Ontogeny of a sexually selected structure in an extant archosaur *Gavialis gangeticus* (Pseudosuchia: Crocodylia) with implications for sexual dimorphism in dinosaurs

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Despite strong evidence for sexual selection in various display traits and other exaggerated structures in large extinct reptiles, such as dinosaurs, detecting sexual dimorphism in them remains difficult. Their relatively small sample sizes, long growth periods, and difficulties distinguishing the sexes of fossil specimens mean that there are little compelling data on dimorphism in these animals. The extant gharial (*Gavialis gangeticus*) is a large and endangered crocodylian that is sexually dimorphic in size, but males also possesses a sexually selected structure, the ghara, which has an osteological correlate in the presence of a fossa associated with the nares. This makes the species a unique model for potentially assessing dimorphism in fossil lineages, such as dinosaurs and pterosaurs, as it is a large, slowly growing, egg-laying archosaur. Here we assess the dimorphism of *G. gangeticus* across 106 specimens and show that the presence of a narial fossa diagnose adult male gharials. Males are larger than females, but the level of size dimorphism, and that of other cranial features, is low and difficult to detect without a priori knowledge of the sexes, even with this large dataset. By extension, dimorphism in extinct reptiles is very difficult to detect in the absence of sex specific characters, such as the narial fossa.

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Abstract

Despite strong evidence for sexual selection in various display traits and other exaggerated structures in large extinct reptiles, such as dinosaurs, detecting sexual dimorphism in them remains difficult. Their relatively small sample sizes, long growth periods, and difficulties distinguishing the sexes of fossil specimens mean that there are little compelling data on dimorphism in these animals. The extant gharial (*Gavialis gangeticus*) is a large and endangered crocodylian that is sexually dimorphic in size, but males also possesses a sexually selected structure, the ghara, which has an osteological correlate in the presence of a fossa associated with the nares. This makes the species a unique model for potentially assessing dimorphism in fossil lineages, such as dinosaurs and pterosaurs, as it is a large, slowly growing, early maturing, egg-laying archosaur. Here we assess the dimorphism of *G. gangeticus* across 106 specimens and show that the presence of a narial fossa diagnose adult male gharials. Males are larger than females, but the level of size dimorphism, and that of other cranial features, is low and difficult to detect without a priori knowledge of the sexes, even with this large dataset. By extension, dimorphism in extinct reptiles is very difficult to detect in the absence of sex specific characters, such as the narial fossa.

Introduction

Sexual selection is a major evolutionary driver of many biological traits in animals, and is important for understanding the anatomy, behavior, and evolution of species and clades. One major indicator of sexual selection is sexual dimorphism where one sex is larger than the other and / or shows some form of exaggerated structure absent in the other, indicating an investment

49   in resources as a means of increasing reproductive success. However, assessing sexual selection

50   in extinct lineages is very difficult in groups such as the non-avian dinosaurs (hereafter simply

51   'dinosaurs') and other reptiles (Knell et al., 2013), and attempts in the past to identify sexual

52   dimorphism in dinosaurs have had no real success (see Mallon, 2017 for a recent review).

53   Lineages may show only sexual size dimorphism, or dimorphism of major osteological traits

54   (e.g., crests and horns), or may be under mutual sexual selection leading to reduced or even

55   absent dimorphism. Further, dimorphic traits are not necessarily linked to evolutionary pressures

56   based around reproductive success or socio-sexual dominance (e.g., see Hone, Naish & Cuthill,

57   2012; Hone & Mallon, 2017; and references therein). As a result, the case for sexual selection in

58   dinosaurs and other extinct reptile lineages has been controversial. In some taxa, however, there

59   is evidence for sexual dimorphism (e.g., *Shringasaurus* Sengupta, Ezcurra & Bandyopadhyay,

60   2017) and for the presence of traits that were likely used as socio-sexual signals (O'Brien et al.,

61   2018). Even so, the detection of sexual dimorphism is an important component of understanding

62   sexual selection, and the current lack of evidence for dimorphism in dinosaurs (e.g., Hone, Naish

63   & Cuthill, 2012; Mallon, 2017 and references therein) remains at least a curious anomaly.

64   There are also limitations to the available models among extant animals for comparison to

65   extinct animals such as dinosaurs. Large mammals may be comparable in size and have some

66   ecological similarities to dinosaurs, but there are major differences in evolutionary histories and

67   growth trajectories. Extant reptiles often show high levels of sexual size dimorphism (Fitch,

68   1981; Cox, Butler & John-Adler, 2007) but most reptiles are small and attain adult size rapidly.

69   The extant phylogenetic bracket for dinosaurs consists of birds and crocodylians, making these

70   two groups potentially better candidates (Witmer, 1995a). However, as with mammals, birds

71   mature rapidly, and their small size and often limited skeletal trait dimorphism also makes them

72   problematic. Crocodylians, in contrast, may be an excellent model with respect to dimorphism.

73   As with many or even most dinosaurs, they reach large sizes, grow slowly over many years, are

74   sexually mature well before maximum size, lay eggs, and have large numbers of offspring.

75   Importantly, at least some show sexual dimorphism in body size (*Caiman* – Thorbjarnarson,

76   1994; *Alligator* - Wilkinson & Rhodes, 1997; *Crocodylus* - Platt et al., 2009).

77   Among extant crocodylians, the gharial (*Gavialis gangeticus*) is a uniquely appropriate

78   example (Fig. 1). Gharials are specialised piscivores having an unusually long and slender snout

79   (Whitaker & Basu, 1983). Now known in the wild only from India, Bangladesh, and Nepal, this

80   species is critically endangered, with the already small wild populations having suffered

81   significant losses in recent decades (Hasan & Alam, 2016; Lang, Chowfin & Ross, 2019). They

82   are among the largest of the extant crocodylians, with the largest recorded animal (a male)

83   reaching 6.25 m in total length and weighting 977 kg, although more typical adults are 3.5–4.5 m

84   long, with males being larger than females (Hasan & Alam, 2016).

85   Gharials show sexual dimorphism not just in body size, but also in their cranial anatomy.

86   Larger males bear a ghara—a growth on the rostrum that is absent in females (Martin & Bellairs,

87   1977; Biswas, Acharjyo & Mohapatra, 1977; Whitaker and Whitaker, 1989). The ghara is a soft-

88   tissue structure that grows behind and over the external nares, and is supported by a depression

89   on the bony rostrum, anterior to the nares (Iordansky, 1973), in the larger male skulls (Martin &

90   Bellairs, 1977). Some early descriptions of the ghara suggest that it is bony and may even be

91   inflated, but this is not the case (Martin & Bellairs, 1977).

92   The exact function of the ghara is uncertain, but as it only appears in larger and presumably

93   sexually mature males (Martin & Bellairs, 1977; Biswas, Acharjyo & Mohapatra, 1978;

94   Whitaker & Whitaker, 1989), it would be reasonable to assume that it functions in sexual

95   display. Large males are seen to be dominant over smaller males and females (Whitaker & Basu,

96   1983). Suggested functions of the ghara include altering the calls of males (a hissing sound not

97   made by females or young males; Whitaker & Whitaker, 1989), or as a visual display signal to

98   females (Martin & Bellairs, 1977). Large males also possess an additional secondary sexual

99   characteristic consisting of a pair of expanded bony bullae on the dorsal aspect of the pterygoid

100   bones (Fig. 2) as also seen in other crocodylians (e.g., *Alligator* – Fig. 3). In gharials, the bullae

101   are not present in small males or apparently in females (though this is uncertain). The egg-shaped

102   bullae are dorsal dilations of the bony nasopharyngeal duct (Wegner, 1958; Witmer, 1995b,

103   1999). Although the resonant properties of the pterygoid bullae have yet to be demonstrated

104   experimentally, they would function as vocal resonating chambers as an inescapable bioacoustic

105   or biophysical consequence of their connection to the vocal tract. Thus, bullae may be linked to

106   the ghara functioning in sound production or modification (Martin & Bellairs, 1977). However,

107   vocalisations are rare (Whitaker & Basu, 1983), potentially arguing against this interpretation.

