. 11
Osteolaemus tetraspis	semiaquatic	Recent	extant, observed	e.g. 11
Tomistoma schlegelii	semiaquatic	Recent	extant, observed	e.g. 11

*The age of the Kayenta Formation may be Pliensbachian-Toarcian, as has been presented in a conference abstract (Marsh et al., 2014, Society of Vertebrate Paleontology Annual Meeting).

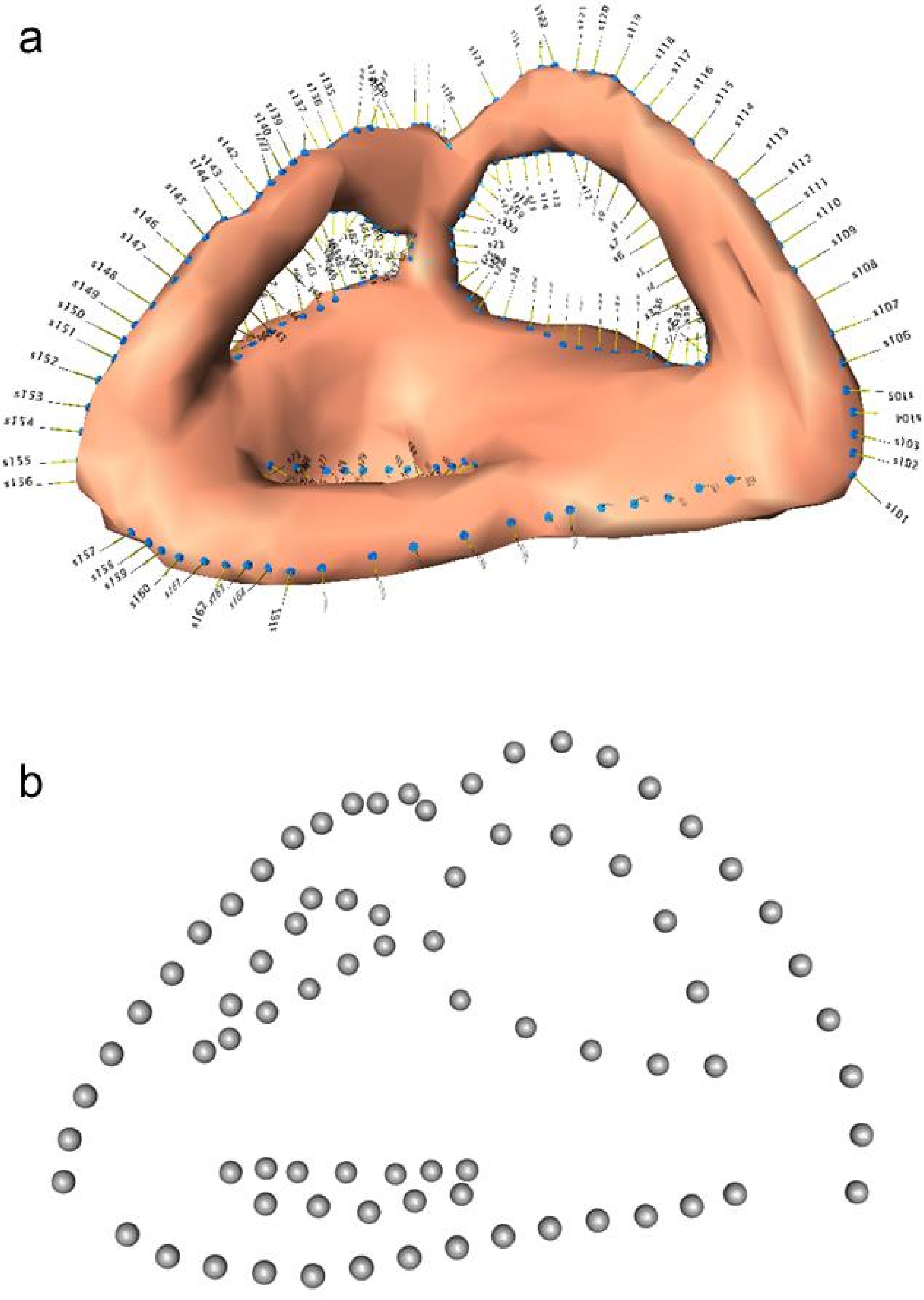

Fig. S1. Landmark placing on the right labyrinth of *Metriorhynchus supercilious* (NHMUK PV R11999). a, landmark placement in the IDAV Landmark software; b, evenly spaced semilandmarks on the three semicircular canals, 11 on the internal surface and 12 on the external surface (see methods section for details).

3. Principal component analysis

Table S3. Results of the Principal Component Analysis. PCA coordinates for the first 31 PC axes.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
AlMi4	-0.025	-0.024	0.035	-0.038	0.013	-0.002	0.009	0.000
AlMi5	-0.022	-0.050	0.025	-0.044	0.000	-0.007	0.010	-0.003
CaCr	-0.051	-0.043	-0.011	-0.037	-0.025	-0.001	0.010	0.028
CrAc	-0.016	-0.056	0.015	0.025	0.022	-0.030	-0.020	-0.006
CrMo	-0.061	-0.021	-0.019	0.013	0.011	0.012	-0.014	-0.004
CrJo	-0.059	-0.003	-0.004	-0.059	0.012	0.000	0.012	-0.028
CrCa	-0.014	-0.085	0.022	0.047	0.011	-0.023	0.005	-0.004
OsTe	-0.030	-0.002	0.049	-0.003	-0.035	-0.044	-0.012	0.034
GaGa1	-0.028	-0.056	0.054	-0.006	0.004	-0.008	0.005	0.004
ToSc1	-0.051	-0.069	0.013	0.027	0.013	0.014	-0.007	0.014
ToSc2	-0.022	-0.071	0.035	0.025	0.009	0.027	-0.017	0.021
GaGa2	-0.032	-0.010	0.058	-0.023	0.037	0.028	-0.019	0.005
AlMi6	-0.038	0.013	0.028	-0.045	0.001	-0.011	0.042	-0.030
CrRh	-0.033	-0.053	0.002	0.039	0.001	0.036	0.001	-0.005
PeTy	0.014	0.084	0.028	0.006	-0.043	0.010	-0.016	-0.002
JuSl	-0.115	0.019	-0.064	0.031	-0.033	-0.056	0.012	0.002
MeSu2	0.057	0.015	-0.016	-0.041	0.038	0.003	0.048	0.032
StBo1	0.011	0.056	0.058	0.023	-0.011	0.013	-0.017	0.013
CrSc	0.104	-0.092	-0.062	-0.005	-0.077	0.060	-0.011	-0.047
EoCo	-0.048	0.066	-0.030	0.009	0.014	0.046	-0.020	-0.021
UnSp	-0.087	0.039	-0.065	-0.008	-0.081	-0.015	0.016	0.012
MeSu1	0.038	0.064	-0.037	-0.004	0.001	0.031	0.031	0.033
StBo2	0.014	0.097	0.059	0.018	-0.012	-0.024	0.006	-0.056
StGr	0.059	0.066	0.029	0.051	-0.018	0.001	0.005	0.001
MeBr	0.072	0.063	-0.009	0.000	0.040	-0.006	0.049	0.005
MeSu3	0.028	0.039	-0.022	0.005	-0.004	0.041	0.029	0.031
CrAu1	0.136	0.008	0.021	-0.074	-0.026	-0.023	-0.073	0.037
PrHa	-0.071	0.101	-0.096	-0.005	0.060	-0.002	-0.071	-0.005
ToCo	0.115	-0.065	-0.110	0.057	0.025	-0.042	0.005	0.017
CrAu2	0.087	-0.028	-0.032	-0.047	0.019	-0.044	-0.003	-0.052
StPi	0.073	0.031	0.068	0.069	0.005	-0.011	0.002	-0.013
ShDj	-0.003	-0.035	-0.025	-0.007	0.027	0.025	0.002	-0.016

