

# Intraspecific variation in the skull morphology of the black caiman *Melanosuchus niger* (Alligatoridae, Caimaninae)

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## Abstract

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*Melanosuchus niger* is a caimanine alligatorid widely distributed in the northern region of South America. This species has been the focus of several ecological, genetic and morphological studies. However, morphological studies have generally been limited to examination of interspecific variation among extant species of South American crocodylians. Here, we present the first study of intraspecific variation in the skull of *M. niger* using a two-dimensional geometric morphometric approach. The crania of 52 sexed individuals varying in size were analysed to quantify shape variation and to assign observed shape changes to different types of intraspecific variation, that is, ontogenetic variation and sexual dimorphism. Most of the variation in this species is ontogenetic variation in snout length, skull depth, orbit size and the width of the postorbital region. These changes are correlated with bite force performance and probably dietary changes. However, a comparison with previous functional studies reveals that functional adaptations during ontogeny seem to be primarily restricted to the postrostral region, whereas rostral shape changes are more related to dietary shifts. Furthermore, the skulls of *M. niger* exhibit a sexual dimorphism, which is primarily size-related. The presence of non-size-related sexual dimorphism has to be tested in future examinations.

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## Introduction

Knowledge of vertebrate morphology and its intraspecific variation (e.g. ontogenetic variation, sexually dimorphic variation, polymorphisms) is crucial for accurate systematic, taxonomic, evolutionary, ecological, physiological and functional hypothesis of the different groups (Sudhaus and Rehfeld 1992; Wiesemüller *et al.* 2003; Carpenter 2010; Porro *et al.* 2011). Among extant crocodylians, previous studies of skull anatomy and intraspecific variation (including ontogenetic variation), evolution and functional morphology include those of Mook (1921), Kälin (1933), Medem (1963), Iordansky (1973), Dodson (1975), Busbey (1989), Hall and Portier (1994), Monteiro and Soares (1997), Brochu (1999, 2001), Verdade (2000), Erickson *et al.* (2003, 2012), McHenry *et al.*

(2006), Piña *et al.* (2007), Wu *et al.* (2006), Sadleir and Makovicky (2008), Platt *et al.* (2009) and Bona and Desojo (2011). Nevertheless, lack of morphological studies and data, especially for osteology, is common to all extant South American crocodylians. This is largely because crocodylian skeletons are rare in South American herpetological collections. This is unfortunate because detailed knowledge of the osteology of extant species and its morphological variation is central to the reconstruction of the evolutionary history of a group, especially given that most of fossil specimens are preserved only by skeletons (and generally as fragments).

Extant South American alligatorids (Caimaninae) are grouped in three genera: *Paleosuchus* Cuvier 1807, *Caiman* Spix 1825 and *Melanosuchus* Spix 1825. Certain taxonomic controversies among caimanines are related to *Melanosuchus*.

This genus is represented by two species: the extinct *Melanosuchus fisheri* Medina, 1976 from the Upper Miocene (Urumaco Formation) of Venezuela (Sánchez-Villagra and Aguilera 2006) and the extant *Melanosuchus niger* Spix, 1825, in which the species status of *M. fisheri* has been questioned (Brochu 1999). The presence of prominent rostral ridges on the skull, shared with the extant *Caiman latirostris* Daudin, 1802, and the extinct *Caiman* cf. *lutescens* (Langston 1965) from the Miocene of South America, supports a sister group relationship of *M. niger* with these two species in morphological cladistic analyses (Norell 1988; Poe 1997; Brochu 1999, 2003, 2010, 2011; Aguilera et al. 2006; Bona 2007). This result has generated differing taxonomic proposals with regard to the putative paraphyly of the genus *Caiman* (Norell 1988; Poe 1997).

*Melanosuchus niger* is particularly interesting among Alligatoridae, because it is one of the largest extant members of the group, with adult males sometimes exceeding 6 m in length (Cott 1926; Brazaitis 1974). It has been the focus of ecological (Otte 1974; Medem 1981; Plotkin et al. 1983; Herron 1991; Pacheco 1994; Horna et al. 2001; Villamarín-Jurado and Suárez 2007; Marioni et al. 2008) and genetic works (Farias et al. 2004; de Thoisy et al. 2006; Vasconcelos et al. 2006), as well as a limited number of morphological studies (Mook 1921; Kálin 1933; Medem 1963). Although there have been some qualitative studies on differently sized specimens of *M. niger* (Mook 1921), its general intraspecific morphological variation is poorly understood. The purpose of the present study is to quantify, describe and interpret the intraspecific variation in the skull of *M. niger* using a geometric morphometric approach.