108   Ontogenetic data are limited to a few scattered accounts. For example, Biswas, Acharjyo &

109   Mohapatra (1978) describe a male of c. 2.5 m total length, and aged 11.5 years, as showing the

110   first signs of a ghara. The same animal was described as showing 'sex play' (which we assume to

111   mean courtship behaviour), aged 12.5 years, suggesting that the growth of the ghara is linked to

112   maturity (females appear to mature at around 2.6 m in length; Whitaker & Basu, 1983).

113   Similarly, Whitaker and Whitaker (1989) described one male as having a snout resembling that

114   of a female until it was 11 years old, when the ghara started to develop; the ghara folded caudally

115   over the nostrils at age 14 years, and reached fully adult form by age 18 years. Martin and

116   Bellairs (1977) suggested that males around 3 m long will exhibit a small ghara, though they also

117   referred to previous reports suggesting that this is normally present only in males in excess of 4.5

118 m long. Clearly, however, this is a feature that is not present in small / young animals. Moore et

119 al. (2019) observed that onset of puberty in male Morelet's crocodiles (*Crocodylus moreletii*),

120 measured by the development of the penile glans, was coincident with changing cranial shape,

121 suggesting a potentially similar pattern.

122   Here we look at sexual dimorphism in the skull of *Gavialis* as a model for detecting sexual

123 dimorphism and the identity of specimens in extinct reptiles, including dinosaurs. We use the

124 largest known sample of gharial data to assess sexual dimorphism in these animals and to

125 examine the feasibility of detecting dimorphism in extinct reptile lineages. This is done by

126 examining the relative growth (allometry) of changes in various measurements and features of

127 the skull, including the fossa and pterygoid bullae, and searching for evidence of bimodality

128 among adult individuals.

129
Abbreviations
130
131
132 BSL, basal skull length (premaxilla to occipital condyle); IW, interorbital width; MW, maximum

133 width of skull (across quadratojugals); MWAO, maximum width across orbits; NFML, narial

134 fossa maximum length; NFMW, narial fossa maximum width; NML, naris maximum length;

135 NMW, naris maximum width; OCW, occipital condyle width; PBL, average pterygoid bulla

136 length; PEMW, premaxillary expansion maximum width; SL_RTO, snout length rostral to

137 orbits; SMW, snout minimum width (mid-length).

138
Materials & Methods
139
140
141   Two binary variables and 13 continuous variables (Fig. 4; Appendix 1) were collected from

142 106 gharial skulls accessioned in 36 museum collections around the world. Where possible, these

143   were measured first-hand with callipers, but it was necessary to measure most of them digitally

144   based on photographs including scale bars. It was impossible to measure all variables because

145   some skulls were incomplete or variably covered with skin. Sex data were not given for any

146   specimens. We therefore assumed that specimens bearing a narial fossa (the osteological

147   correlate of the ghara) were male; those lacking a narial fossa were assumed to be immature

148   and/or female. The narial fossa (Figs. 1, 2, 4) is the depression in the premaxillary bones adjacent

149   to the bony nasal aperture (i.e., the opening into the nasal passage). A small ghara has been

150   reported in a captive animal that, when dissected, was seen to have ovaries, but this was assumed

151   to have been a pathological individual (Martin & Bellairs, 1977). It is therefore reasonable to

152   assume that animals with a narial fossa are male, and hereafter all mentions of male specimens

153   are based on this assumption.

154   To assess allometry in those continuous variables, it was necessary to first choose a

155   regressor. Visual inspection of the skulls, and prior published work (Piras et al., 2014), suggested

156   that variables associated with the snout vary widely in the adults, so we chose maximum skull

157   width (MW), measured across the outside of the quadratojugals, as our regressor, which is

158   consistent with the recommendations of O'Brien et al. (2019). The data were initially log-

159   transformed then subjected to reduced major axis (RMA) regression, which accounts for

160   measurement error in both the independent and dependent variables. Isometry was rejected if the

161   confidence intervals of the regression slope did not bound a value of 1. Negative allometry was

162   manifest if the confidence intervals were < 1; positive allometry was manifest if the confidence

163   intervals were > 1.

164   We used the gharial data to attempt to model the detection of sexual dimorphism in the fossil

165   record by disregarding sex information (inferred from narial fossa presence/absence). As

166   advocated by Mallon (2017), we tested for dimorphism in the continuous data by first subjecting

167   the residuals of the RMA regressions to Shapiro-Wilk and Anderson-Darling tests for normality

168   ($\alpha = 0.05$). Residuals were then subjected to a supplemental Hartigan's dip test, which yields the

169   likelihood that the data are distributed unimodally (Hartigan & Hartigan 1985). Residuals were

170   also subjected to mixture analysis, a maximum-likelihood procedure used to estimate univariate

171   parameters (e.g., mean, standard deviation) of two or more univariate normal distributions from a

172   pooled sample. The fit of the models was assessed using the Akaike Information Criterion (AIC).

173   As a final attempt to quantify sexual dimorphism, we reasoned that dimorphic structures

174   should exhibit higher variance of the RMA residuals than non-dimorphic structures. To test for

175   this, we used Levine's test for homogeneity of variance from means, with follow-up F-test

176   pairwise comparisons. The multiple comparisons were adjusted using Holm–Šidák correction.

177

Results

General observations

180   Maximum skull width (MW) ranges between 13 mm and 356 mm (embryonic and large adult

181   skulls, respectively) in our dataset, with basal skulls lengths (BSL) being from 33 mm to 864

182   mm, and total estimated lengths of the animals between 17 cm and 5.9 m (see Appendix 1). More

183   than 30 of our specimens represent animals of estimated total length in excess of 5 m, showing

184   that this dataset is biased towards larger animals, presumably at least in part as a result of

185   selective acquisition of large specimens for museums. The smallest skull having a narial fossa is

186   the Madras Crocodile Bank Trust male, where MW = 217 mm and BSL = 581 mm (Fig. 5) or

187   approximately 60% maximum size. Above MW = 280 mm (BSL c. 715 mm), all skulls possess a

188   narial fossa; thus, the largest skulls are male. The smallest skull possessing pterygoid bullae (but

189   lacking a narial fossa) is from the American Museum of Natural History (AMNH) 110145,

190   where MW = 179 mm (BSL = 459 mm).

191   Thirty-one of the 106 skulls possess narial fossae. Where determinable (some lack palates or

192   are otherwise obscured), all of these possess pterygoid bullae, indicating that they are

193   predominantly, if not universally, present in males. There are, however, 11 skulls lacking a narial

194   fossa but having bullae (Fig. 5). Of these, six are smaller than the unnumbered Madras Crocodile

195   Bank Trust male, and all are smaller than MW = 280 mm (BSL = 743 mm), which is the lower

196   threshold at which the narial fossa is consistently expressed (Fig. 5). If having a pterygoid bulla

197   is indicative of the male sex, which seems likely, it shows up earlier in ontogeny, at

198   approximately 50% maximum size, than does the narial fossa.

