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Abstract

Crocodylians today live in tropical to subtropical environments, occupying mostly shallow waters. Their body size changes drastically during ontogeny, as do their skull dimensions and bite forces, which are associated with changes in prey preferences. Endocranial neurosensory structures have also shown to change ontogenetically, but less is known about the vestibular system of the inner ear. Here we use 30 high-resolution computed tomography (CT) scans and three-dimensional geometric morphometrics to investigate the size and shape changes of crocodylian endosseous labyrinths throughout ontogeny, across four stages (hatchling, juvenile, subadult, and adult). We find two major patterns of ontogenetic change. First, the labyrinth increases in size during ontogeny, with negative allometry in relation to skull size. Second, labyrinth shape changes significantly, with hatchlings having shorter semicircular canal radii, with thicker diameters, and an overall dorsoventrally shorter labyrinth than those of more mature individuals. We argue that the modification of the labyrinth during crocodylian ontogeny is related to constraints imposed by skull growth, due to fundamental changes in the crocodylian braincase during ontogeny (e.g. verticalization of the basicranium), rather than changes in locomotion, diet, or other biological functions or behaviours.

1 INTRODUCTION

Living crocodylians are mostly large, semiaquatic ambush predators living in shallow waters. The nine living crocodylian genera belong to three families (Alligatoridae,

51 Crocodylidae, and Gavialidae) and are distributed mostly across tropical and

52 subtropical regions. During their development from embryo to adult, crocodylians

53 undergo major ontogenetic changes that go far beyond simply increasing their

54 overall size.

55   During ontogeny, crocodylians change their diet, locomotion, and the

56 architecture of their skull, among other modifications (e.g. Fernandez Blanco et al.,

57 2018). Hatchlings prey on small animals such as insects, fish and amphibians, and

58 as they grow bigger they shift to larger prey like small reptiles, birds and mammals

59 (Gignac & Erickson, 2015). Fully grown adults can also include turtles or large

60 mammals, such as deer, into their diet (Dodson, 1975). In concert with these dietary

61 shifts, crocodylian snout shape changes during ontogeny: the snout flattens, which

62 includes nasal rotation (Witmer, 1995), and morphs from being relatively broad in

63 hatchlings to a longer-snouted morphology in more mature individuals (Dodson,

64 1975). Additionally, alligators modify their teeth from needle-like in hatchlings to

65 bulbous shapes in adults, which correspond to changes in bite force during ontogeny

66 (Erickson et al., 2003, 2004, 2014; Gignac & Erickson, 2015). Furthermore, young

67 American alligators are thought to be more agile than adult individuals, with relatively

68 longer limbs compared to the rest of their body (Allen et al., 2010), which means that

69 they can more easily move and spend more time on land. Finally, other marked

70 ontogenetic modifications are the verticalization of the basicranium, where the

71 basisphenoid and basioccipital become dorsoventrally elongated (Tarsitano et al.,

72 1989; Brochu, 1996). This verticalization process also affects the paratympanic

73 sinuses (Dufeau & Witmer, 2015), as well as the angle of the jaw adductor muscles

74 (Tarsitano et al., 1989). Ontogenetic studies in crocodylians have generally focused

75 on such osteological transformations.

76   Sensory systems, however, also undergo significant changes during

77   ontogenetic growth although these have received far less study. In crocodylians, the

78   brain (and thus the brain endocast) becomes anteroposteriorly more elongated from

79   juvenile to more mature individuals (Jirak & Janacek, 2017; Hu et al., 2020), the

80   tubes for the pharyngotympanic and median pharyngeal sinus structures become

81   vertically longer (Dufeau & Witmer, 2015), and the semicircular canals have recently

82   been shown to undergo negative allometric growth in relation to the bony otic

83   capsule (Kuzmin et al., 2021). Thus, it can be hypothesized that most endocranial

84   systems are affected by ontogeny, but much work remains to document and interpret

85   these changes. Given the life-history shifts discussed in the prior paragraph it is

86   important to untangle which ontogenetic sensory system changes reflect functional

87   shifts in diet, locomotion, or other biological attributes, and which are by-products of

88   how skulls (and other features) transform in shape during growth.

89   We here focus on one crucial sensory system, the vestibular system of the

90   inner ear (Fig. 1), which includes the three semicircular canals and the vestibule.