Geometric morphometrics is widely regarded as a powerful tool for taxonomic identification and functional interpretations (Rohlf and Marcus 1993; Zelditch et al. 2004) and has great potential to characterize developmental and genetic effects on morphological shape (Klingenberg 2010). This method quantifies differences in shape between objects from coordinates of homologous landmark locations, after the effects of nonshape variation (position, size and rotation) are mathematically held constant (Adams et al. 2004; Zelditch et al. 2004). Geometric landmark-based analysis captures and retains more information about shape than traditional morphometric measurements (e.g. linear distances, ratios and measurements of angles), which often fail to capture the full geometry of the original object (Rohlf and Marcus 1993; Rohlf 2000; Hammer and Harper 2006). Geometric morphometrics has been used successfully to document intraspecific variation and to test specific taxonomic and ontogenetic biological hypotheses (Richtsmeier et al. 1993; O'Higgins and Collard 2002; Bookstein et al. 2003; Elewa 2004; Zelditch et al. 2004). However, only a few analyses of extant crocodylian skulls using a geometric morphometric approach have been previously conducted. Monteiro et al. (1997) studied ontogenetic changes in three *Caiman* species, and Pierce et al. (2008) described the cranial morphospace of extant crocody-

lians and its correlation with functional morphology based on finite element modelling (FEM). Piras et al. (2009) investigated the influence of phylogeny and ecological factors (climate change) on the skull shape of Alligatoroidea and Crocodyloidea, and Piras et al. (2010) compared allometric trajectories in different crocodylian taxa to test phylogenetic hypotheses about the relationships between gavials (*Gavialis gangeticus*) and false gavials (*Tomistoma schlegelii*).

In the context of quantifying skull shape variation within *M. niger*, we want to classify ontogenetic variation and sexual dimorphism and to test whether skull shape is correlated with bite force performance (which is used as a functional proxy) in this species. The results are compared with published data for other crocodylian species to identify probable key patterns in intraspecific variation in cranial shape and how these patterns might be related to ecology and function.

## Material and methods

### Specimen sampling

The crania of 52 individuals of *M. niger* (Table S1, Supporting information) were analysed using a two-dimensional geometric morphometric approach. Most of the specimens ( $n = 40$ ) are deposited in the Zoologische Staatssammlung, Munich (Germany), which possesses one of the oldest and largest collections of extant crocodylian skulls in the world. These specimens were collected mainly on Marajó Island (NE Brazil) between 1906 and 1925 during expeditions made by the Zoologische Staatssammlung. Additional material ( $n = 12$ ) was examined in the Senckenberg Naturmuseum Frankfurt (Germany), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (Germany), Zoologisches Museum Hamburg (Germany) and Naturhistorisches Museum Wien (Austria). The length of the skulls varies from approximately 5–50 cm (Table S1, Supporting information). All specimens, for which historical notes are available, represent wild individuals. This is crucial as skull shape can vary between wild and captive crocodylians (Erickson et al. 2004), which could influence the results of shape analyses.

Determination of the sex of each specimen was based on original collection data. Unfortunately, most specimens were collected almost 100 years ago, so we were not able to ascertain how sex was originally determined (e.g. direct inspection of the cloaca, see Chabreck 1963; Ziegler and Olbort 2007), and no historical notes exist describing this procedure (F. Glaw, personal communication). Therefore, it is possible that the data set includes some misidentifications of sex, especially between small males and females within the same size range. However, the skull of the largest male is approximately 14 cm (i.e. about 30%) longer than that of the largest female (see Table S1, Supporting information), which represents a percentile size difference between females and males similar to that documented for other crocodylian species (Chabreck and Joanen 1979; Wilkinson and Rhodes 1997; Platt et al.

2009). Based on this observation, some specimens were classified as males by one of the authors (CF) based on their larger size (see Table S1, Supporting information).