199

200   **Allometry**

201   The results for the all-inclusive allometric analyses are summarized in Figure 6 and Table

202   S1. MW is a good predictor of all continuous cranial variables ($R^2 > 0.92$, $p < 0.0001$). Positively

203   allometric variables include PEMW (premaxillary expansion maximum width) and IW

204   (interorbital width). Negatively allometric variables include BSL (basal skull length), OCW

205   (occipital condyle width), NML (naris maximum length), and MWAO (maximum width across

206   orbits). The three remaining variables—SL_RTO (snout length rostral to orbits), SMW (snout

207   minimum width), and NMW (naris maximum width)—grow isometrically.

208   The largest of our presumed males consistently plot above the regression line for SMW,

209   PEMW, and NMW (Fig. 6), suggesting that these variables increase very rapidly at large body

210   sizes. Follow-up allometric analyses of just the male data (having pterygoid bullae and narial

211 fossae) reveal positive allometry in all three variables (Table S2), with slopes greater than those

212 reported for the entire dataset, albeit with slightly reduced goodness of fit ($R^2 > 0.75$, $p <$

213 0.0001).

214 NFML and NFMW (narial fossa maximum length and width, respectively) scale with positive

215 allometry, but the relationship with MW is insignificant (Table S2). PBL (average pterygoid

216 bulla length) is weakly but positively correlated with skull size in males. We were unable to

217 reject the null hypothesis of isometry (Table S2).

218

219 **Sexual dimorphism**

220 Presumed males categorically differ from females in the presence of a narial fossa (~ ghara)

221 and, ostensibly, the presence of pterygoid bullae. Males are further distinguished by their

222 absolutely larger skulls at maturity (MW > 287 mm, BSL > 715 mm), relatively shorter and

223 wider rostra, and wider terminal rosettes that support larger nares.

224 Without knowing the sexes a priori (as in fossil taxa), it is otherwise difficult to detect

225 dimorphism in those continuous variables. With the exception of NML, the residuals for all

226 cranial variables are significantly non-normal, but in no case are they significantly non-unimodal

227 (Table S3). Mixture analysis shows that pooled BSL values are best modelled by two normal

228 distributions, but further investigation shows that these distributions distinguish between juvenile

229 and more mature individuals, not sexual dimorphs (Group 1 mean = -0.205 ± 0.0739, Group 2

230 mean = 0.00617 ± 0.0312). The ability to detect dimorphism in the three most obviously

231 dimorphic continuous variables (SMW, PEMW, and NMW) does not increase by considering

232 only adults (MW ≥ 179 mm, BSL ≥ 459 mm the smallest presumed male having pterygoid

233   bullae). The adult NMW residuals are not significantly non-normal, and none of the residuals are

234   either significantly non-unimodal or best fit by two normal distributions (Table S3).

235   On average, the SMW, PEMW, and NMW residuals exhibit higher variances (≥ 0.004) than

236   the non-dimorphic residuals (Fig. 7). Levene's test for homogeneity of variance from means is

237   highly significant ($p < 0.0001$). Follow-up pairwise comparisons (Table S4) reveal that variance

238   for the SMW, PEMW, and NMW residuals is usually significantly higher compared to the other

239   residuals. Variance does not differ significantly between any of the three dimorphic variables.

240

241   **Discussion**

242   **Sexual dimorphism and sexual selection in *Gavialis***

243   The results here broadly align with previous assessments of dimorphism and the ghara in

244   *G. gangeticus*. Males are larger than females, and the former show both a fossa associated with

245   the nares and bullae on the palate. These latter features appear only in larger animals, and thus

246   with the onset of sexual maturity. The smallest specimen with a narial fossa in our sample is

247   slightly smaller, at 581 mm in basal skull length (MW = 217 mm), than the smallest reported by

248   Martin and Bellairs (1977; 69 cm), but the samples are broadly comparable. There are several

249   large animals (with BSL > 700 mm, MW > 270 mm) that lack a fossa, and these would be

250   considered females, though they would be unusually large with body sizes over 4.5 m.

251   Martin and Bellairs (1977) stated that a ghara appears in males of around 3 m in total

252   length, which, following their head to body ratio of 1:6, would equate to a basal skull length of

253   approximately 42 cm. This is considerably smaller than the smallest skull with a narial fossa

254   recorded here. We infer from this finding that the ghara may be growing for some time before

255   the ghara's soft tissues are extensive enough to generate the bony fossa that supports it (just as

256 muscle scars tend to be subtle in small animals and more prominent in large animals). This

257 would match with the apparent development of the bullae prior to the presence of the fossa and

258 would indicate that the ghara and bulla develop nearly simultaneously. Above a BSL of 680 mm

259 (MW > 240 mm), there are 23 specimens where the presence of a fossa and bullae can be

260 reliably determined (see Appendix 1). Of these, 20 possess both, two possess neither, but one

261 specimen (Royal Scottish Museum RSM 1948.58.1) has bullae and no fossa. Thus there is not a

262 perfect 1:1 ratio between larger animals possessing both a fossa and bullae or neither, though

263 clearly a strong majority do fall into this category. We therefore provisionally consider the bullae

264 to be a feature of adult male animals, but recognise that this may not be exclusive.

265   The narial fossa shows strong positive allometry compared to other traits in the skull (Fig.

266 6), which would suggest that the affixed ghara functions as a sexually selected display feature

267 (cf. O'Brien et al., 2018). This also fits with the observation of Dinets (2013) that males have a

268 sex-specific head-up posture on land, which elevates the ghara. The ghara would also be a major

269 handicap to males when hunting, and thus would form an honest signal of the fitness of the

270 owner. The large size of the ghara (Fig. 1) might also increase visibility to prey, and would

271 certainly offer considerable drag on the otherwise thin snout of an animal hunting in water

272 (Martin & Bellairs, 1977), presumably incurring a cost to feeding effectiveness. This is

273 especially true since an extra drag generated near the tip of the jaws would be much greater than

274 closer to the rear of the skull, as drag is a function of distance from the joint squared. The

275 extreme variation of the morphology of the ghara (Fig. 1) also points to it being a socio-sexual

276 signal (see Hone & Naish, 2013 and references therein) that would be under selection.

277   Initially the pterygoid bullae must grow rapidly as the smallest record of them in our sample

278 is still sizeable (37 mm long on the Field Museum of Natural History (FMNH) 22025, BSL =

279 611 mm, MW = 218 mm), although it is possible that at smaller sizes they are hidden in

280 photographs of the palate. However, bullae growth is isometric, which suggests that although

281 they are important structures, their size is not critical. We hypothesise, therefore, that these

282 features function as an acoustic signal to females (or perhaps other males) that the male is

283 mature, but that there is no additional information about the size and quality of the male

284 possessing them or otherwise their growth would be expected to be positively allometric.