91   This system provides information on angular and linear acceleration of the head,

92   respectively (contributing to vestibulo-ocular and vestibulo-collic reflexes), and is

93   involved in the control of balance and equilibrium (e.g. de Burlet, 1934; Cox &

94   Jeffery, 2007). Semicircular canal morphology has previously been associated with

95   habitat, behaviour and locomotion in various vertebrate groups (e.g. Spoor et al.,

96   2002; Neenan et al., 2017; Schwab et al., 2019, 2020; Hanson et al., 2021; see also

97   Bronzati et al., 2021). More limited study has assessed labyrinth changes in an

98   ontogenetic context, but only in a small sample of species, with most focus on

99   mammals. They generally exhibit no discernible labyrinth shape changes during

100   post-natal ontogeny, as adult labyrinth shape and size are reached in utero (Hoyte,

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101   1961; Jeffery & Spoor, 2004; Mennecart & Costeur, 2016; Costeur et al., 2017;

102   Schellhorn, 2017).

103   On the other hand, reptilians appear to be different in these regards from

104   mammals, and only a few species have been studied. The labyrinth of ostriches

105   increases only in size and does not change shape (Romick, 2013). Avian labyrinths

106   have long been known to exhibit extremely high shape variability across taxa, which

107   has widely been interpreted to relate to differences in flight capability (Hadžiselimovic

108   & Savkovic, 1964); however this variability appears to be also a result of the

109   constraints of needing to fit long and sensitive semicircular canals along with large

110   eyes and a large brain into a small, aerodynamically constrained head (Benson et

111   al., 2017; Walsh & Knoll, 2018). In the ornithischian dinosaur *Dysalotosaurus*, the

112   labyrinth did not change significantly during development (Lautenschlager & Hübner,

113   2013). In the sauropod dinosaur *Massospondylus*, however, the labyrinth continued

114   to grow throughout ontogeny but changed only subtly in shape (Neenan et al., 2018).

115   Clearly, more data are needed to understand the diversity of reptilian labyrinth

116   growth trajectories, and assess whether ontogenetic changes in the labyrinth (if

117   present) are related to biological functional change during growth or side effects of

118   other ontogenetic or allometric changes in morphology. It is especially important to

119   target extant species, for which large samples across the ontogenetic series from

120   hatchling to adult are available.

121   Here we examine changes in the size and shape of the vestibular system of

122   the inner ear during ontogeny in extant crocodylians. Our sample includes members

123   of the three extant families Gavialidae, Alligatoridae and Crocodylidae. We used

124   high-resolution computed tomography (CT) imagining to create three-dimensional

125   labyrinth models of 30 extant crocodylians spanning four ontogenetic stages

126 (hatchling, juvenile, subadult and adult), quantified their shape with three-

127 dimensional geometric morphometrics, and used morphospace-based statistical

128 approaches to test for ontogenetic changes and patterns. Our analyses reveal two

129 major results: (1) hatchling labyrinths are generally smaller, than those of more

130 mature individuals, with the labyrinth growing with negative allometry in relation to

131 skull size (Fig. 2); and (2) a significant shape change occurs during crocodylian

132 ontogeny, as hatchlings generally have smaller anterior and posterior semicircular

133 canal radii, with larger diameters and a dorsoventrally shorter labyrinth compared to

134 adults and subadults (Fig. 3). We argue that this morphological change in the

135 labyrinth through ontogeny is most likely a product of space limitations in the skull

136 and the morphological modifications of the braincase, such as the verticalization of

137 the braincase, which allows the labyrinth to expand during growth, rather than a

138 functional adaptation that signifies divergent biological or behavioural attributes

139 between less mature and more mature crocodylians.

140

141 **2 MATERIALS AND METHODS**

142 **2.1 Institutional abbreviations**

143 **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **MNB**, National

144 Museum of the Bahamas, Nassau, The Bahamas; **NMS**, National Museum Scotland,

145 Edinburgh, U.K.; **OUVC**, Ohio University Vertebrate Collection, Athens, Ohio, U.S.A.;

146 **TMM**, Texas Memorial Museum, University of Texas, Austin, U.S.A.; **UF**, University

147 of Florida, Florida Museum of Natural History, Gainesville, U.S.A.; **USNM**, National

148 Museum of Natural History; Smithsonian Institution; Washington, U.S.A..

149 **2.2 Specimen**

150 We complied a dataset of 30 crocodylian endosseous labyrinths using CT scans.

151 This dataset includes skulls from the three extant families (Gavialidae, Alligatoridae

152 and Crocodylidae) and eight genera (*Alligator*, *Caiman*, *Crocodylus*, *Gavialis*,

153 *Mecistops*, *Melanosuchus*, *Osteolaemus*, and *Tomistoma*). Divided into four

154 ontogenetic stages, these specimens include 10 hatchlings, six juveniles, four

155 subadults, and 10 adults (see Table S1 for details). Two of the hatchling specimens

156 were excluded from the main statistical analysis due to their poorly fused bones,

157 which might have caused segmentation errors. We included those specimens in

158 additional analyses in the supplementary material (Fig. S3).

