Ontogeny of a sexually selected structure in an extant archosaur *Gavialis gangeticus* with implications for sexual selection in dinosaurs

David W. E. Hone[1], Jordan C. Mallon[2,3], Patrick J. Hennessey[1, 4], Lawrence M. Witmer[5]

1. School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London, E1 4NS, UK.
2. Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada.
3. Department of Earth Sciences, Carleton University, 2115 Herzberg Laboratories, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada.
4. Georgia Southern University, 4324 Old Register Rd, PO Box 8042-1, Statesboro, GA, 30460, USA.
5. Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Ohio Center for Ecology and Evolutionary Studies, Ohio University, Athens, OH 45701, USA.

Corresponding Author:

David W. E Hone

School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London, E1 4NS, UK Email address: d.hone@qmul.ac.uk

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Abstract

Detecting sexual dimorphism in extinct reptiles is difficult given their long growth periods and the uncertain sex of fossil specimens. The extant gharial (*Gavialis gangeticus*) is a large crocodylian that in males possesses a sexually selected structure – the ghara – that has an osteological correlate in the presence of a fossa that is associated with the nares. This makes the species a unique model for potentially assessing dimorphism in lineages such as dinosaurs and pterosaurs. Here we assess the dimorphism of *G. gangeticus* across 106 specimens and show that the presence of a narial fossa and pterygoid bullae diagnose adult male gharials. Males are larger than females; however, the level of size dimorphism and that of other cranial features is low between the two and is difficult to detect. Dimorphism in fossil reptiles is very difficult to detect without 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. The problem of assessing possible sexual selection in extinct lineages is especially acute in groups such as the non-avian dinosaurs (hereafter simply 'dinosaurs') and other reptiles (Knell et al., 2013). Lineages may show only sexual size dimorphism, or dimorphism in terms of major osteological traits (e.g., crests and horns), or may be under mutual sexual selection leading to a lack of dimorphism, and dimorphic traits are not necessarily linked to evolutionary pressures based around reproductive success or socio-sexual dominance (e.g., see Hone, Niash & Cuthill, 2012; Hone & Mallon, 2017 and references therein). As a result, the case for sexual selection in dinosaurs and other fossil reptile lineages has been controversial. In some taxa, however, there is

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evidence for sexual dimorphism (e.g., Sengupta, Ezcurra & Bandyopadhyay, 2017) and for the presence of traits that were likely used as socio-sexual signals (O'Brien et al., 2018).

There are also limitations to the available models among extant animals for potential comparisons to animals such as dinosaurs. Large mammals may be comparable in size to some dinosaurs and have some ecological similarities but have a huge evolutionary difference and grow rapidly to adult size. Extant reptiles often show high levels of sexual size dimorphism (Fitch, 1981; Cox, Butler & John-Adler, 2007), but most reptiles are small and attain adult size rapidly. The extant phylogenetic bracket for dinosaurs consists of birds and crocodylians, making them potentially better candidates (Witmer, 1995a). However, as with mammals, birds mature rapidly, and their small size and often limited dimorphism also makes them problematic. Crocodylians, in contrast, may be an excellent model with respect to dimorphism. As with many or even most dinosaurs, they reach large sizes, grow slowly over many years, are sexually mature well before maximum size, lay eggs, have large numbers of offspring, and often show sexual size dimorphism.

Among extant crocodylians, the gharial (*Gavialis gangeticus*), now known in the wild only from the Indian subcontinent, is a uniquely appropriate example (Fig. 1). These specialised piscivores may reach 6 m or more in length (Hasan & Alam, 2016). Other crocodylians often show body size dimorphism and some other limited degrees of dimorphism (see Moore et al., 2019), but the gharial shows sexual dimorphism not just in body size (Hasan & Alam, 2016). The larger males also bear a ghara – a growth of tissue on the rostrum that is absent in females (Martin & Bellairs, 1977; Biswas, Acharjyo & Mohapatra, 1977; Whitaker and Whitaker, 1989). The ghara is a soft tissue structure that grows behind and over the external nares but is supported by an osteological change to the rostrum with a depression anterior to the nares (Iordansky,

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1973) seen in skulls of larger males (Martin & Bellairs, 1977). Some early descriptions of the ghara suggest that it is bony and may even be inflated, but this is not the case (Martin & Bellairs, 1977).