285   Although it has been noted that gharials rarely produce calls, they are known to vocalise

286 (Whitaker & Basu, 1983), including 'buzzing' during courtship (Dinets, 2013). Many

287 crocodylians communicate using very low-frequency vocalizations (Garrick, Lang & Herzog,

288 1978), some of which extend into the infrasonic range (i.e., below the range of normal human

289 hearing; Todd, 2007). Although gharials are unusual among the larger crocodylians, in that they

290 are not known to produce infrasonic calls (Dinets, 2013), these or other vocalisations may not

291 have been detected by previous researchers. The bullae are connected to the vocal/respiratory

292 tract and would act as acoustic resonators, potentially lowering the frequencies of sounds

293 produced. Whether the pterygoid bullae are important for acoustic signalling remains

294 unconfirmed. They are, however, large structures that we presume have some positive function,

295 in that they occupy space in the orbit and palatal regions, and would presumably adversely affect

296 other functions (e.g., the bullae expand into the adductor chamber and hence decrease the

297 available space for jaw adductor muscles such as *M. pterygoideus dorsalis*). They appear in

298 larger, mature males, and infrasonic calls of other crocodylians are produced only by males

299 (Dinets, 2013). The vocal capabilities of alligators are well known (Garrick, Lang & Herzog,

300 1978; Vliet, 1989; Todd, 2007), and alligators also possess inflations of the nasopharyngeal ducts

301 known as the pterygopalatine bullae (Wegner, 1958; Witmer, 1995b, 1999; though these are

302 presumably non-homologous), perhaps lending some credence to an acoustic resonance function

303 in gharials, as well (Fig. 3). Dinets (2013) reported specifically that gharials do not use

304 infrasound, but the basis for this assertion is not clear, and we regard acoustic signalling

305 (potentially including an emphasis on low-frequency sounds, perhaps even infrasound) as the

306 current best-supported hypothesis for the function of the pterygoid bullae.

307 When analysed in the presumed males alone, some of the traits in the skull also show

308 positive allometry. The premaxillary expansion maximum width (PEMW), the snout minimum

309 width (SMW), and the naris maximum width (NMW) are all disproportionately larger in the

310 largest males (Fig. 7). All are potentially associated with the ghara and the size increase of the

311 fossa to which it attaches. We suggest here that the expansion of the premaxillary rosette and

312 relative increase of the snout minimum width could help strengthen the skull given the drag of a

313 large ghara, but could also potentially have an ecological function permitting engaging of larger

314 prey.

315 Given that the pterygoid bullae ontogenetically appear in presumed males that would be of

316 breeding age, we suggest that they provide a general infrasonic acoustic signal that would

317 function to advertise their maturity to females (and also perhaps to other males). This signal

318 would serve to attract attention to the male (even while out of line of sight such as underwater),

319 and the primary visual signal of status and quality would be the ghara. The visual signal is

320 enhanced by a spray of water emerging from the ghara itself upon exhalation, accompanied by an

321 audible hiss and hum (Whitaker & Whitaker, 1989).

322

323 **Detecting sexual dimorphism in the fossil record**

324   To date, no dinosaur has been determined to exhibit sexual dimorphism under rigorous

325   analysis (Mallon, 2017). Tests for dimorphism in fossil taxa may be confounded by a

326   combination of small sample sizes and protracted growth, coupled with uncertainty of the age or

327   sex of most specimens. These conspire to ensure that young individuals of the larger sex are

328   conflated with older individuals of the smaller sex (Hone & Mallon, 2017). Dinosaurs matured

329   sexually before they reached growth asymptotes (e.g., Erickson et al., 2007; Lee & Werning,

330   2008), and as a result may be expected to have initiated the growth of a sexually selected

331   structure earlier in ontogeny than in animals where they reach maximum size at a similar time to

332   sexual maturity. This also fits with the high juvenile mortality of dinosaurs, and thus may have

333   promoted early reproduction (Hone & Mallon, 2017). Thus, although we may expect to, and do,

334   see strong positive allometry for features such as crests and horns under sexual selection (Hone,

335   Wood & Knell, 2016; Brown, 2017), these features may start earlier and grow more slowly than

336   in traditional models, such as large mammals.

337   Our results support these general contentions that dimorphism is very difficult to detect in

338   taxa showing growth over considerable periods of time. Were these animals recovered from the

339   fossil record, the presence of the fossa and bullae give clear osteological characters that are not

340   obviously functional (sensu Hone, Naish & Cuthill, 2012) and appear only in larger specimens,

341   and these would likely be regarded as indicative of sex. *Gavialis gangeticus* is identified by

342   numerous osteological traits (Iordansky, 1973) present in all specimens that would signify all

343   specimens as belonging to a single species. However, in the absence of these discrete traits,

344   determining dimorphism would be very difficult. Hone and Mallon (2017) assessed detection of

345   sexual dimorphism in alligators based on body size, and suggested a minimum of 60 animals

346   might be needed to statistically support dimorphism, even when the difference between sexes

347   was strong and could be measured effectively. Here in the gharials, there is no clear statistical

348   signal for any continuous traits producing two clusters across all specimens, despite a dataset of

349   over 100 specimens. Even when our approach is restricted to osteological mature individuals, the

350   signal is weak and arguably present only in some features that are also associated with the ghara.

351   Were these fossilized gharial specimens, and having no *a priori* knowledge of their dimorphism,

352   there would be little to separate out the sexes.

353   There few datasets in the fossil record for dinosaurs in excess of even 50 specimens where

354   traits such as size and potentially dimorphic display features can be reliably measured. The

355   sample sizes and levels of specimen completeness in most assemblages are low enough that

356   dimorphism will be hard to detect unless there are clear presence/absence traits or very different

357   morphologies between sexes. This is not say that sexual dimorphism was not present in

358   dinosaurs—and more detailed analyses of assemblages with large samples and completeness

359   (e.g., *Coelophysis*; Griffin, 2018) are merited—only that it is difficult to demonstrate

360   quantitatively.

361

362   **Future work and conservation implications**

363   Further work is needed to confirm the hypotheses laid out here. An exact relationship

364   between the timing of sexual maturity and the physical expression of the ghara, narial fossa, and

365   pterygoid bullae is key to understanding gharial reproductive biology. A formal assessment of

366   any social or mating displays, and the differing acoustic and visual components of this, are also

367   important and may provide information critical to breeding efforts given the severe extinction

368   risk of this species (Lang, Chowfin & Ross, 2019).

369   This study also raises additional issues regarding the functional morphology of gharials,

370   which may also be important for understanding their ecology and behaviour. The ghara will

371   induce severe drag on the jaws during prey apprehension underwater, while the bullae will affect

372   the palatal muscles, which will influence the functioning of the jaws.

373   Finally, we note that the largest narial fossae are associated with an increase in the size of

374   the terminal rosette and a broadening of the snout (increased minimum width), and this may

375   increase the ability of males to catch larger prey. Although we did not measure tooth size across

376   all specimens, we note that some of the largest males (e.g., Grant Museum - LDUCZ X215)

377   apparently have disproportionately large teeth compared to smaller animals, and this would

378   likely allow them to tackle larger prey than may be expected. Given the great differences in size

379   between osteologically mature gharials and young juveniles, there would be niche partitioning

380   between various different growth stages, as seen in other crocodylians (Dodson, 1975). However,

381   there may also be separation between larger (and presumably fitter) gharial males and other adult

382   animals, and if so, this may also be a very important consideration for sustaining populations. If

383   high-quality males are removed from a population, this has the potential for profoundly negative

384   effects in small populations (Knell & Martínez-Ruiz, 2017). So if our hypothesis about prey

385   preference is correct, suitable prey for larger males must be a consideration in establishing

386   suitable habitats for sustainable gharial populations or they may be at risk.