159 **2.3 Terminology**

160 Ontogenetic stages were mostly defined based on the literature, their assignment by

161 those collecting the data/museum collections and absolute size. There are not

162 definite, major osteological indicators of ontogenetic stage in crocodylian skulls.

163 Hatchling conditions usually persist for one or two years after hatching and this is

164 when changes in the crocodylian braincase occur during ontogeny. In the

165 verticalization of the basicranium one sees a reorientation of the basisphenoid and

166 basioccipital ("verticalization"), the development of a planar skull table, and

167 reconfiguration of the supratemporal fenestrae from shallow oval depressions to

168 deeper and more circular openings (Tarsitano et al., 1989; Witmer, 1995; Brochu,

169 1996; Gold et al., 2014; Dufeau & Witmer, 2015). The demarcation between

170 subadults and adults is particularly gradual, and thus challenging to distinguish; our

171 results reinforce this finding (see below).

172   To quantitatively describe semicircular canal features, we use the term

173 'radius' of the canals, which is used for the overall size of the canal curvature, and

174 the term canal 'diameter' as the cross-sectional diameter of the canal itself. The 'M'

175 shape of the canals is defined as the dorsal region of the labyrinth, from the anterior

176 to the posterior canal.

2.4 Methods

178 The crocodylian specimens were scanned at various facilities, and scanning

179 parameters vary (Table S2). Many of the specimens were scanned with an X-ray

180 microtomography instrument designed and constructed in house at the University of

181 Edinburgh, School of Geosciences. Specimens were scanned with a peak

182 accelerating voltage of 120 kV and a target power of 2.6 W. A total of 2000

183 projections, each with a 2 second exposure time, were acquired over a 360° rotation

184 of each specimen. Data were reconstructed by filtered back projection using

185 Octopus® software v. 8.9 (Dierick et al., 2004).

186 The crocodylian bony labyrinths were digitally segmented using Materialise

187 Mimics software versions 19.0 and 20.0, using the livewire and lasso tools. Only right

188 labyrinths were used for this study, as no substantial left-right variation in the

189 labyrinth has been previously noticed (Cerio & Witmer, 2019; Schwab et al., 2020).

190 To characterise shape, we used three-dimensional geometric morphometrics.

191 On each of the three-dimensionally reconstructed labyrinths, two series of

192 semilandmarks were placed using the IDAV Landmark software (Wiley et al., 2005),

193 one series on the internal surface and the other series on the external surface of

194 each of the three semicircular canals (Fig. S1). The landmarks were digitised in

195 RStudio (R Core Team, 2018) and evenly spaced along the semicircular canals,

196 using the 'geomorph' 3.1.2. package (Adams et al., 2019). Internal landmarks were

197 treated as closed structures and external ones as open structures. Then Procrustes

198 superimposition was applied to reduce the effects of size and orientation using the

199 *gpagen* function in 'geomorph'.

8

200 We performed statistical analysis on the landmark dataset to investigate

201 differences in labyrinth shape and size during crocodylian ontogeny. Using the

202 landmark coordinates, we conducted a principal component analysis (PCA) in

203 'geomorph' to quantify and visualise labyrinth shape variation. This analysis returns a

204 set of PC scores that summarises the labyrinth shape of each of the specimens and

205 places them in a morphospace (Fig. 3). We performed a PCA for the whole dataset

206 and separate PCAs for the genus *Alligator* and for Crocodylinae (Fig. 4), as those

207 include most of the specimens in the study, and in order to focus more strictly on

208 ontogenetic changes within certain groups.

209 We applied a PERMANOVA to the PC coordinates to test whether the

210 morphospace occupation of the ontogenetic stages (hatchling, juvenile, subadult,

211 adult) are statistically separated from each other, using the pairwiseAdonis() function

212 in the 'vegan' 2.5–3 package (Oksanen et al., 2018). In other words, this tests

213 whether there is significant overlap in morphospace between different ontogenetic

214 stages, or whether these stages have unique shapes that do not significantly overlap

215 with each other. We also performed a canonical variates analysis (CVA) using the

216 'morpho' package (Schlager, 2017), which assigns each of the specimens to their

217 ontogenetic stage a priori, and then tests the accuracy of the PC scores to assign

218 each specimen to its known ontogenetic stage.