	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16
AlMi4	0.028	-0.006	-0.019	0.014	-0.035	-0.013	-0.002	0.039
AlMi5	0.016	-0.002	0.026	-0.018	-0.009	-0.018	0.008	0.008
CaCr	0.008	-0.005	-0.012	-0.020	0.014	0.003	-0.024	0.008
CrAc	0.042	-0.010	0.014	-0.023	0.040	0.005	0.015	0.002
CrMo	-0.023	-0.018	-0.003	-0.014	0.011	0.015	0.006	0.005
CrJo	-0.030	-0.022	-0.008	0.022	-0.004	0.008	0.026	-0.013
CrCa	-0.032	-0.010	0.024	0.005	0.012	-0.010	0.023	0.001
OsTe	0.012	-0.040	0.003	-0.001	-0.022	0.034	-0.015	-0.012
GaGa1	0.014	0.018	0.010	0.004	-0.002	0.007	-0.001	0.006
ToSc1	-0.013	0.017	0.005	0.006	0.010	-0.017	-0.003	-0.005
ToSc2	0.032	0.013	0.006	0.024	-0.020	-0.036	-0.005	-0.026
GaGa2	0.008	0.028	-0.012	-0.011	0.014	0.026	-0.015	-0.013
AlMi6	-0.002	-0.034	-0.017	-0.022	0.009	-0.024	-0.022	-0.017
CrRh	-0.025	-0.015	-0.004	0.017	-0.006	0.018	0.004	0.024
PeTy	-0.017	-0.014	0.002	-0.011	0.007	-0.022	-0.013	0.015
JuSl	0.005	0.045	-0.053	-0.014	-0.010	-0.003	0.027	-0.004
MeSu2	-0.023	0.009	0.024	-0.006	-0.015	0.008	0.026	0.009
StBo1	-0.016	0.021	0.007	-0.017	-0.030	0.015	0.001	-0.004
CrSc	0.036	-0.009	-0.008	-0.010	-0.006	0.013	0.018	-0.003
EoCo	-0.007	0.001	0.004	-0.006	-0.030	-0.008	-0.005	-0.015
UnSp	-0.007	0.005	0.041	0.044	0.013	0.003	-0.012	-0.005
MeSu1	0.028	0.012	-0.013	0.012	0.026	-0.010	-0.006	0.017
StBo2	0.006	0.012	0.013	-0.009	-0.002	0.012	-0.003	0.008
StGr	-0.022	-0.011	0.002	-0.022	0.005	-0.032	0.012	-0.002
MeBr	0.033	-0.024	-0.013	0.022	0.002	0.006	0.016	-0.021
MeSu3	-0.001	0.020	0.018	-0.025	0.011	0.017	0.000	-0.007
CrAu1	-0.025	0.002	-0.021	0.011	0.012	-0.008	0.017	-0.005
PrHa	0.027	-0.018	0.015	0.004	0.003	-0.002	0.003	0.008
ToCo	-0.010	-0.016	-0.002	-0.015	-0.025	0.001	-0.028	-0.001
CrAu2	-0.005	0.045	0.023	0.009	0.000	-0.001	-0.020	0.000
StPi	0.011	0.001	-0.020	0.040	0.012	0.011	-0.006	0.005
ShDj	-0.048	0.004	-0.031	0.011	0.016	0.002	-0.023	0.000

	PC17	PC18	PC19	PC20	PC21	PC22	PC23	PC24
AlMi4	-0.013	0.000	-0.005	-0.001	-0.005	0.018	0.002	0.002
AlMi5	-0.012	0.000	0.018	0.009	-0.003	-0.006	-0.015	-0.015
CaCr	-0.011	-0.008	0.008	0.001	0.033	-0.004	0.002	0.011
CrAc	-0.007	0.007	0.006	-0.007	-0.002	0.007	-0.009	0.013
CrMo	-0.011	0.010	0.004	-0.004	0.004	0.001	0.009	-0.019
CrJo	-0.004	-0.002	0.016	0.011	0.001	-0.011	0.011	0.017
CrCa	0.012	-0.011	-0.003	-0.002	0.003	0.015	0.011	0.000
OsTe	0.027	0.014	-0.008	-0.008	-0.002	-0.001	-0.005	0.001
GaGa1	0.012	-0.003	0.002	0.004	-0.002	-0.015	-0.002	-0.009
ToSc1	-0.007	0.001	-0.023	-0.023	0.005	-0.008	0.000	0.002
ToSc2	-0.001	0.006	0.004	0.004	-0.008	-0.009	0.005	0.007
GaGa2	0.005	-0.029	-0.014	0.022	-0.003	0.005	0.003	-0.006
AlMi6	0.008	0.003	-0.004	-0.003	-0.014	0.012	0.010	-0.004
CrRh	0.014	0.004	0.011	0.001	-0.003	-0.013	0.000	-0.007
PeTy	0.006	0.002	-0.009	0.013	-0.002	-0.014	-0.006	0.010
JuSl	0.007	0.002	0.000	0.004	-0.004	-0.001	-0.004	-0.001
MeSu2	0.011	-0.007	-0.020	-0.001	0.000	0.003	-0.009	0.010
StBo1	-0.026	0.021	-0.006	0.000	0.006	0.006	0.016	0.002
CrSc	0.002	-0.001	-0.015	0.002	0.000	0.002	0.001	0.001
EoCo	0.017	-0.015	0.019	-0.018	0.015	0.013	-0.013	-0.001
UnSp	-0.015	-0.009	-0.005	0.005	-0.004	0.010	-0.003	-0.005
MeSu1	0.021	0.000	0.007	-0.012	-0.002	-0.003	0.017	-0.003
StBo2	-0.012	-0.021	0.001	-0.021	-0.010	-0.015	0.003	0.003
StGr	0.006	0.002	-0.006	0.016	0.011	0.001	-0.003	-0.007
MeBr	-0.017	0.004	-0.009	-0.003	0.013	-0.010	-0.005	-0.012
MeSu3	-0.004	0.014	0.022	0.002	-0.017	0.006	-0.002	0.006
CrAu1	-0.004	-0.009	0.009	-0.011	-0.006	0.002	0.000	-0.006
PrHa	0.002	0.006	-0.011	0.009	-0.003	-0.002	0.003	0.001
ToCo	-0.011	-0.018	0.007	0.005	-0.008	-0.005	0.005	0.002
CrAu2	0.017	0.023	0.001	0.003	0.013	0.001	0.005	-0.003
StPi	0.000	0.001	0.013	0.011	0.005	0.014	-0.007	0.006
ShDj	-0.011	0.014	-0.009	-0.005	-0.010	0.000	-0.019	0.003