387   Moore et al. (2019) noted an increase in size in the anterior teeth of male Morelet's

388   crocodiles (*Crocodylus moreletii*) at sexual maturity and suggested that this increase was linked

389   to male-male interactions over females. This could also be the case in gharials. However,

390   developmentally this change occurs much earlier in the crocodile than the shift suggested here,

391   and it was only the anterior teeth that changed in the crocodile and not the entire tooth row, as we

392 observed in *Gavialis*. This difference implies that these respective changes in tooth morphology

393 are not synonymous. In any case, as noted by Moore et al. (2019), increased head size is

394 correlated with increased bite power and opportunities to tackle larger prey (Erickson et al.,

395 2012). So regardless of the selective pressures that might produce more robust crania and teeth in

396 large males, the hypothesised dietary shift may still be present.

397
398
399 **Conclusions**
400
401 We agree with previous studies that the ghara and associated narial fossa, and probably

402 the pterygoid bullae, are male traits of gharials, and most likely have a socio-sexual function in

403 displays. Limited dimorphism in size and various cranial traits are exhibited with males being

404 larger than females.

405 In the absence of key traits, determining moderate sexual dimorphism (body size or other

406 measurements) is going to be extremely difficult, even with good sample sizes and complete sets

407 of data. Doing so for such fossil taxa as dinosaurs (but also many other extinct reptiles and

408 amphibians) is extraordinarily difficult unless the degrees of dimorphism are extreme. Prolonged

409 growth, and the overlap of males and females in terms of body size and even features linked to

410 sexually selected structures (such as the width of the terminal rosette seen here), make the sexual

411 identity of individual specimens highly cryptic.

412
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426

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436

437

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533

534

535   **Figure captions**

536   Figure 1. (A) bony snout of two male *Gavialis gangeticus*. The black arrows point to the fossae

537   to which the ghara attaches. (B-F) various male *G. gangeticus* in the wild showing the range of

538   size and morphology of the ghara. Image B provided by Nikhil Whitaker and images C-F

539   provided by Gharial Ecology Project, all used with permission.

540

541   Figure 2. Pterygoid bullae of *Gavialis gangeticus* (UF 118998) based on volume renders of

542   computed tomographic data of a dried skull. (A) Dorsolateral oblique view of the full skull

543   showing the immature narial fossa and the pterygoid bulla, the latter being seen through the

544   orbit. (B–E) Dorsolateral oblique views of (B) the pterygoid bulla enlarged, (C) with the skull

545   roof digitally removed to reveal both bullae, and (D) with the dorsal portions of the bullae

546   removed to show the thin walls and the connection with the nasopharyngeal duct. (E) Close-up

547   ventral view of the pterygoid bullae projecting into the adductor muscle chamber. (F) Ventral

548   view of the full skull. All scale bars equal 5 cm. A and F are at the same scale, as are B–F.

549

550   Figure 3. Pterygopalatine bullae of *Alligator mississippiensis* (OUVC 10615) based on volume

551   renders of computed tomographic data of a fleshy head. (A) Dorsolateral oblique view of the full

552   skull showing the pterygopalatine bulla as seen through the orbit. (B) Dorsolateral oblique view

553   of the pterygopalatine bulla enlarged with the skull roof digitally removed to reveal both bullae.

554   (C) Same presentation as in (B) but in dorsal view and enlarged. (D) Medial (internal) view of

555   the right side of a parasagittaly sectioned head, showing the pterygopalatine bulla emerging as a

556   dorsal dilation of the nasopharyngeal duct. (E) Ventral view of the full skull showing that the

557   pterygopalatine bulla is not visible in ventral view. All scale bars equal 5 cm. A and E are at the

558   same scale, as are B and D, whereas C has its own scale.

559

560   Figure 4. Measurements used in the present study. Left inset details measurements from the

561   rostrum; right inset details measurement from the palate. See main text for the key to the

562   abbreviations.

563

564   Figure 5. Distribution of narial fossa and pterygoid bullae presence/absence across gharial skulls

565   of different sizes (measured as MW). Insets at right illustrate the variable in question.

566

567   Figure 6. Reduced major axis regressions for nine of the continuous variables examined here. (A)

568   log BSL vs. log MW, (B) log OCW vs. log MW, (C) log SL_RTO vs. log MW, (D) log SMW

569   vs. log MW, (E) log PEMW vs. log MW, (F) log NMW vs. log MW, (G) log NML vs. log MW,

570   (H) log MWAO vs. log MW, (I) log IW vs. log MW. Males (possessing narial fossae) are

571   identified with blue triangles. Black dots represent osteologically immature individuals and/or

572   females.

573

574   Figure 7. Residual variances (± 95% confidence intervals) for the nine continuous variables

575   examined. Numbers provided above each of the variables indicate sample size.

Figure 1

Gharial snouts and the ghara

Figure 1. (A) bony snout of two male *Gavialis gangeticus*. The black arrows point to the fossae to which the ghara attaches. (B-F) various male *G. gangeticus* in the wild showing the range of size and morphology of the ghara. Image B provided by Nikhil Whitaker and images C-F provided by Jeffrey Lang, all used with permission.
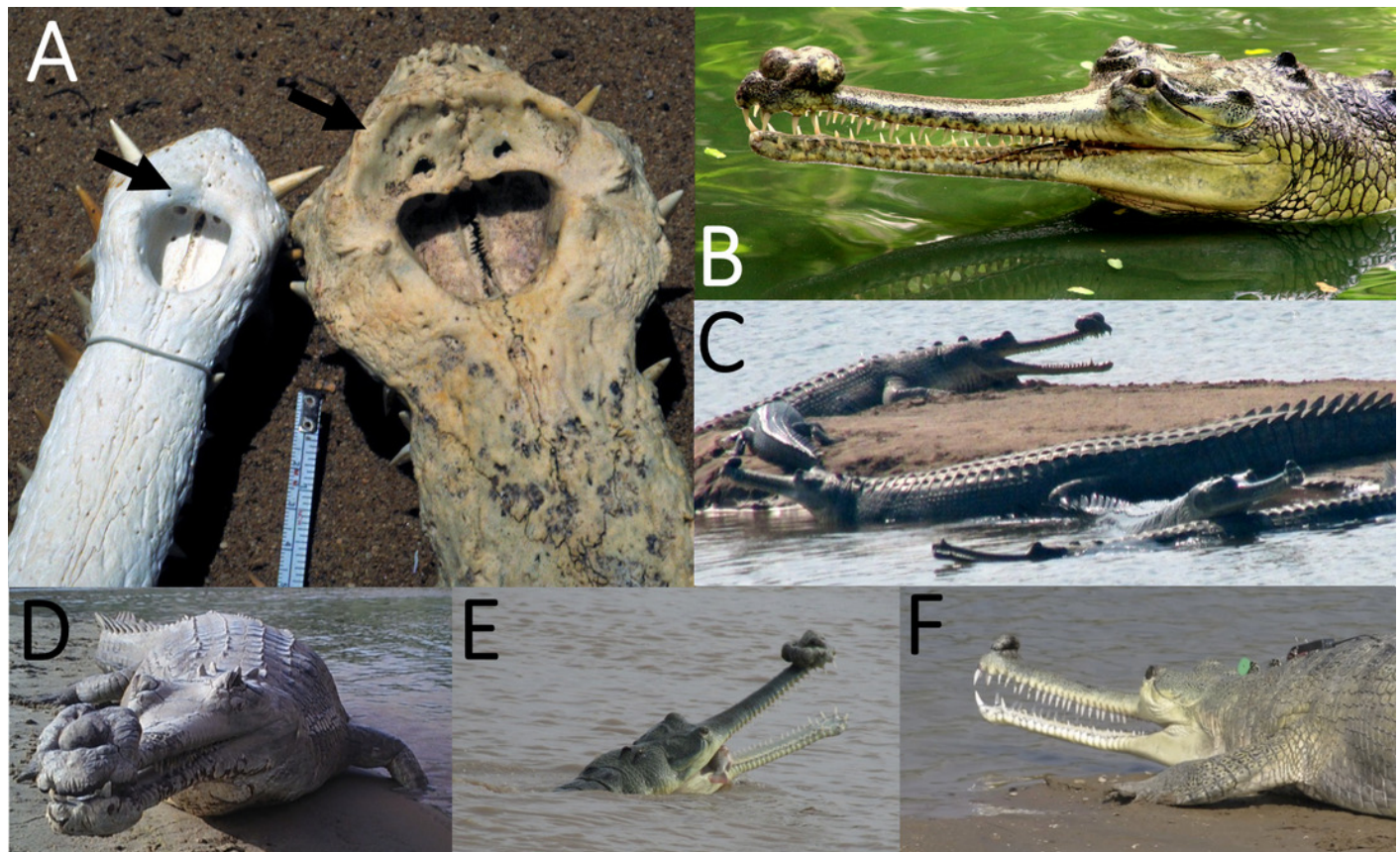
Figure 2