219 We tested for allometry using measurements of skull size and labyrinth size.

220 Skull length was used as a proxy for body size, and was measured as the basicranial

221 length from the most anterior point of the premaxilla to the posterior surface of the

222 occipital condyle. Labyrinth size was quantified as the anteroposterior length,

223 measured from the most lateral base of the anterior canal to the most lateral base of

224   the posterior canal (Neenan et al., 2017). Those measurements were log

225   transformed and plotted against each other to show allometric relationships.

226

227   **3 RESULTS**

228   Our geometric morphometric analysis (landmark based PCA) found that crocodylian

229   labyrinths undergo major morphological change through ontogeny (Fig. 3, 4).

230   Hatchling crocodylians (Fig. 5A-E) have a relatively dorsoventrally shorter labyrinth

231   with smaller anterior and especially smaller posterior canal radii, larger canal

232   diameters, and also no prominent 'M' shape, which is present in most of the more

233   mature individuals. Juveniles are morphologically intermediate between hatchlings

234   and adults/subadults (Fig. 5F-J). Adult and subadult specimens (Fig. 5K-O),

235   however, develop a larger anterior and posterior canal radius, and have a generally

236   larger labyrinth with the characteristic 'M' shape in most specimens.

237   The PCA of all specimens produces a morphospace that visually groups

238   crocodylians into three clusters based on their ontogenetic stage (hatchling, juvenile

239   and subadult/adult). The first three PC axes explain 52.98% of the total shape

240   variation (Fig. 3). The first PC axis, explaining 25.87% of the cumulative variance,

241   represents the radius of the anterior and posterior semicircular canals, the presence

242   of an 'M' shape, and the dorsoventral height of the vestibular labyrinth. The hatchling

243   specimens have the most positive PC1 scores, whereas the adult and subadult

244   specimens have the most negative scores. On PC1, the most obvious visual

245   separation is between the hatchling and adult/subadult groups. PC2 and PC3

246   (16.35% and 10.76% of the variance, respectively) represent ontogenetic differences

247   to a lesser degree and do not show major differences between groups.

248   Our separate PCAs for the genus *Alligator* (first two PC axes explain 55.6% of

249   the overall variance) and the subfamily Crocodylinae (first two PC axes explain

250   55.49% of the overall variance) show the same morphospace occupation patterns as

251   the combined analysis, with separations based on PC1 (Fig. 4).

252   The PERMANOVA test of the entire dataset finds that each of the four

253   ontogenetic groups is significantly separated from the others in morphospace (P

254   value < 0.005). There is only one exception, the adult and subadult specimens are

255   not significantly different, in line with the visual overlap between them in

256   morphospace (Table S8).

257   The CVA finds that PC scores of labyrinth shape are highly effective at

258   assigning specimens to their known ontogenetic stage, with an overall classification

259   accuracy of 82.14%. Specimens incorrectly identified are only adults and subadults,

260   which can be confused for each other due to their overlap in morphospace—in other

261   words, due to their similar size and shape (Fig. 6; Table S7).

262   Labyrinth size correlates with skull size, exhibiting an allometric relationship

263   (Fig. 2). This shows that the labyrinth continues to grow throughout ontogeny, with

264   generally larger crocodylian individuals having larger labyrinths than smaller

265   individuals, but the labyrinth grows with a negative allometry in relation to skull size

266   (slope = 0.45, R^2 = 0.95, std error = 0.042, p-value < 0.001).

267

268   **4 DISCUSSION**

269   We found two main results that characterize morphological changes in the

270   endosseous labyrinth of modern crocodylians during their ontogeny. First, the

271   labyrinth continues to grow, with hatchlings having smaller labyrinths compared to

272   adult specimens, and labyrinths grow with negative allometry in relation to the skull

273 length (Fig. 2). Secondly, in crocodylians, the labyrinth changes shape through

274 ontogeny. Hatchling crocodylians have relatively smaller overall canal radii, with

275 thicker canal diameters, and a dorsoventrally shorter labyrinth than adults and

276 subadults (Fig. 5, 8). However, subadult and adult taxa occupy the same region in

277 morphospace and do not show significant morphological differences. Juveniles

278 occupy an intermediate position between hatchlings and subadults/adults, showing

279 features of both other clusters but are still significantly separated from both of them.

280 Thus, we recognise three distinct ontogenetic labyrinth shapes: those of hatchlings,

281 juveniles, and subadults/adults.