	PC25	PC26	PC27	PC28	PC29	PC30	PC31
AlMi4	-0.001	-0.002	-0.014	0.005	0.000	0.002	0.001
AlMi5	0.001	-0.003	0.010	-0.007	0.001	-0.010	0.008
CaCr	0.010	-0.001	0.002	0.001	-0.004	-0.003	-0.006
CrAc	-0.010	-0.004	0.000	0.001	0.010	0.008	-0.001
CrMo	-0.015	-0.005	-0.005	-0.008	-0.015	0.005	-0.002
CrJo	-0.004	-0.004	-0.002	0.005	0.000	0.002	0.008
CrCa	0.018	0.006	-0.007	-0.010	0.002	-0.004	0.001
OsTe	0.002	-0.008	-0.004	-0.001	-0.001	-0.004	0.005
GaGa1	0.010	0.015	0.003	0.007	-0.006	0.018	0.003
ToSc1	-0.010	0.007	-0.001	0.011	-0.003	-0.010	0.008
ToSc2	0.000	-0.010	-0.001	-0.007	-0.004	0.001	-0.009
GaGa2	-0.005	-0.005	-0.005	-0.001	0.005	-0.003	0.001
AlMi6	-0.002	0.009	0.011	0.004	0.000	-0.001	-0.005
CrRh	-0.004	0.000	0.004	0.006	0.013	-0.006	-0.011
PeTy	-0.010	0.015	-0.009	-0.012	0.002	0.001	0.001
JuSl	0.000	0.002	0.001	-0.002	0.001	-0.002	-0.002
MeSu2	-0.007	-0.003	0.010	-0.003	-0.006	0.002	-0.006
StBo1	0.002	0.004	0.012	-0.003	0.009	0.004	0.003
CrSc	0.003	0.001	0.003	0.000	-0.003	-0.001	0.002
EoCo	-0.004	0.004	-0.002	-0.001	0.003	0.005	0.002
UnSp	-0.003	-0.002	0.001	0.002	0.003	0.004	-0.001
MeSu1	0.000	-0.009	0.005	-0.006	0.004	0.002	0.008
StBo2	0.006	-0.009	-0.001	-0.001	-0.004	-0.002	-0.004
StGr	0.004	-0.017	-0.003	0.014	-0.001	0.003	0.001
MeBr	0.003	0.008	-0.009	-0.003	0.007	-0.001	-0.003
MeSu3	0.006	0.007	-0.013	0.007	-0.006	-0.006	-0.001
CrAu1	0.000	0.003	0.001	0.002	0.001	0.000	-0.004
PrHa	0.011	0.003	0.006	0.003	-0.004	-0.004	-0.001
ToCo	-0.005	0.002	0.001	0.001	0.001	0.002	0.003
CrAu2	-0.005	-0.002	-0.006	0.000	0.002	-0.003	-0.002
StPi	-0.005	0.006	0.011	0.000	-0.011	-0.005	0.002
ShDj	0.014	-0.009	0.001	-0.006	0.002	0.005	0.003

Table S4. Results of the Principal Component Analysis. Variance (%) and Cumulative Proportion (%) for the first 31 principal component axes.

	Variance (%)	Cumulative Proportion (%)
PC1	22.269	22.269
PC2	18.443	40.713
PC3	12.386	53.099
PC4	7.336	60.435
PC5	5.641	66.076
PC6	4.605	70.681
PC7	4.183	74.864
PC8	3.487	78.351
PC9	3.100	81.450
PC10	2.368	83.819
PC11	2.124	85.943
PC12	1.951	87.894
PC13	1.702	89.596
PC14	1.525	91.121
PC15	1.454	92.575
PC16	1.006	93.581
PC17	0.918	94.498
PC18	0.769	95.267
PC19	0.748	96.015
PC20	0.597	96.612
PC21	0.540	97.152
PC22	0.483	97.635
PC23	0.409	98.044
PC24	0.374	98.418
PC25	0.325	98.743
PC26	0.309	99.053
PC27	0.262	99.315
PC28	0.197	99.511
PC29	0.196	99.707
PC30	0.167	99.874
PC31	0.126	100.000

4. Morphospace clustering analysis

Table S5. Results of the PERMANOVA, to test if the three habitat groups are statistically significantly different form each other.

pairs	F Model	R2	p value	p adjusted
semiaquatic vs. terrestrial	4.875	0.223	0.002	0.003
semiaquatic vs. pelagic	5.302	0.218	0.002	0.003
terrestrial vs. pelagic	4.543	0.431	0.012	0.012

5. Canonical variate analysis

Table S6. Results for the canonical variate analysis (CVA). Showing the classification of the three habitat groups (pelagic, semiaquatic, terrestrial) with an overall classification accuracy of 100%.

	pelagic	semiaquatic	terrestrial
pelagic	100	0	0
semiaquatic	0	100	0
terrestrial	0	0	100

overall classification accuracy: 100 %

	CV 1	CV 2
AlMi4	-1.033	0.846
AlMi5	-0.485	1.594
CaCr	-0.128	-0.364
CrAc	-2.027	0.536
CrMo	-3.402	0.029
CrJo	-2.502	-0.035
CrCa	-3.322	1.787
OsTe	-3.384	-0.204
GaGa1	-2.031	1.215
ToSc1	-2.747	0.397
ToSc2	-1.644	0.679
GaGa2	-2.243	2.108
AlMi6	-2.406	2.322
CrRh	-3.277	1.411
PeTy	-1.567	0.197
JuSl	-1.680	-7.193
MeSu2	5.803	1.926
StBo1	-1.803	1.280
CrSc	5.133	1.732
EoCo	-1.782	-1.412
UnSp	0.071	-7.272
MeSu1	5.550	-1.380
StBo2	-2.583	0.189
StGr	-0.300	2.021
MeBr	4.587	0.826
MeSu3	4.047	0.695
CrAu1	4.832	0.948
PrHa	-0.600	-6.291
ToCo	6.925	-0.480
CrAu2	5.415	-0.885
StPi	-1.109	1.514
ShDj	-0.307	1.266

6. Phylogenies used for phylogenetic comparative methods

The main phylogenetic framework used herein is based on the results from Young *et al*. (12). This dataset (the ‘H+Y dataset’) is the latest in the ongoing Crocodylomorph SuperMatrix Project, a continuously updated dataset investigating the evolutionary relationships of crocodylomorph archosaurs. It was first presented in Ristevski *et al*. (13), and has been subsequently updated (e.g. 14–17). It is one of three datasets that form the core of the Crocodylomorph SuperMatrix Project, the other two also being presented in a modified form in Ősi *et al*. (14).

However, there are some taxa we use in our datasets that are known to have differing positions phylogenetically. The first of which is *Eopneumatosuchus colberti*. It has been recovered as the basal-most thalattosuchian in the ‘H+Y dataset’. However, in Young *et al*. (12), the position of *Eopneumatosuchus* can change depending on use of implied weighting or using Bayesian methods. In those analyses, *Eopneumatosuchus* is recovered as the sister taxon to Shartegosuchoidea + Mesoeucrocodylia. To test whether this second possible position of *Eopneumatosuchus* alters our result, we ran a series of sensitivity analyses with *Eopneumatosuchus* placed as the sister taxon to Thalattosuchia + (*Shamosuchus* + Crocodylia).

The second species we ran sensitivity analyses on was *Pelagosaurus typus*. While the more recent and large-sampled thalattosuchians phylogenetic datasets recover *Pelagosaurus* as the basal-most member of Metriorhynchoidea (papers using the ‘H+Y’ dataset, 18), some earlier datasets and pre-phylogenetic opinions considered *Pelagosaurus* to be a teleosauroid (e.g. 4, 19; although see Buffetaut (20) for a metriorhynchid-like opinion). We tested this alternate position of *Pelagosaurus* to see if it impacted upon our results.

There are also some competing hypotheses for the relationships of extant crocodylians in our dataset. In particular, there is no consensus on whether *Osteolaemus tetraspis* is more closely related to *Mecistops* or *Crocodylus*, in either molecular or morphological phylogenies (21). Additionally, the position of *Gavialis gangeticus* differs between molecular and morphological datasets. Molecular datasets recover *Gavialis* as the sister taxon to *Tomistoma* (being within Crocodylidae) – a position the Young *et al*. (12) dataset also recovers (e.g. 21, 22). However, most morphology-only datasets recover *Gavialis* as the basal-most living species, being the sister taxon to Alligatoridae + Crocodylidae (for further analyses and discussion see 23). However, as these both concern small nuances of the relationships of extant crocodylians—all of which have semiaquatic-type ears—these rearrangements would not affect our results.