Pterygoid bullae of gharials

Pterygoid bullae of *Gavialis gangeticus* (UF 118998) based on volume renders of computed tomographic data of a dried skull. (A) Dorsolateral oblique view of the full skull showing the immature narial fossa and the pterygoid bulla, the latter being seen through the orbit. (B–E) Dorsolateral oblique views of (B) the pterygoid bulla enlarged, (C) with the skull roof digitally removed to reveal both bullae, and (D) with the dorsal portions of the bullae removed to show the thin walls and the connection with the nasopharyngeal duct. (E) Close-up ventral view of the pterygoid bullae projecting into the adductor muscle chamber. (F) Ventral view of the full skull. All scale bars equal 5 cm. A and F are at the same scale, as are B–F.
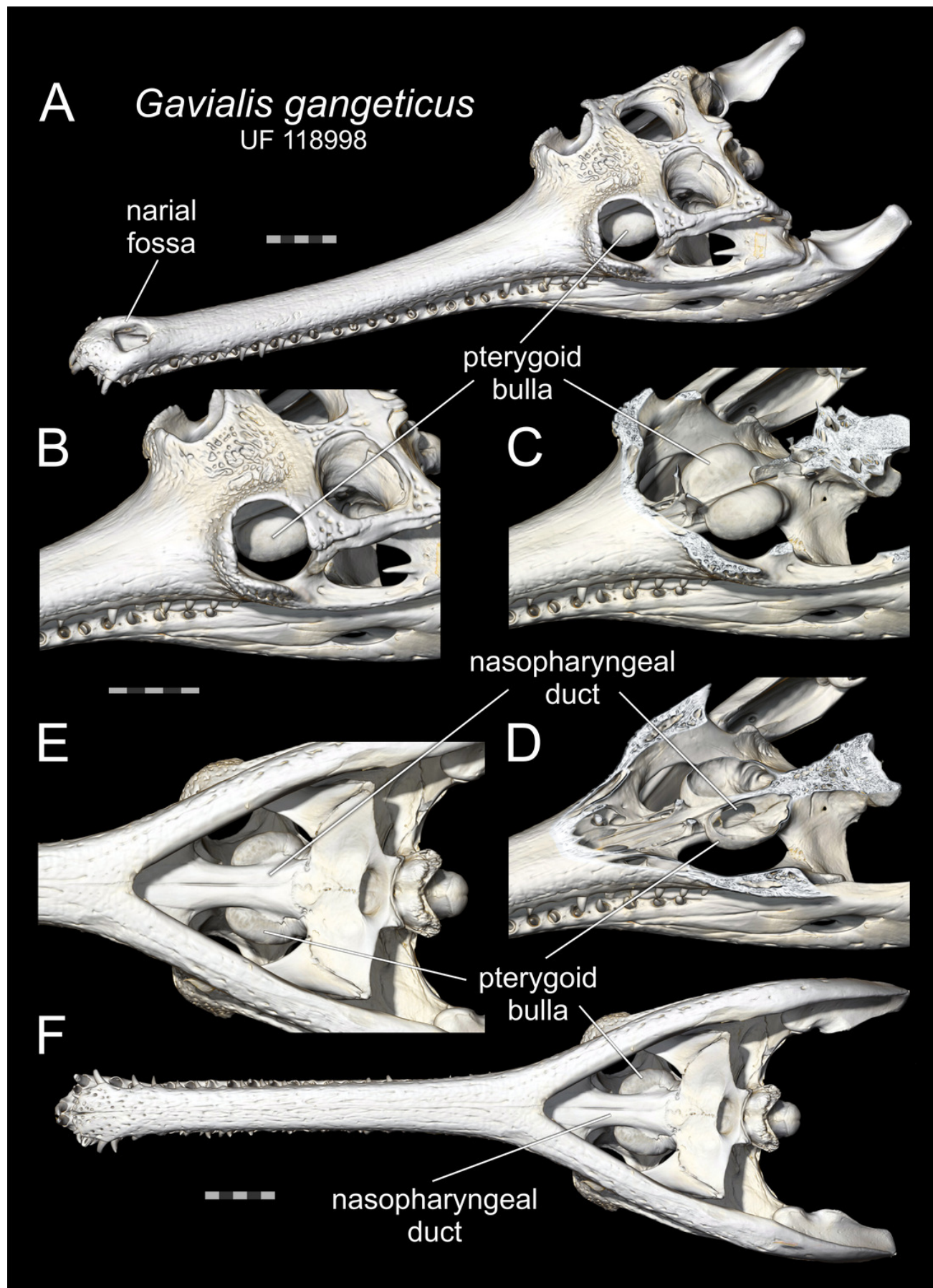
Figure 3

Pterygopalatine bullae of *Alligator*

Pterygopalatine bullae of *Alligator mississippiensis* (OUVC 10615) based on volume renders of computed tomographic data of a fleshy head. (A) Dorsolateral oblique view of the full skull showing the pterygopalatine bulla as seen through the orbit. (B) Dorsolateral oblique view of the pterygopalatine bulla enlarged with the skull roof digitally removed to reveal both bullae. (C) Same presentation as in (B) but in dorsal view and enlarged. (D) Medial (internal) view of the right side of a parasagittaly sectioned head, showing the pterygopalatine bulla emerging as a dorsal dilation of the nasopharyngeal duct. (E) Ventral view of the full skull showing that the pterygopalatine bulla is not visible in ventral view. All scale bars equal 5 cm. A and E are at the same scale, as are B and D, whereas C has its own scale.