282   We can compare our results in crocodylians to what is currently known about

283 ontogenetic labyrinth size and shape changes in other tetrapods, to show differences

284 but also similarities with other groups. First, and most notably, crocodylians are

285 markedly unlike placental mammals, in which labyrinth size does not change after

286 birth, even as an individual grows a larger head and body. This is most likely due to

287 a developmental constraint (defined as factors that limit variation; Pearce 2011). The

288 ossification of the bony labyrinth (otic capsule) within the petrosal bone occurs during

289 gestation, as part of the development of the intricate mammalian middle ear and

290 sophisticated hearing system (Luo, 2011), and there are usually no substantial

291 changes after birth. This is the case, for example, in ruminants, in which ossification

292 of the labyrinth occurs in utero (Mennecart & Costeur, 2016). Only open structures

293 such as the endolymphatic duct change shape (in this instance, becoming more

294 elongated) to stay in contact with the skull. Likewise in cetaceans the inner ear

295 reaches near adult dimensions after only one third of the gestation period (Thean et

296 al., 2017). This general placental ontogenetic pattern has also been observed in the

297 domestic cat (*Felis silvestris catus*; Schellhorn, 2017), rabbits (*Oryctolagus*; Hoyte,

298   1961) and humans (*Homo*; Jeffery & Spoor, 2004). It is not surprising that

299   crocodylians are distinct from placental mammals, as their bony labyrinths are not

300   held within a dense petrosal bone that ossifies early in development as part of a

301   highly derived hearing system, but rather within the prootic, opisthotic, and epiotic

302   bones on the side of the braincase that grow and fuse with other braincase bones

303   during ontogeny.

304   We do note that marsupials are different from placental mammals in that the

305   petrosal and otic capsule are not yet ossified at birth (Larsell et al., 1935; Sánchez-

306   Villagra & Schmelzle, 2007; Ekdale, 2010). This is related to the unique marsupial

307   reproductive strategy, in which they give live birth at such an early developmental

308   stage that the adult middle ear ossicle chain and typical mammalian squamosal-

309   dentary jaw articulation are not yet assembled (Filan, 1990). After ossification of the

310   otic capsule, there are no major ontogenetic changes in the labyrinth, which is similar

311   to placental mammals (Ekdale, 2010).

312   Crocodylians are more similar to other reptiles/archosaurs in how their

313   labyrinth changes during ontogeny, although few reptiles have been studied, and

314   there is not a general pattern as in placental mammals. We can compare

315   crocodylians to two dinosaurian archosaurs whose labyrinth ontogeny has recently

316   been documented: the Early Jurassic sauropodomorph *Massospondylus* (Neenan et

317   al., 2018) and the Late Jurassic ornithischian *Dysalotosaurus* (Lautenschlager &

318   Hübner, 2013). In *Massospondylus*, the labyrinth continued to grow with slight

319   negative allometry in relation to skull size, as we observed in crocodylians (Neenan

320   et al., 2018). Although there were only slight changes in labyrinth geometry as

321   juveniles become adults, which is unlike what we observed in crocodylians. In

322   *Dysalotosaurus*, the size and shape of the endocranium changed during ontogeny,

323 but the inner ears were already well developed early in ontogeny, and do not show

324 clear changes in size or shape during growth (Lautenschlager & Hübner, 2013). The

325 labyrinth of living birds appears to scale with skull size (Romick, 2013), and unlike

326 crocodylians does not involve shape change during ontogeny. Investigation into

327 ontogenetic change in avian labyrinths has so far focused only on the ostrich

328 *Struthio*, which retains open cranial sutures into adulthood and is ground-dwelling,

329 where continued growth in the endocranium is less constrained, and balance

330 requirements are likely to be less critical than they would be for aerobatic flyers

331 (Walsh & Knoll, 2018). Investigation into ontogenetic changes in volant taxa may

332 reveal that labyrinth shape change occurs if canal length exceeds the available

333 endocranial space resulting in a morphological change, as moving through 3D

334 environments such as air and water might require similar sensory system

335 adaptations. These limited comparisons seem to indicate that reptiles are more

336 plastic than mammals in changing their labyrinths as they grow, with variability in

337 whether, and how, size and shape transform.

338   As the inner ear is involved in the sensation of balance and equilibrium, it has

339 previously been demonstrated that morphological changes in crocodylomorphs and

340 various other vertebrate groups over evolutionary time and across phylogeny are

341 linked to their lifestyle and ecology (e.g. Spoor et al., 2002; Neenan et al., 2017;

342 Schwab et al., 2019, 2020). The vestibular system, including the three semicircular

343 canals, plays an important role in head and gaze stabilisation (vestibulo-ocular and

344 vestibulo-collic reflexes), and hence is crucial for an animal to balance its body in

345 complex three-dimensional environments. Significant differences in labyrinth

346 morphology have been noted between secondarily fully aquatic (pelagic) amniote

347 species and their more terrestrial or semi-aquatic ancestors (Spoor et al., 2002;

348 Neenan et al., 2017; Schwab et al., 2020). Other differences have also been

349 recognized within taxonomic groups associated with different lifestyles and hunting

350 strategies (Pfaff et al., 2015; Capshaw et al., 2019; Schwab et al., 2019). This raises

351 the question: if labyrinth size and shape changes across phylogeny were linked to

352 changes in habitat or behaviour, do labyrinth size and shape changes across

353 ontogeny correlate with behavioural or biological shifts in crocodylians?