7. Pagel’s Lambda analysis

Table S7. Results for the phylogenetic influence tested with the Pagel's lambda tested for three different phylogenies: our primary phylogeny (first listed) and two alternative trees, for sensitivity analysis (see Section 6 above). 0 → no correlation between species; 1 → correlation between species equal to the Brownian expectation/the structure of the phylogeny alone can explain changes in traits.

Primary phylogeny

	lambda	logL	logL0	p value
PC1	0.99996	28.705	16.435	0.00000073
PC2	0.69646	31.134	22.893	0.00004913
PC3	0.99993	31.597	18.921	0.00000048

***Eopneumatosuchus colberti* placed as the sister taxon to Thalattosuchia + (*Shamosuchus* + Crocodylia)**

	lambda	logL	logL0	p value
PC1	0.77400	27.769	16.506	2E-06
PC2	0.65831	30.953	22.949	6E-05
PC3	0.99993	32.243	19.051	3E-07

***Pelagosaurus typus* positioned as a teleosauroid**

	lambda	logL	logL0	p value
PC1	0.77400	27.769	16.506	2E-06
PC2	0.65831	30.953	22.949	6E-05
PC3	0.99993	32.243	19.051	3E-07

8. pGLS regressions

Table S8. Results for Ordinary least squares (OLS) and phylogenetic generalised least squares (pGLS), using our primary phylogeny. First correlating the raw PC scores and centroid size (labyrinth size); second, correlating the raw PC scores and habitat; third correlating the residuals from the PC scores and centroid size with habitat.

Primary phylogeny

Model	Type	AICc	intercept	p value	slope	p value	R2
PC1~centroid size	OLS	-61.319	-4.706	0.111	4.662	0.112	0.071
	pGLS	-78.643	-5.078	0.034	4.993	0.035	0.111
PC2~centroid size	OLS	-64.049	-0.531	0.845	0.527	0.845	-0.044
	pGLS	-76.99	8.307	0.002	-8.208	0.002	0.418
PC3~centroid size	OLS	-88.324	7.205	0.0002	-7.149	0.0002	0.451
	pGLS	-81.948	5.787	0.011	-5.751	0.011	0.315
PC1~pelagic	OLS	-78.162	-0.028	0.012	0.116	2.65e-05	0.559
	pGLS	-70.159	-0.035	0.370	0.083	0.042	0.385
PC2~pelagic	OLS	-64.329	0.0033	0.81	-0.016	0.59	0.013
	pGLS	-60.347	0.002	0.974	-0.060	0.222	-0.165
PC3~pelagic	OLS	-76.934	0.0035	0.734	-0.046	0.056	0.156
	pGLS	-68.628	-0.031	0.445	-0.050	0.226	-0.193
PC1.residuals~pelagic	OLS	-72.660	-0.019	0.110	0.089	0.00143	0.377
	pGLS	-59.892	0.018	0.703	0.089	0.0005	-0.061
PC2.residuals~pelagic	OLS	-64.505	0.004	0.769	-0.019	0.522	0.019
	pGLS	-49.136	-0.038	0.522	0.007	0.801	-0.861
PC3.residuals~pelagic	OLS	-88.418	0.001	0.895	-0.005	0.773	0.004
	pGLS	-68.295	0.003	0.940	0.008	0.847	-1.304

Table S9. Results for phylogenetic generalised least squares (pGLS), using the two alternative phylogenies. First correlating the raw PC scores and centroid size (labyrinth size); second, correlating the raw PC scores and habitat; third correlating the residuals from the PC scores and centroid size with habitat.

***Eopneumatosuchus colberti* placed as the sister taxon to Thalattosuchia + (*Shamosuchus* + Crocodylia)**

Model	Type	AICc	intercept	p value	slope	p value	R2
PC1~centroid size	pGLS	-76.721	-4.918	0.069	4.838	0.069	0.532
PC2~centroid size	pGLS	-77.183	7.885	0.005	-7.790	0.005	0.422
PC3~centroid size	pGLS	-83.430	5.577	0.019	-5.544	0.019	0.356
PC1~pelagic	pGLS	-70.159	-0.035	0.370	0.083	0.042	0.385
PC2~pelagic	pGLS	-60.347	0.002	0.974	-0.060	0.222	-0.165
PC3~pelagic	pGLS	-68.628	-0.031	0.445	-0.049	0.226	-0.192
PC1.residuals~pelagic	pGLS	-55.657	0.009	0.859	0.092	0.001	-0.266
PC2.residuals~pelagic	pGLS	-47.624	-0.032	0.594	0.013	0.666	-0.983
PC3.residuals~pelagic	pGLS	-70.355	0.003	0.939	0.011	0.544	-1.114

***Pelagosaurus typus* positioned as a teleosauroid**

Model	Type	AICc	intercept	p value	slope	p value	R2
PC1~centroid size	pGLS	-80.371	-5.328	0.023	5.230	0.024	0.598
PC2~centroid size	pGLS	-77.218	8.343	0.002	-8.242	0.002	0.423
PC3~centroid size	pGLS	-82.687	5.655	0.012	-5.627	0.012	0.336
PC1~pelagic	pGLS	-71.177	-0.042	0.279	0.078	0.041	0.410
PC2~pelagic	pGLS	-60.562	0.0002	0.997	-0.059	0.214	-0.154
PC3~pelagic	pGLS	-69.841	-0.038	0.345	-0.052	0.174	-0.134
PC1.residuals~pelagic	pGLS	-55.436	0.008	0.887	0.089	0.001	-0.278
PC2.residuals~pelagic	pGLS	-48.265	-0.039	0.536	0.007	0.809	-0.930
PC3.residuals~pelagic	pGLS	-70.095	0.004	0.916	0.005	0.782	-1.137

9. Labyrinth character optimization on phylogeny

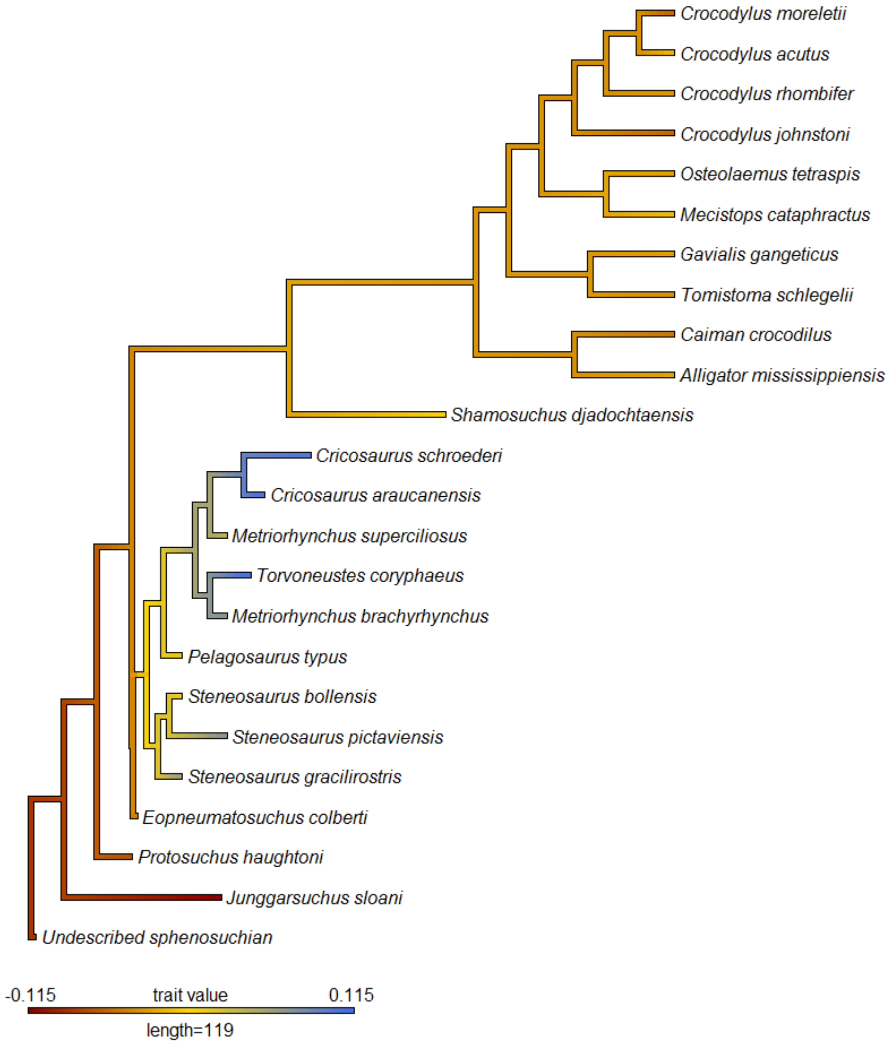

Fig. S2. PC1 scores optimized on our primary phylogeny to predict ancestral states for the major clades and assess evolutionary trends.