A *Alligator mississippiensis*
OUVC 10615

pterygopalatine bulla

B

C

D

pterygo-palatine bulla

nasopharyngeal duct

E
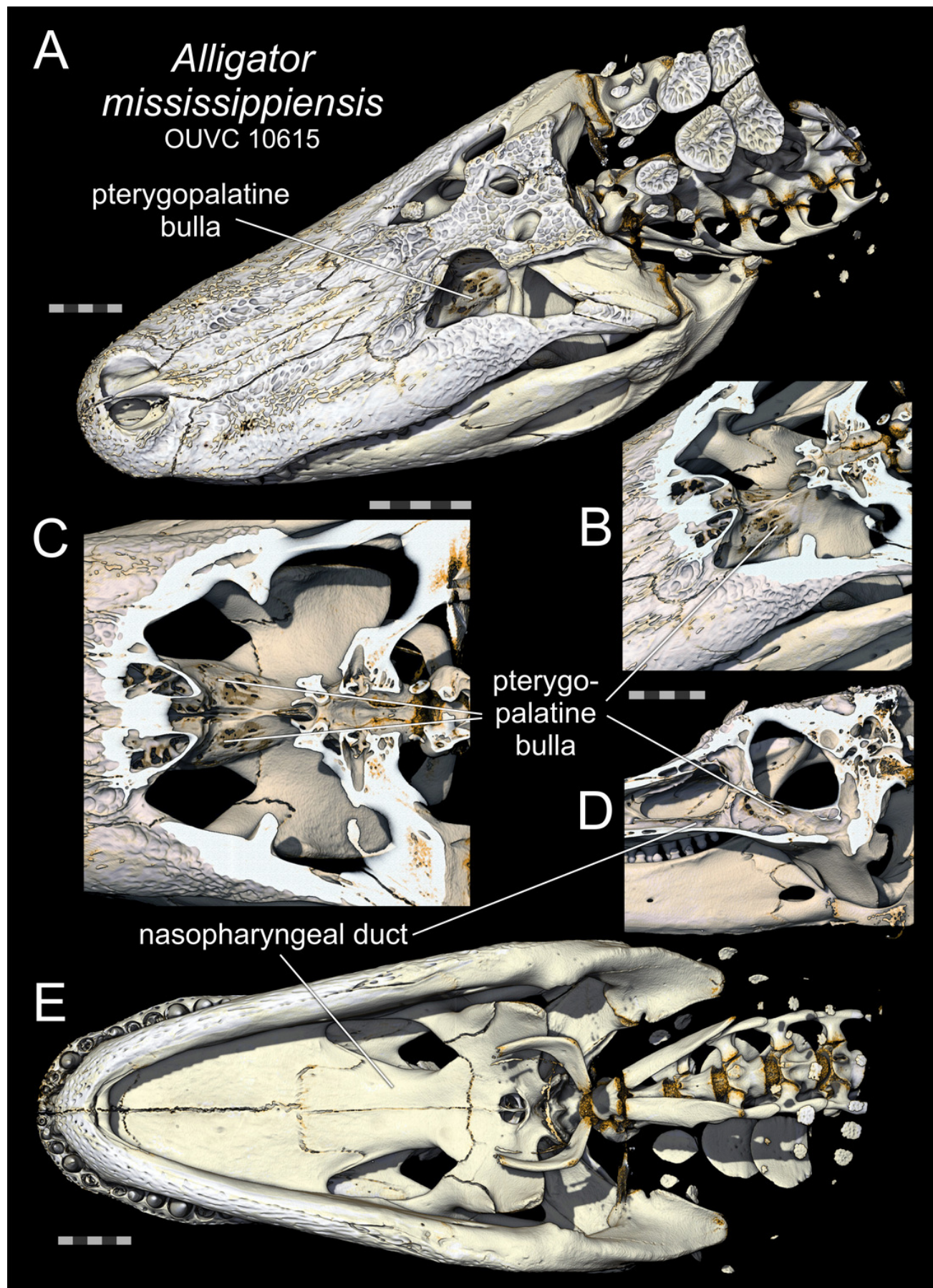
Figure 4

Measurements used in the present study

Measurements used in the present study. Left inset details measurements from the rostrum; right inset details measurement from the palate. See main text for the key to the abbreviations.
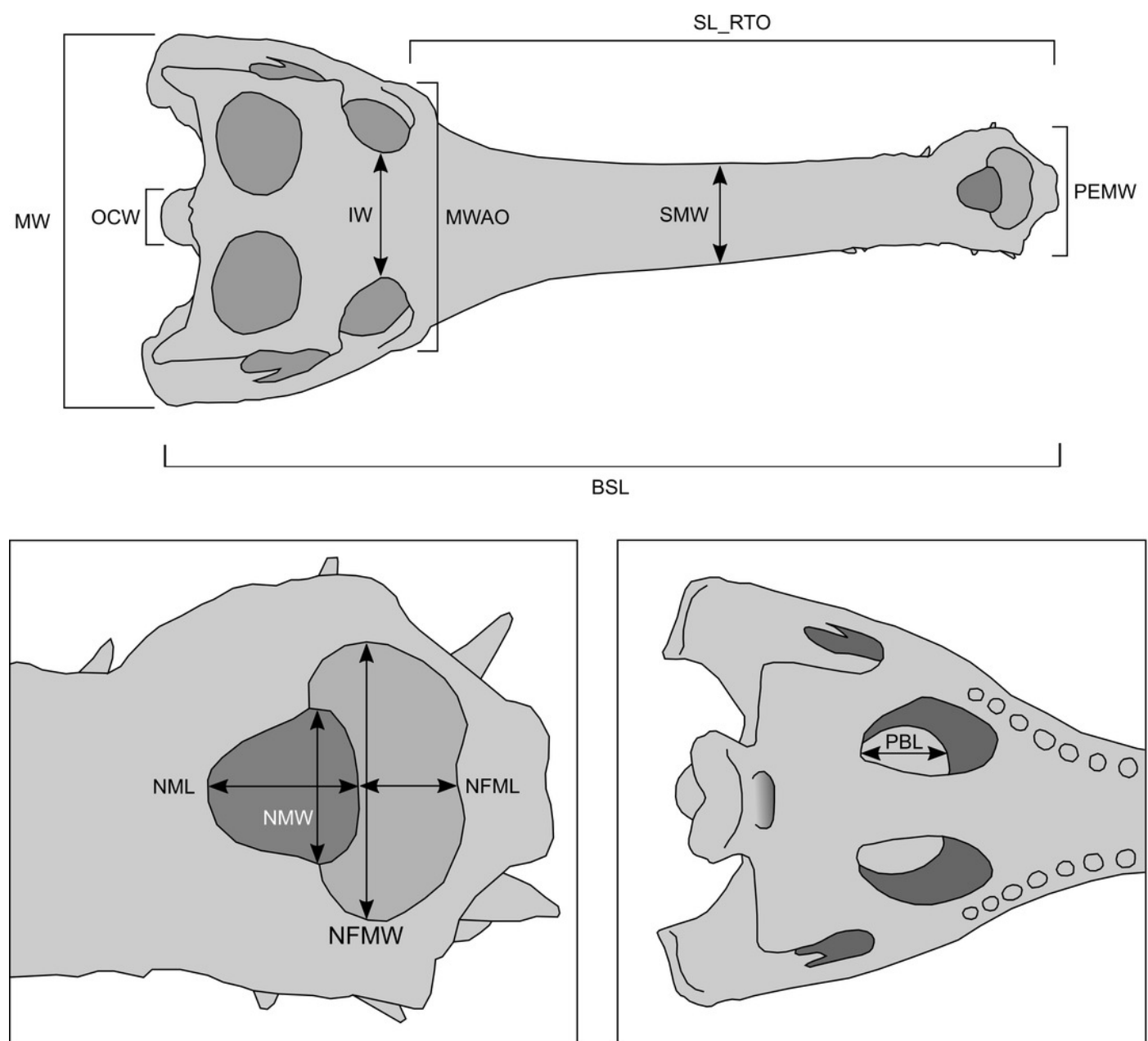
Figure 5