354   To first address this question, we must consider how crocodylian biology

355 changes from hatchling to adult. Extant crocodylians do not exhibit major changes in

356 locomotion or head posture during ontogeny. However, they do change their body

357 mass dramatically as they mature (Britton et al., 2012), which impacts ecology, as

358 larger body size allows them to feed on larger prey and venture into new habitats.

359 Hatchlings feed on small prey until their increased body size allows them to secure

360 larger prey items (Gignac & Erickson, 2015). There is also an ontogenetic shift in the

361 crocodylian feeding apparatus, including changes in their snout morphology (e.g.

362 Witmer, 1995; Brochu, 2001), dentition, and bite performance (Erickson et al., 2014;

363 Gignac & Erickson, 2015). Alligators are more agile during early stages of their

364 development, due to relatively long limbs compared to their body, which allows them

365 to spend more time in terrestrial settings as they can more easily move around

366 compared to their adult conspecifics (Allen et al., 2010).

367   While the prey envelope of crocodylians expands during ontogeny, their

368 overall ecomorphology does not change. They continue to be largely submerged

369 ambush predators (although adults of smaller-bodied species and juveniles of larger-

370 bodied species are known to frequent and forage in more terrestrial habitats). As

371 such, ontogenetic behavioural differences can be considered relatively minor.

372 Therefore, we hypothesize that the ontogenetic change in labyrinth morphology is

373 not primarily driven by function or behaviour.

374 Instead, we suggest that skull dimensions, and how they change through

375 ontogeny (which do, of course, have an impact on feeding ecology), primarily

376 underpin changes in labyrinth size and shape. There are major transformations in

377 crocodylian cranial morphology during ontogeny. In the first year of life, the

378 braincase in particular undergoes radical change: a verticalization process (Tarsitano

379 et al., 1989). This verticalization of the basicranium (Fig. 7), especially the

380 basisphenoid and the basioccipital, results in a dorsoventral expansion of the

381 braincase, and a reorientation of the quadrate and the jaw musculature. This

382 verticalization process also impacts the pharyngotympanic and median pharyngeal

383 (Eustachian) tubes, which become vertically elongated, together with an overall

384 expansion of the braincase, and the flattening of the skull roof and snout interlinked

385 with nasal rotation during ontogeny (Witmer, 1995; Gold et al., 2014; Dufeau &

386 Witmer, 2015; Morris et al. 2021). Such morphological changes in the braincase

387 during ontogeny have also been recognised in ichthyosaurs (Miedema & Maxwell,

388 2019) and ceratopsian dinosaurs (Bullar et al., 2019), and might reflect a more

389 general reptilian pattern.

390 Here we propose that the change in labyrinth morphology is fundamentally a

391 result of the morphological change of the braincase, as for example, the deepening

392 of the braincase (verticalization) during ontogeny would allow the labyrinth to expand

393 dorsoventrally and increase the size of the semicircular canals. We suggest that

394 immature skulls may be structurally constrained relative to the larger adult skulls with

395 more vertical braincases, and that this limits labyrinth growth and might explain the

396 morphological difference between hatchling/juvenile and subadult/adult crocodylians.

397   We however also note that even if the skull increases in size during ontogeny, the

398   sensory systems do not grow at the same rate (negative allometry). It is still under

399   debate if, in reptiles, skull dimensions generally have more impact on inner ear size

400   and shape than lifestyle and locomotion or phylogeny, and how all of these factors

401   might interact to shape inner ear evolution across phylogeny and evolutionary time

402   (e.g. Benson et al., 2017; Bronzati et al., 2021; Hanson et al., 2021). Our results

403   indicate that care must be taken when selecting specimens to include in broad

404   comparative and deep-time studies, so that ontogenetic variation is not conflated

405   with other potential influences on inner ear morphology. We recommend that such

406   studies do not include various ontogenetic stages together, but if possible, focus

407   solely only on adult and subadult specimens.