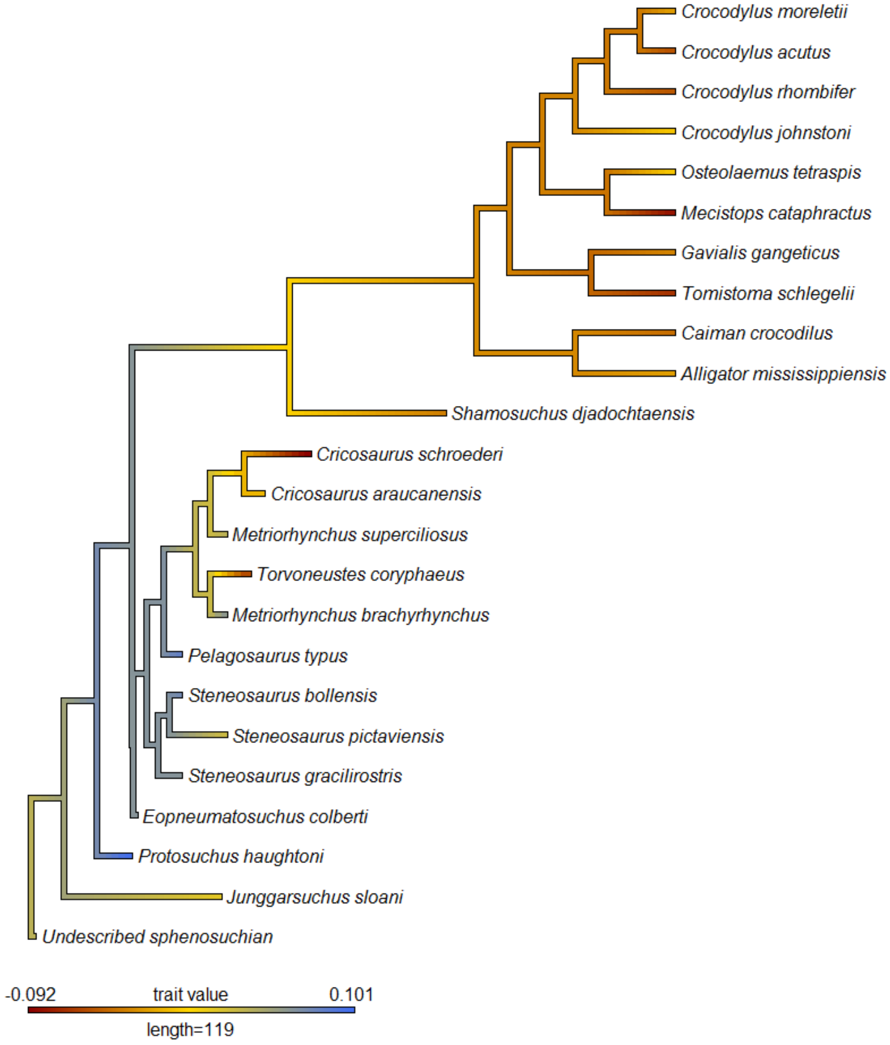

Fig. S3. PC2 scores optimized on our primary phylogeny to predict ancestral states for the major clades and assess evolutionary trends.

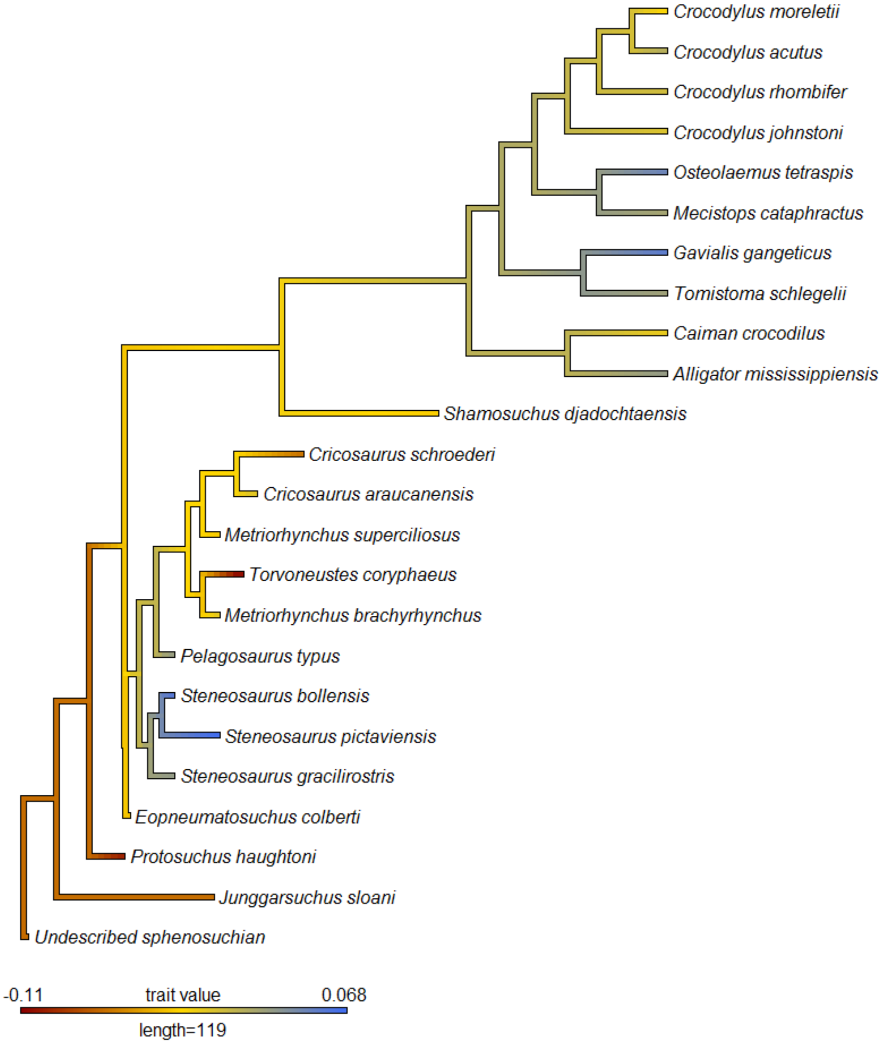

Fig. S4. PC3 scores optimized on our primary phylogeny to predict ancestral states for the major clades and assess evolutionary trends.