Gharial narial fossa and pterygoid bullae presence/absence

Distribution of narial fossa and pterygoid bullae presence/absence across gharial skulls of different sizes (measured as MW). Insets at right illustrate the variable in question.
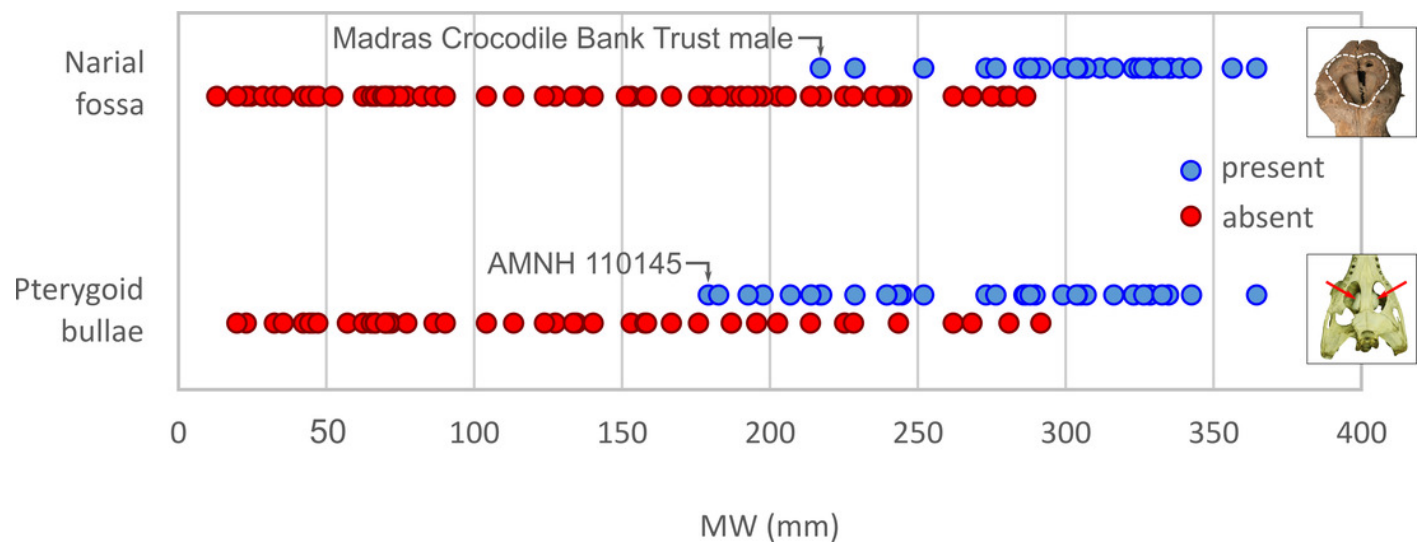
Figure 6

Reduced major axis regressions for nine of the assessed continuous variables

Reduced major axis regressions for nine of the continuous variables examined here. (A) log BSL vs. log MW, (B) log OCW vs. log MW, (C) log SL_RTO vs. log MW, (D) log SMW vs. log MW, (E) log PEMW vs. log MW, (F) log NMW vs. log MW, (G) log NML vs. log MW, (H) log MWAO vs. log MW, (I) log IW vs. log MW. Males (possessing narial fossae) are identified with blue triangles. Black dots represent osteologically immature individuals and/or females.
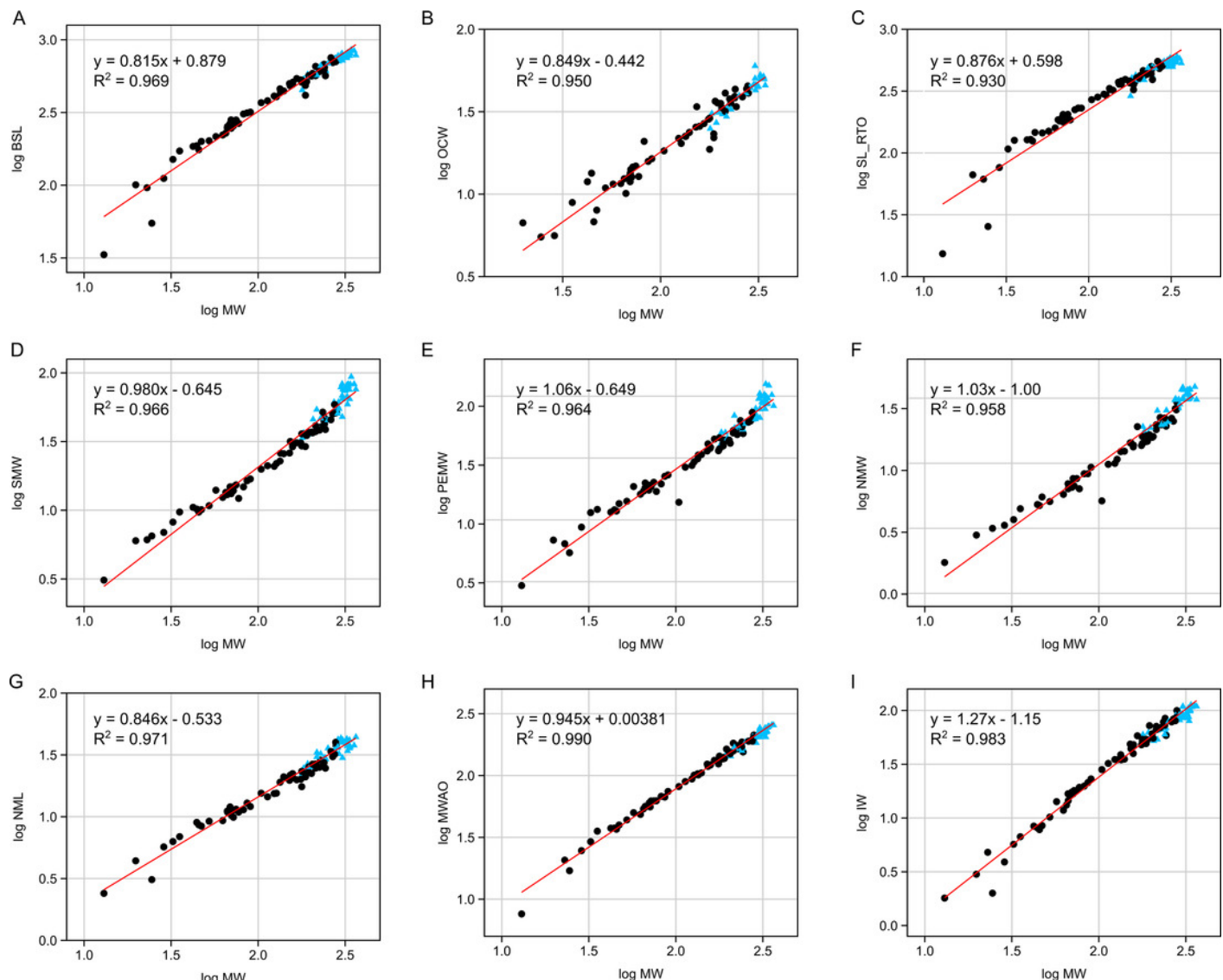
Figure 7

Residual variances for the nine continuous variables examined.

Residual variances (± 95% confidence intervals) for the nine continuous variables examined. Numbers provided above each of the variables indicate sample size.