Unfortunately, there is no information on the sex of the smallest specimens, and little is known about the reproduction biology of *M. niger*. According to Herron (1991), it reaches sexual maturity at total body length of c. 2 m. Assuming isometric growth between body length and skull length (Webb and Messel 1978; Verdade 2000; Wu *et al.* 2006) and a similar relation between body length at maturity and maximum body length as in *Alligator mississippiensis* (Chabreck and Joanen 1979; Wilkinson and Rhodes 1997), the skull length of a *M. niger* individual reaching sexual maturity is approximately 22–26 cm. Based on this estimation, specimens with skull lengths <22 cm were treated as immature juveniles in all analyses.

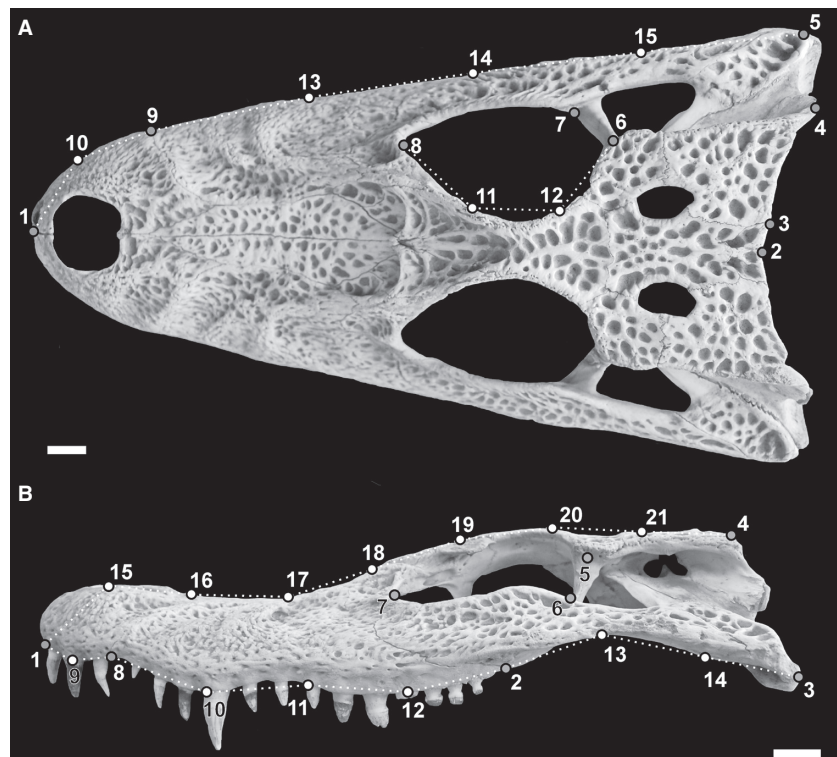
Furthermore, the age and the place of capture of each specimen investigated in this study are unknown. Thus, it is not possible to test geographical variation in *M. niger* with the current data set.

#### Geometric morphometrics

The majority of specimens were macerated skulls. Skulls were photographed in dorsal and lateral views. Because macerated skull material of juvenile *M. niger* is rare, we additionally X-rayed the skulls of alcohol-preserved specimens in dorsal and lateral views (Table S1, Supporting information). The

X-ray data were outputted as digital images. Skull shape was captured using eight (lateral view) and nine (dorsal view) homologous landmarks (Fig. 1, see Supporting information for full description of landmarks), which were digitized onto photographs/X-ray images using the program tpsDig2 (Rohlf 2005). We used landmarks of types 1 (good evidence for anatomical homology, such as points where two bone sutures meet) and 2 (good evidence for geometric homology, such as points of maximal curvature or extremities) following the terminology of Bookstein (1991). Because the detection of some bone sutures and the determination of the shape of the lateral temporal fenestra were difficult or unfeasible in the X-ray images, we additionally captured the outer shape of the skull and the shape of the orbit with help of six (dorsal view) and 13 (lateral view) semilandmarks. For dorsal view, we used a unilateral configuration for the right skull side, because a mirroring of the landmark and semilandmarks would not add more information (Young *et al.* 2010), but in contrast would inflate the degrees of freedom in the statistical analyses (Pierce *et al.* 2008).