408   Interestingly, we note that the crocodylian hatchling labyrinth morphology

409   shows similarities to the labyrinths of adults of a group of extinct crocodylomorphs,

410   the pelagic metriorhynchids of the Jurassic and Cretaceous, with both having a

411   dorsoventrally short labyrinth and enlarged semicircular canal diameters (Schwab et

412   al., 2020). This might simply be coincidental, or it could indicate a heterochronic shift

413   in braincase development during the evolution of these highly unusual ocean-

414   adapted extinct crocodylomorphs. Perhaps retention of juvenile labyrinth size and

415   shape (which we suggest is a product of constraint in the juvenile skull) may have

416   helped metriorhynchids adapt their sensory systems to life in the open water, where

417   shorter labyrinths and thicker canals may have been biologically useful (see

418   discussion in Schwab et al., 2020). It is interesting to note that metriorhynchids are

419   the only crocodylomorph group suggested to have some form of live birth (e.g.

420   Herrera et al. 2017), and therefore may not have had the same structural constraints

421   on embryonic braincase development as egg-laying species. However, this

422   hypothesis requires further testing, such as looking at sensory development through

423   an ontogenetic series in a metriorhynchid species, but unfortunately, such a series is

424   currently unknown. It also needs to be determined if the ontogenetic changes of

425   extant crocodylians are plesiomorphic for crocodylomorphs (and thus the ancestral

426   baseline for metriorhynchids and other extinct species), or a derived feature of the

427   modern-day species.

428   Finally, our finding that crocodylians changed labyrinth size and shape during

429   ontogeny corresponds to other observed changes in neurosensory systems as

430   crocodylians grow. Recent work shows that *Alligator* brain endocasts unfold during

431   ontogeny, with hatchlings having a bird-like shape (an S-shaped endocast with the

432   forebrain region located anterodorsal to the hindbrain region) and adults a more

433   elongated and straight endocast (Jirak & Janacek, 2017; Hu et al., 2020).

434   Crocodylian proportional brain volume also varies considerably through ontogeny,

435   with the brain occupying a smaller proportion of the endocast in later ontogenetic

436   stages (Watanabe et al., 2019). In contrast, birds show relatively little ontogenetic

437   variation in their brain endocasts (Kawabe et al., 2015; Hu et al., 2020), probably due

438   at least in part to their rapid maturation from hatchling to adult. The previously

439   recognised changes in brain shape and size during ontogeny, and the changes in

440   vestibular labyrinth size and shape that we recognise here, together indicate that

441   there is a general pattern of neurosensory system transformation seen throughout

442   crocodylian ontogeny. It remains to be tested whether the anatomical undergirding of

443   other sensory systems, such as vision and hearing, also undergo ontogenetic shifts,

444   and if so, whether they are mere by-products of skull shape changes (as we propose

445   for the labyrinth) or are involved with any biological, dietary, behavioural, or

446 functional shifts as crocodylians hatched from eggs, endured the juvenile phase, and

447 matured into adults.

448

5 CONCLUSIONS

450 The bony labyrinth of crocodylians shows two major shifts during ontogeny: (1) a

451 change in labyrinth size, with hatchlings having a smaller labyrinth compared to

452 adults/subadults, and the labyrinth growing with negative allometry; and (2) a change

453 in shape, with hatchling specimens having smaller semicircular canal radii, thicker

454 canal diameters and a dorsoventrally shorter labyrinth compared to the more mature

455 individuals. We propose that this is due to morphological change in the crocodylian

456 braincase during ontogeny (e.g. verticalization of the basicranium), allowing the

457 labyrinth to expand in the braincase, rather than being a response to any ontogenetic

458 shifts in function or behaviour. We hypothesise that hatchling skulls are structurally

459 constrained, and that the ontogenetic shape changes seen in endocranial anatomy

460 (inner ear, brain, sinus systems) are largely a consequence of the growth patterns in

461 crocodylian crania. Ontogenetic studies such as these allow us to better understand

462 intraspecific patterns of sensory system change, which in turn gives us better

463 confidence in examining the neuroanatomy of extinct species and macroevolutionary

464 patterns through time. However, given that the crocodylian endosseous labyrinth

465 undergoes both size and shape changes during ontogeny, comparative studies,

466 must be careful to select ontogenetically similar specimens. We recommend that

467 macroevolutionary studies on the crocodylomorph inner ear be based solely on adult

468 and subadult specimens.

469

479 **Author contributions**

480 JAS designed and performed the research, analysed the data and wrote the paper;

481 MTY, SAW, LMW, YH, CAB, SLB helped with the interpretation of the data and

482 reviewed drafts of the paper; IB acquired the scans.

483

484 **Data Availability Statement**

485 Three dimensional models will been uploaded to MorphoSource

486 (https://www.morphosource.org/) and can be accessed at

487 https://www.morphosource.org/projects/000384666.