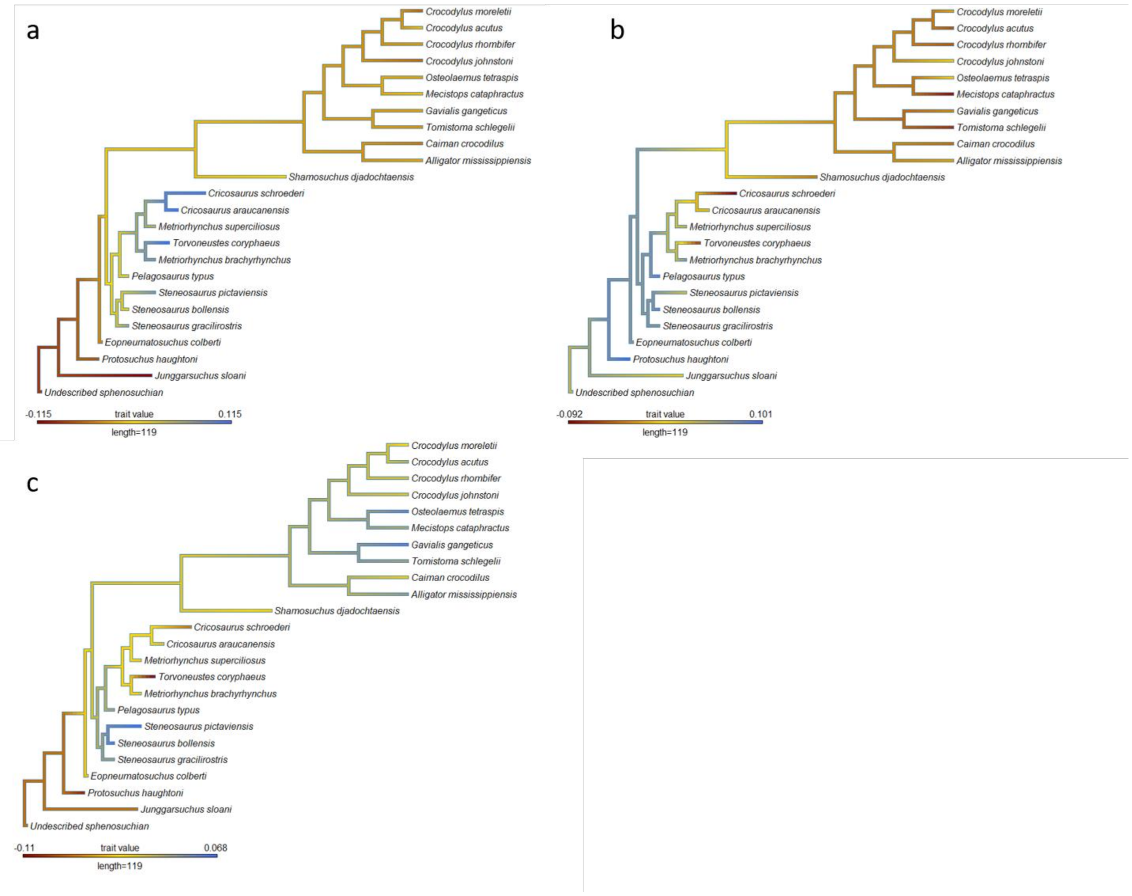

Fig. S5. PC scores of the first three principal components, optimized on the phylogeny with *Eopneumatosuchus colberti* placed as the sister taxon to Thalattosuchia + (*Shamosuchus* + Crocodylia), to predict ancestral states for the major clades and assess evolutionary trends. a, PC1; b, PC2; c, PC3.

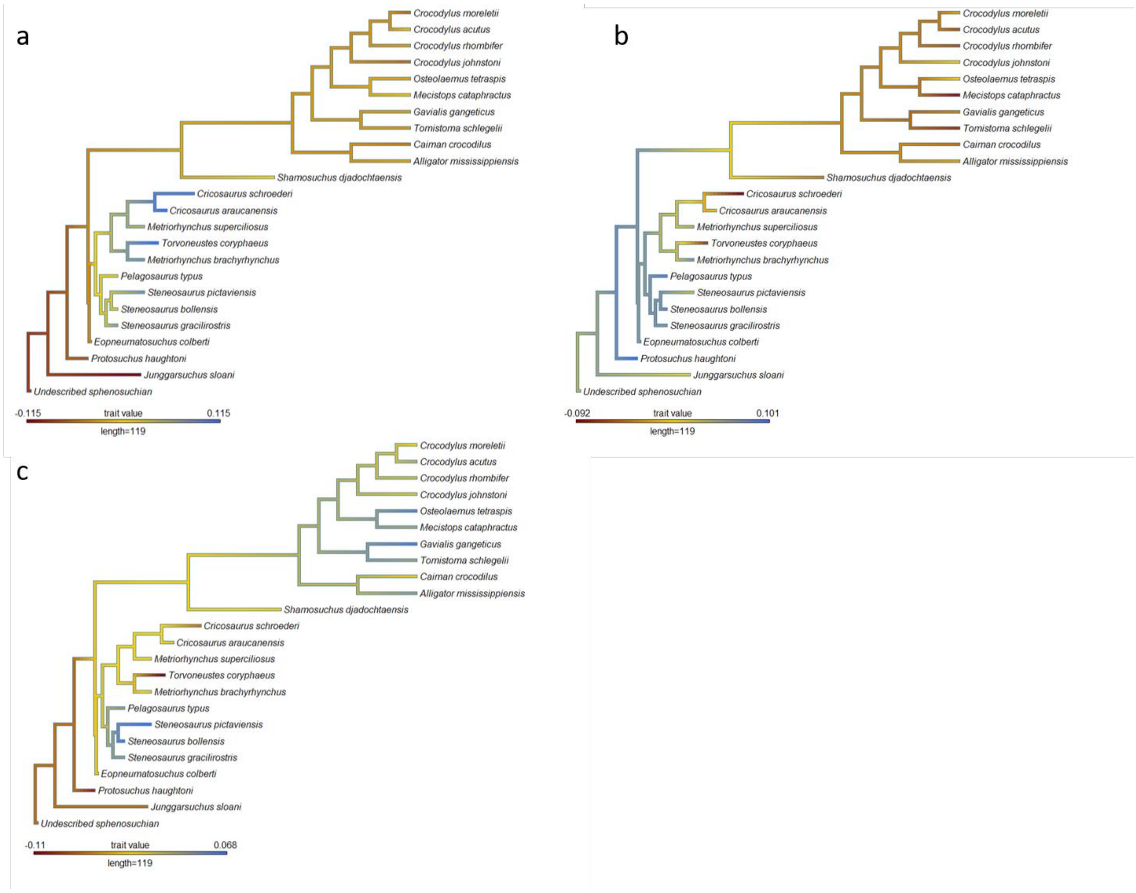

Fig. S6. PC3 scores optimized on the phylogeny with *Pelagosaurus typus* positioned as a teleosauroid, to predict ancestral states for the major clades and assess evolutionary trends. a, PC1; b, PC2; c, PC3.

10. Evolutionary model fitting

Table S10. Five standard models fitted on the first three principal component axes showing the AIC scores. The models are: BM (Brownian motion), OU (Ornstein-Uhlenbeck), EB (Early-burst), trend (Brownian motion with trend) and lambda (Pagel).