The exact function of the ghara is uncertain, but as it only appears in larger, and presumably sexually mature, males (Martin & Bellairs, 1977; Biswas, Acharjyo & Mohapatra, 1978; Whitaker & Whitaker, 1989) it would be reasonable to assume it functions in sexual display. Large males are seen to be dominant over smaller males and females (Whitaker & Basu, 1983). Suggested functions of the ghara include making alterations to the calls of males (a hissing sound not made by females or young males; Whitaker & Whitaker, 1989), or as a visual display signal to females (Martin & Bellairs, 1977). Large males also possess an additional secondary sexual characteristic consisting of a pair of expanded bullae on the dorsal aspect of the pterygoid bones (Fig. 2), not present in small males or apparently in females (though this is uncertain). Being connected to the vocal tract, the pterygoid bullae could function as a resonating chamber and thus may be linked to the possibility of the ghara functioning in sound production or modification (Martin & Bellairs, 1977), though vocalisations are rare (Whitaker & Basu, 1983; Dinets, 2013) arguing against this interpretation.

Ontogenetic data are limited to a few scattered accounts. For example, Biswas, Acharjyo & Mohapatra (1978) described a male of c. 2.5 m total length and aged 11.5 years as showing the first signs of a ghara, with that animal showing 'sex play' (which we assume to mean courtship behaviour) aged 12.5 years suggesting the growth of this feature is linked to maturity (females appear to mature at around 2.6 m in length – Whitaker & Basu, 1983). Similarly, Whitaker and Whitaker (1989) described one male as having a snout resembling that of a female until it was 11 years old when the ghara started to develop; the ghara folded caudally over the nostrils at age 14

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years and reached fully adult form by age 18 years. Martin & Bellairs (1977) suggested that males of around 3 m or so in total length will exhibit a small ghara though they also referred to previous reports suggesting this is normally present only in males in excess of 4.5 m. Clearly, this is a feature that is not present in small / young animals. Moore et al. (2019) observed that onset of puberty in the male Morelet's crocodiles (*Crocodylus moreletii*) as taken by the development of the penile glans was coincident with changing cranial shape suggesting a potentially similar pattern.

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Here we look at sexual dimorphism in the skull of *Gavialis* based on a large dataset of specimens as a model for detecting sexual dimorphism and the identity of specimens in extinct reptiles, including dinosaurs. We use the largest known sample of gharial data to assess sexual dimorphism in these animals and to examine the feasibility of detecting dimorphism in extinct reptile lineages.

Abbreviations

BSL, basal skull length (premaxilla to occipital condyle); IW, interorbital width; MW, maximum width of skull (across quadratojugals); MWAO, maximum width across orbits; NFML, narial fossa maximum length; NFMW, narial fossa maximum width; NML, naris maximum length; NMW, naris maximum width; OCW, occipital condyle width; PBL, average pterygoid bulla length; PEMW, premaxillary expansion maximum width; SL_RTO, snout length rostral to orbits; SMW, snout minimum width (mid-length).

Materials & Methods

Two binary variables and 13 continuous variables (Fig. 3; Appendix 1) were collected from 106 gharial skulls accessioned in 36 museum collections around the world. Where possible, these

were measured first-hand with calipers, but it was necessary to measure most of them digitally based on photographs including scale bars. It was impossible to measure all variables because some skulls were incomplete or variably covered with skin. Sex data were not given for most specimens, and when they were, it was unclear whether the sex was confirmed by observation of the gonads, or whether it was inferred from the presence/absence of the ghara. To both avoid uncertainty and increase the sample size of sexed individuals, we assumed that specimens bearing a narial fossa (the osteological correlate of the ghara) were male; those lacking a narial fossa were assumed to be immature and/or female. A small ghara has been reported in a captive animal that, when dissected, was seen to have ovaries, but this was assumed to have been a pathological individual (Martin & Bellairs, 1977). It is therefore reasonable to assume that animals with a narial fossa are male.

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To assess allometry in those continuous variables, it was necessary to first choose a regressor. Visual inspection of the skulls, and prior published work (Piras et al., 2014), suggested that variables associated with the snout vary widely in the adults, so we chose maximum skull width (MW), measured across the outside of the quadratojugals, as our regressor. The data were initially log-transformed then subjected to reduced major axis (RMA) regression, which accounts for measurement error in both the independent and dependent variables. Isometry was rejected if the confidence intervals of the regression slope did not bound a value of 1. Negative allometry was manifest if the confidence intervals were < 1; positive allometry was manifest if the confidence intervals were > 1.

We used the gharial data to attempt to model the detection of sexual dimorphism in the fossil record by disregarding sex information (inferred from narial fossa presence/absence). Following the methodology of Mallon (2017), we tested for dimorphism in the continuous data by first

subjecting the residuals of the RMA regressions to Shapiro-Wilk and Anderson-Darling tests for normality. Residuals deemed significantly non-normal ($\alpha = 0.05$) were subjected to a supplemental Hartigan's dip test, which yields the likelihood that the data are distributed unimodally (Hartigan & Hartigan 1985).