488

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647

648   **Figure captions**

649

650   **FIGURE 1** Lateral view of the skull and right endosseous labyrinth of a hatchling

651   specimen of *Crocodylus niloticus* (NMS Z.1859.13.804). (a) semi-transparent skull

652   showing the position of the endosseous labyrinth; right endosseous labyrinth in (b)

653   lateral; (c) medial; (d) anterior; (e) posterior; (f) dorsal views. Abbreviations: asc,

654   anterior semicircular canal; cc, crus commune; cd, cochlear duct; lsc, lateral

655   semicircular canal; psc, posterior semicircular canal. Scale bar equals 1cm.

656

657   **FIGURE 2** Relationship between skull length (mm) and labyrinth length (mm), in

658   crocodylians (log transformed) with 95% confidence interval indicating that the

659   labyrinth grows with negative allometry in relation to the skull. Colours and shapes

660   indicate ontogenetic stages; blue/squares, adults; turquoise/rhombus, subadults;

661   orange/triangle, juvenile; magenta/circle, hatchling.

662

663 **FIGURE 3** Principal component analysis (PCA) with morphospace occupation based

664 on ontogenetic stages, showing three distinct clusters, hatchling, juvenile and

665 subadult/adult. (a) PC1 vs. PC2; (b) PC1 vs PC3. Blue/squares, adults;

666 turquoise/rhombus, subadults; orange/triangle, juvenile; magenta/circle, hatchling.

667

668 **FIGURE 4** Principal component analysis (PCA) with morphospace occupation based

669 on ontogenetic stages for two crocodylian genera for PC1 vs. distinct clusters,

670 hatchling, juvenile and subadult/adult. (a) *Alligator*; (b) Crocodylidae. Blue/squares,

671 adults; turquoise/rhombus, subadults; orange/triangle, juvenile; magenta/circle,

672 hatchling.

673

674 **FIGURE 5** Ontogenetic variation in the right endosseous labyrinth of *Alligator*

675 *mississippiensis*. (a-e) hatchling (NMS Unreg.); (f-j) juvenile (UF herp 21461); (k-o)

676 adult (USNM 211232) in (a,f,k) lateral; (b,g,l) anterior; (c,h,m) posterior; (d,i,n)

677 medial; (e,j,o) dorsal views. Scale bars equal 5mm.

678

679 **FIGURE 6** Bony labyrinth shape morphospace, separating hatchling, juvenile and

680 subadult/adults specimen based on a canonical variate analysis (CVA) of the PCA

681 scores. Blue/squares, adults; turquoise/rhombus, subadults; orange/triangle,

682 juvenile; magenta/circle, hatchling.

683

684 **FIGURE 7** Verticalization of the braincase in *Alligator mississippiensis*. (a) occipital

685 view, (b) cross section of hatchling (NMS Unreg.); (c) occipital view, (d) cross section

686 of adult (USNM 211232). Abbreviations: an, angular; ar, articular; bo, basioccipital;

687 bs, basisphenoid; ls, laterosphenoid; oc, occipital condyle; ot, otoccipital; pa, parietal;

688   pro, prootic; pt, pterygoid; qua, quadrate; so, supraoccipital; sq, squamosal. Scale

689   bar equals 5mm in a, b and 10cm in c, d.

690

691   **FIGURE 8** Lateral (first, third and fifth rows) and dorsal (second, fourth and sixth

692   rows) views of various crocodylian endosseous labyrinths. (a) *Osteolemus tetrapis*

693   (FMNH 98936); (b) *Gavialis gangeticus* (UF-herp-118998); (c) *Crocodylus acutus*

694   (FMNH 59071); (d) *Mecistops cataphractus* (TMM M-3529); (e) *Crocodylus*

695   *rhombifer* (MNB AB50.0171); (f) *Crocodylus moreletti* (TMM M-4980); (g) *Crocodylus*

696   *johnstoni* (TMM M-6807); (h) *Caiman crocodylus* (FMNH 73711); (i) *Gavialis*

697   *gangeticus* (TMM M-5490); (j) *Crocodylus palustris* (NMS Z.1968.13.55); (k)

698   *Crocodylus porosus* (OUVC 10899); (l) *Gavialis gangeticus* (NMS Unreg.); (m)

699   *Melanosuchus niger* (NMS Z.1859.13.804); (n) *Crocodylus porosus* (NMS

700   Z.1925.9.1131); (o) *Mecistops* sp. (NMS Z.1859.13). (a-f) adults; (g-i) subadults; (j-k)

701   juveniles; (l-o) hatchlings. Scale bars equal 5mm.