Primary phylogeny

	BM	OU	EB	trend	lambda
PC1	-74.485	-71.856	-79.996	-63.232	-71.856
PC2	-69.521	-68.680	-69.084	-64.574	-67.822
PC3	-74.591	-73.483	-78.519	-64.725	-71.962

Primary phylogeny (fossil specimens only)

	BM	OU	EB	trend	lambda
PC1	-36.607	-33.298	-33.297	-39.191	-33.305
PC2	-35.977	-34.494	-32.667	-38.418	-33.666
PC3	-42.606	-40.841	-39.524	-36.884	-39.297

Eopneumatosuchus colberti **placed as the sister taxon to Thalattosuchia + (*****Shamosuchus*** **+ Crocodylia)**

	BM	OU	EB	trend	lambda
PC1	-72.911	-70.283	-78.911	-61.215	-70.283
PC2	-72.719	-71.107	-71.698	-67.207	-70.091
PC3	-78.059	-76.365	-80.978	-67.787	-75.429

Pelagosaurus typus **positioned as a teleosauroid**

	BM	OU	EB	trend	lambda
PC1	-76.211	-73.582	-81.262	-65.216	-73.582
PC2	-69.629	-68.789	-69.289	-64.601	-67.825
PC3	-75.373	-74.759	-79.190	-65.683	-72.745

11. Evolutionary rates

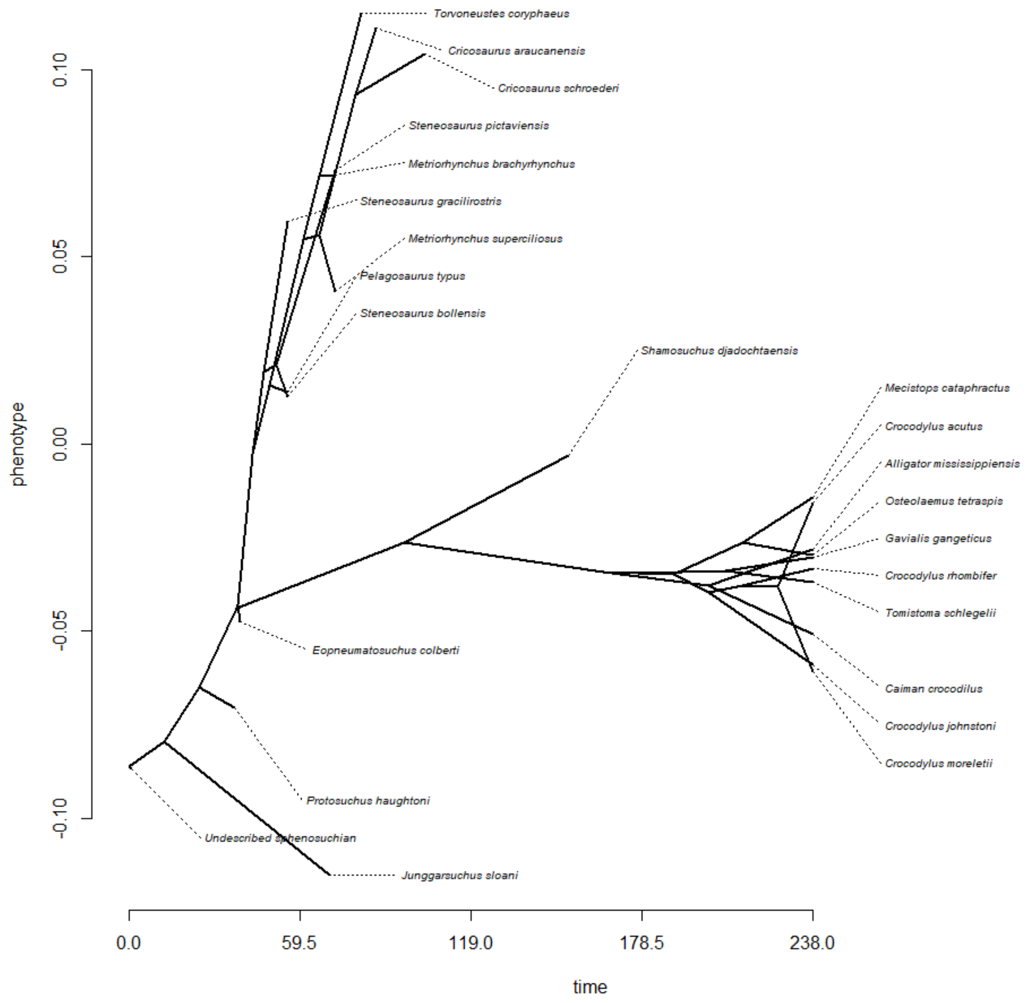

Fig. S7. The primary phylogeny is plotted such that the x-axis is scaled to time and the y-axis to PC1 score.

12. Cochlear measurements

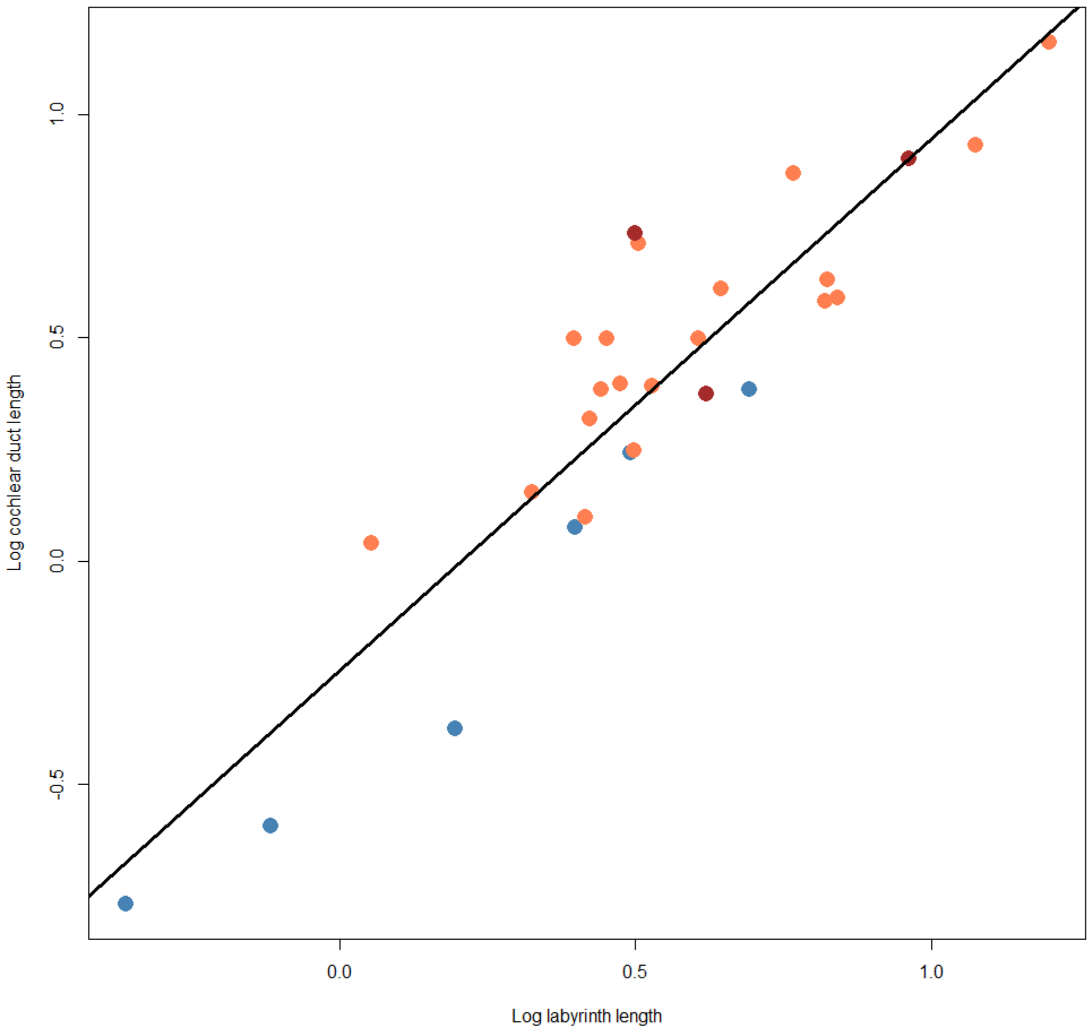

Fig. S8. Logarithmic plot of labyrinth length and cochlear duct length. Blue, pelagic; orange, semiaquatic; red, terrestrial.