As a final attempt to quantify sexual dimorphism, we reasoned that dimorphic structures should exhibit higher variance of the RMA residuals than non-dimorphic structures. To test for this, we used Levine's test for homogeneity of variance from means, with follow-up F-test pairwise comparisons. The multiple comparisons were adjusted using Holm–Šidák correction.

Results

General observations

Maximum skull width (MW) varies between 13 mm and 365 mm (embryonic and large adult skulls, respectively) in our dataset. The smallest skull having a narial fossa is the Madras Crocodile Bank Trust male, where MW = 217 mm (Fig. 4) or approximately 60% maximum size. Above MW = 280 mm, all skulls possess a narial fossa; thus, the largest skulls are male. The smallest skull possessing pterygoid bullae (but lacking a narial fossa) is from the American Museum of Natural History (AMNH) 110145, where MW = 179 mm.

Thirty-one of the 106 skulls possess narial fossae. Where determinable (some lack palates or are otherwise obscured), all of these possess pterygoid bullae. The bullae thus appear to be universally present in males. There are, however, 11 skulls lacking a narial fossa but having bullae (Fig. 4). Of these, six are smaller than the Madras Crocodile Bank Trust male, and all are smaller than MW = 280 mm, which is the lower threshold at which the narial fossa is consistently expressed (Fig. 4). If the bullae are indicative of the male sex, which seems likely, they show up earlier in ontogeny, at approximately 50% maximum size.

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184 **Allometry**

185 The results for the all-inclusive allometric analyses are summarized in Figure 5 and Table
186 S1. MW is a good predictor of all continuous cranial variables ($R^2 > 0.92$, $p < 0.0001$). Positively
187 allometric variables include PEMW and IW. Negatively allometric variables include BSL, OCW,
188 NML, and MWAO. The three remaining variables (SL_RTO, SMW, and NMW) grow
189 isometrically.

190 The largest males consistently plot above the regression line for SMW, PEMW, and
191 NMW (Fig. 5), suggesting that these variables increase very rapidly at large body sizes. Follow-
192 up allometric analyses of just the male data (having pterygoid bullae/narial fossa) reveal positive
193 allometry in all three variables (Table S2), with slopes greater than those reported for the entire
194 dataset, albeit with slightly reduced goodness of fit ($R^2 > 0.75$, $p < 0.0001$).

195 NFML and NFMW scale with positive allometry, but the relationship with MW is
196 insignificant (Table S2). PBL is weakly but positively correlated with skull size in males. We
197 were unable to reject the null hypothesis of isometry (Table S2).

198

199 **Sexual dimorphism**

200 Males categorically differ from females in the presence of a narial fossa (~ ghara) and,
201 ostensibly, the presence of pterygoid bullae. Males are further distinguished by their absolutely
202 larger skulls at maturity (MW > 287 mm), relatively shorter and wider rostra, and wider terminal
203 rosettes that support larger nares.

204 Without knowing the sexes a priori (as in fossil taxa), it is otherwise difficult to detect
205 dimorphism in those continuous variables. With the exception of NML, the residuals for all

cranial variables are significantly non-normal, but in no case are they significantly non-unimodal (Table S3). The ability to detect dimorphism in the three most obviously dimorphic continuous variables (SMW, PEMW, and NMW) does not increase by considering only adults (MW ≥ 179 mm, the smallest male having pterygoid bullae). The adult NMW residuals are not significantly non-normal, and the adult SMW and PEMW residuals are not significantly non-unimodal (Table S3).

On average, the SMW, PEMW, and NMW residuals exhibit higher variances (≥ 0.004) than the non-dimorphic residuals (Fig. 6). Levene's test for homogeneity of variance from means is highly significant ($p < 0.0001$). Follow-up pairwise comparisons (Table S4) reveal that variance for the SMW, PEMW, and NMW residuals is usually significantly higher compared to the other residuals. Variance does not differ significantly between any of the three dimorphic variables.

Discussion

Sexual dimorphism and sexual selection in *Gavialis*

The results here broadly align with previous assessments of dimorphism and the ghara in *G. gangeticus*. Males are larger than females, and the former show both a fossa associated with the nares and bullae on the palate. These latter features appear only in larger animals and thus with the onset of sexual maturity. The smallest specimen with a narial fossa in our sample is slightly smaller, at 58 cm in skull length, than the smallest reported by Martin and Bellairs (1977; 69 cm), but the samples are broadly comparable.