13. Inclusion of *Crocodylus porosus* juvenile

The extant crocodylian *Crocodylus porosus* often ventures further offshore than other extant species. We do not include *C. porosus* in our dataset as the scan we acquired is of a juvenile, and we are limiting our analysis to adults. However, to demonstrate that *C. porosus* has an inner ear that is similar in shape to other extant crocodylians, and distinct in shape from pelagic extinct thalattosuchians, we provide an auxiliary analysis in which this juvenile specimen is included in our PCA morphospace below (analysis conducted following the same protocol as our primary PCA analysis, described above and in the main text). This demonstrates that the exclusion of *C. porosus* should not greatly affect our results, as its ear is exceedingly similar to the many other extant crocodylians in our dataset. We also acknowledge that extant species other than *C. porosus* are frequently encountered in brackish or saline environments, including one of the species in our analysis, *C. acutus*, and that swimming behavior in extant crocodylians appears to be the same whether an individual is in fresh or salt water. Hence, we wouldn't expect substantial differences in inner ear morphology between coastal and fluviolacustrine extant forms.

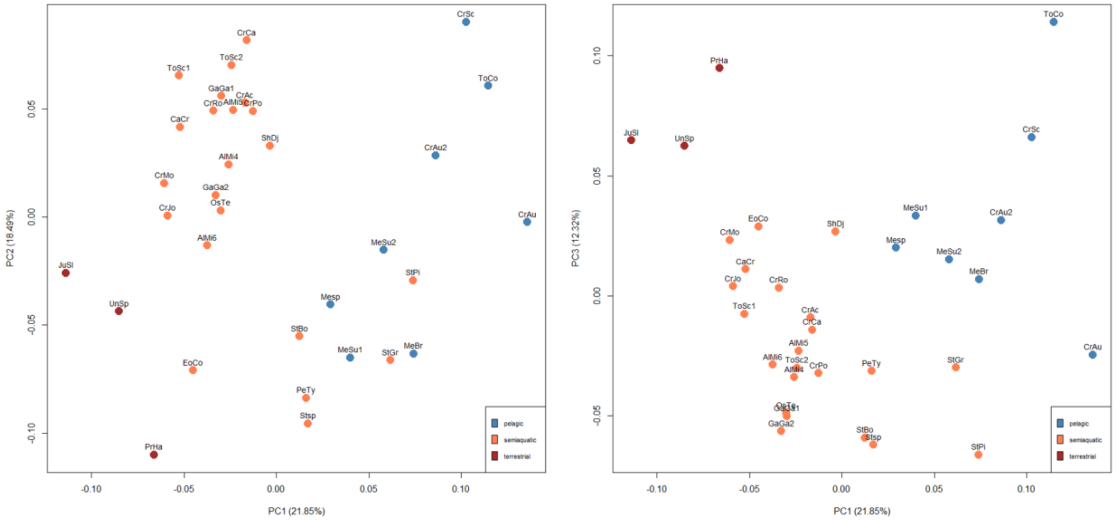

Fig. S9. PCA including the juvenile *Crocodylus porosus* (OUVC:10899; CrPo).

14. Left-Right Ear Asymmetry

To our knowledge, the only study testing whether left and right inner ear labyrinths of an archosaur are consistent in shape is a recent study of wild turkeys (24). The analyses in our paper use right labyrinths or mirrored left labyrinths. We here test whether mirrored left labyrinths resemble the shape of the right labyrinths in individuals of three key extant species, one from each major crocodilian subgroup. Importantly, we find that, for each individual, the mirrored left and actual right labyrinths fall out very close to each other in PCA morphospace (Fig. S10, analysis conducted following the same protocol as our primary PCA analysis, described above and in the main text), demonstrating that any asymmetry between left and right sides is minimal compared to the much greater amount of variation between species and between habitat groups. Thus, the inclusion of both right and mirrored left labyrinths in our dataset should not provide any serious bias. We visually show the actual left and right labyrinths of the three extant individuals in Fig. S11, which further demonstrates how similar in shape they are.

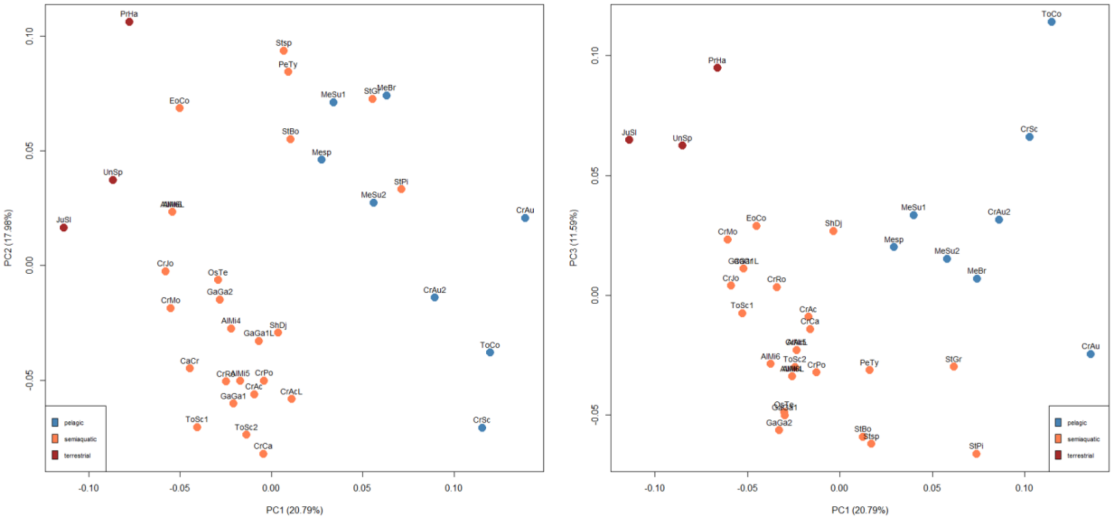

Fig. S10. PCA including the left mirrored labyrinths *for Alligator mississippiensis* (OUVC 9761; AlMi6L), *Crocodylus acutus* (FMNH 59071; CrAcL) and *Gavialis gangeticus* (TMM M-5490; GaGa1L).

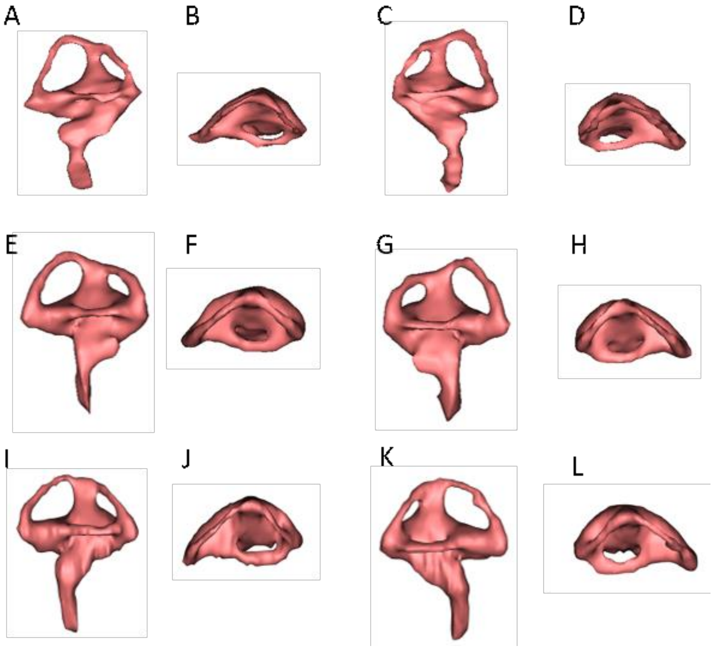

Fig. S11. Bony labyrinths of *Alligator mississippiensis* (OUVC 9761), *Crocodylus acutus* (FMNH 59071) and *Gavialis gangeticus* (TMM M-5490). A, E, I left lateral view; B, F, J left dorsal view; C, G, K right lateral view; D, H, L right dorsal view.

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