Martin and Bellairs (1977) stated that a ghara appears in males of around 3 m in total length, which following their head to body ratio of 1:6 would equate to a skull length of approximately 42 cm. This is considerably smaller than the smallest skull recorded here with a narial fossa and suggests that the ghara may be growing before a fossa is developed. This would

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match with the apparent development of the bullae prior to the presence of the fossa and would indicate that the ghara and bulla develop nearly simultaneously.

The narial fossa shows strong positive allometry compared to other traits in the skull (Fig 5) which would suggest that the ghara attaching to the fossa functions as a display feature (cf. O'Brien et al., 2018). The ghara would also be a major handicap to males when foraging and thus would form an honest signal of the fitness of the owner. The large size of the ghara (Fig. 1) might also increase visibility to prey, but would certainly offer considerable drag on the otherwise thin snout of an animal hunting in water (Martin & Bellairs, 1977), presumably incurring a cost to feeding effectiveness. This is especially true since an extra drag generated near the tip of the jaws would be much greater than closer to the rear of the skull, as drag is a function of distance from the joint squared. The extreme variation of the morphology of the ghara (Fig. 1) also points to it being a socio-sexual signal (see Hone & Naish, 2013 and references therein).

Initially the pterygoid bullae must grow rapidly as the smallest record of them in our sample are still sizeable structures (37 mm long on the Field Museum of Natural History (FMNH) specimen 22025, a skull 61 cm long), although it is possible that at smaller sizes they are hidden in photographs of the palate. However, bullae growth is isometric which suggests that although they are important structures, their size is not critical. We hypothesise therefore that these features function as a signal to females that the male is mature but that there is no additional information about the size and quality of the male possessing them or otherwise their growth would be expected to be positively allometric.

The pterygoid bullae likely function in sound production. Although it has been noted that gharials rarely produce calls (Whitaker & Basu, 1983; Dinets, 2013), many crocodylians

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communicate using very low-frequency vocalizations (Garrick, Lang & Herzog, 1978), some of which extend into the infrasonic range (i.e., below the range of normal human hearing; Todd, 2007) and so gharial calls may not have been detected by previous researchers. The bullae are dorsal dilations of the nasopharyngeal duct (Wegner, 1958; Witmer, 1995b, 1999) and thus are connected to the vocal/respiratory tract and would act as acoustic resonators, potentially lowering the frequencies of sounds produced. Whether the pterygoid bullae are important for acoustic signaling remains unconfirmed, but they are large structures that presumably have some positive function in that they occupy space in the orbit and palatal regions and would presumably adversely affect other functions (e.g., restricting the attachments of jaw adductor muscles such as *M. pterygoideus dorsalis*). The vocal capabilities of alligators are well known (Garrick, Lang & Herzog, 1978; Vliet, 1989; Todd, 2007), and alligators have similar (but presumably nonhomologous) inflations of the nasopharyngeal ducts known as the pterygopalatine bullae (Wegner, 1958; Witmer, 1995b, 1999), perhaps lending some credence to an acoustic resonance function in gharials, as well. Dinets (2013) reported specifically that gharials do not use infrasound, but the basis for this assertion is not clear, and we regard acoustic signaling (potentially including an emphasis on low-frequency sounds, perhaps even infrasound) as the current best-supported hypothesis for the function of the pterygoid bullae.

When analysed in the males alone, some of the traits in the skull also show positive allometry. The premaxillary expansion maximum width, the snout minimum width, and the naris maximum width are all disproportionately larger in the largest males. All are potentially associated with the ghara and the increase of the fossa to accommodate it. The expansion of the premaxillary rosette and relative increase of the snout minimum width could help strengthen the

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skull given the drag of a large ghara but could also potentially have an ecological function permitting engaging of larger prey.

Given that the pterygoid bullae ontogenetically appear in males of breeding age, we suggest that they provide a general infrasonic acoustic signal that would function to advertise their maturity to females (and also perhaps to other males). This signal would serve to attract attention to the male (even while out of line of sight such as underwater), and the primary visual signal of status and quality would be the ghara. The visual signal is enhanced by a spray of water emerging from the ghara itself upon exhalation, accompanied by an audible hiss and hum (Whitaker & Whitaker, 1989).

Detecting sexual dimorphism in the fossil record

To date, no dinosaur has been determined to exhibit sexual dimorphism under rigorous analysis (Mallon, 2017). Tests for dimorphism in fossil taxa may be confounded by a combination of small sample sizes and protracted growth coupled with uncertainty of the age or sex of most specimens so that small males may be similar in size to large females (Hone & Mallon, 2017). Dinosaurs matured sexually before they reached growth asymptotes, and as a result may expect to have initiated the growth of a sexually selected structure earlier in ontogeny than in animals that reach maximum size at a similar time to sexual maturity. This also fits with the high juvenile mortality of dinosaurs, and thus may have promoted early reproduction (Hone & Mallon, 2017). Thus although we may expect to, and do, see strong positive allometry for features such as crests and horns under sexual selection (Hone, Wood & Knell, 2016; Brown, 2017), these features may start earlier and grow more slowly than seen in traditional models such as large mammals.

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304 The results here support these general contentions that dimorphism is very difficult to detect
305 in taxa showing growth over considerable periods of time. Were these animals recovered from
306 the fossil record, the presence of the fossa and bullae give clear osteological characters that are
307 not obviously functional and appear only in larger specimens, and these would likely be
308 identified as a separate sex to the smaller specimens that lacked these features. *Gavialis*
309 *gangeticus* is identified by numerous osteological traits (Iordansky, 1973) present in all
310 specimens, which would mark out both sexes as being one species. However, in the absence of
311 these discrete traits, determining dimorphism would be very difficult. Hone and Mallon (2017)
312 assessed detection of sexual dimorphism in alligators based on body size and suggested a
313 minimum of 60 animals might be needed to statistically support dimorphism. Here there is no
314 clear statistical signal for any continuous traits producing two clusters across all specimens
315 despite a much larger dataset. Even when restricted to those we have identified as adult males
316 and females, the signal is weak and present only in some features which are also associated with
317 the ghara. Were these fossil animals there would be little to separate out the sexes.
318
319 **Future work and conservation implications**
320 Further work is needed to confirm the hypotheses laid out here. An exact relationship
321 between the timing of sexual maturity and the physical expression of the ghara, narial fossa, and
322 pterygoid bullae is key to understanding gharial reproductive biology. A formal assessment of
323 any social or mating displays and the differing acoustic and visual components of this are also
324 important and may provide information critical to breeding efforts given the severe extinction
325 risk of this species.

This study also raises additional questions about the functional morphology of gharials which may also be important for understanding their ecology and behaviour. The ghara will induce severe drag on the jaws on an animal catching prey underwater, while the bullae will affect the palatal muscles which will influence the function of the jaws.

Finally, we note that the largest narial fossae are associated with an increase in the size of the terminal rosette and a broadening of the snout (increased minimum width) and this may increase the ability of males to catch larger prey. Although we did not measure tooth size across all specimens, we note that some of the largest males (e.g., Grant Museum - LDUCZ X215) apparently have disproportionately large teeth compared to smaller animals and this would likely allow them to tackle larger prey than may be expected. Given the great differences in size between mature gharials and young juveniles, there would be niche partitioning between various different growth stages, as seen in other crocodylians (Dodson, 1975). However, there may also be ecological separation between larger (and presumably fitter) gharial males and other adult animals and if so, this is also a very important possible consideration for sustaining populations. Removal of high-quality males has the potential for profoundly negative effects in small populations (Knell & Martínez-Ruiz, 2017) so if our hypothesis about prey choice is correct, suitable prey for larger males must be a consideration in establishing suitable habitats for sustainable gharial populations.

Moore et al. (2019) noted an increase in size in the anterior teeth of male Morelet's crocodiles (*Crocodylus moreletii*) at sexual maturity and suggested this was lined to male-male interactions over females and this could be the case here. However, developmentally this is much earlier in the crocodile than the shift suggested here, and it was only the anterior teeth not the entire tooth row, implying that these two developments are not synonymous. In any case, as

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noted by Moore et al. (2019), increased head size is correlated with increased bite power and opportunities to tackle larger prey (Erickson et al., 2012), so regardless of the selective pressures that might produce more robust crania and teeth in large males, the hypothesised dietary shift may still be present.

Conclusions

We agree with previous studies in that the ghara and associated narial fossa and the pterygoid bullae are male traits of extant gharials and most likely have a socio-sexual function in displays. Limited dimorphism in size and various cranial traits are exhibited with males being larger than females.

In the absence of key traits, determining moderate sexual dimorphism (body size or other measurements) is going to be extremely difficult, even with good sample sizes and complete sets of data. Doing so for the fossil record for taxa such as dinosaurs (but also many other extinct reptiles and amphibians) is extraordinarily difficult unless the degrees of dimorphism are extreme. Prolonged growth and the overlap of males and females in terms of body size and even features linked to sexually selected structures (such as here, the width of the terminal rosette) make the identity with regards to sex of individual specimens highly cryptic.

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Figure captions

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

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

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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. 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 4. 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 5. 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 are identified with blue triangles.

Figure 6. Residual variances (± 95% confidence intervals) for the nine continuous variables examined.