The landmark and semilandmark coordinates of both data sets were superimposed separately using generalized Procrustes analysis in tpsrelw (Rohlf 2003), which serves to minimize nonshape variation between species, including that caused by size, location and orientation (Gower 1975; Rohlf and Slice 1990). To reduce the effects of variation due to the arbitrary spacing of the semilandmarks over the sampled curves, semilandmarks were slid along their



**Fig. 1**—Visualization of the landmarks and semilandmarks used for the geometric morphometric analyses. —**A.** Specimen ZSM 86/1911 in dorsal view. —**B.** Specimen ZSM 68/1911 in lateral view. Landmark points are shown in grey, and semilandmark points are shown in white. The shape described by semilandmarks is shown as dotted line. Scale bar 2 cm.

tangent to align with the perpendicular of corresponding semilandmarks, minimizing the Procrustes distance. Thus, semilandmarks capture primarily information about the bowing of the sampled curve (Bookstein 1997; Zelditch *et al.* 2004).

Before starting the analyses, the percentage error for each landmark and semilandmark was computed for two specimens (one represented by a photograph and the other by an X-ray image; with  $n = 10$  repetitions), each in dorsal and lateral view after the method of Singleton (2002) (Table S2, Supporting information). The methodological error for plotting landmarks by hand varies between 0.08% and 1.27% and should have no significant impact on the shape analyses. Afterwards, the superimposed landmarks and semilandmark data of each data set were imported into MorphoJ 1.05d (Klingenberg 2011) and subjected to principal component analysis by generating a covariance matrix. This procedure assimilates data from all Procrustes coordinates and allows the underlying variation in the data to be characterized based on few axes that account for maximum variance (Hammer and Harper 2006).

#### *Ontogenetic patterns*

To assign the observed shape changes to different types of intraspecific variation and to visualize ontogenetic changes in skull shape, we performed a multivariate regression in MorphoJ on the Procrustes coordinates as well as the scores of the first two PC axes against log-transformed centroid size. If an ontogenetic signal is present, then a statistical correlation between size and shape should be detectable. The degree of correlation was estimated as a percentage of total shape variation, with a corresponding  $P$  value computed by a permutation test with 10 000 permutations and a null hypothesis of independence (Drake and Klingenberg 2008). Additionally, we tested the correlation between shape and size by performing a two-block partial least squares (2B-PLS) in MorphoJ using the Procrustes coordinates and centroid size. This method explores the pattern of covariation between two sets of variables by constructing pairs of variables that are linear combinations of the variables within each of the two sets, and it accounts for as much as possible of the covariation between the original data sets. In contrast to linear regression models (which casts one set of variables as dependent on the other), 2B-PLS treats the two sets of variables symmetrically in an attempt to find relationships between them without assuming that one is the cause of the other (Rohlf and Corti 2000; Zelditch *et al.* 2004). The strength of the correlation is given by the RV coefficient (Robert and Escoufier 1976) and a  $P$  value generated by 10 000 permutations. To test whether the results could be falsified by the use of two different sources of samples (i.e. photographs and X-ray images), we repeated the analyses excluding all specimens represented by X-ray images and compared the results with the previous analyses.

#### *Sexual dimorphism*

To determine whether skull shape is related to sex, we created a second data set including only mature males and females and performed a new generalized Procrustes fit. We assessed the statistical significance of differences between males and females based on the Procrustes coordinates using nonparametric multivariate analysis of variance (NPMANOVA) with 10 000 permutations and Euclidian distances (= Procrustes distances) using the software PAST 2.09 (Hammer *et al.* 2001). This approach tests for significant differences in the distribution of groups within the morphospace (Anderson 2001). One of the strengths of this approach is that it does not assume or require normality from the multivariate data. The test generates  $F$  and  $P$  values, with a significant difference between the sexes indicated when the  $F$  value is high and the  $P$  value is less than 0.05. Due to size differences between males and females, it is possible that apparent sexual dimorphism is largely due to size. To detect evidence for non-size-related sexual dimorphism, we repeated the analysis mentioned above with the nonallometric residuals, which were separated from the Procrustes coordinates by a multivariate regression against log-transformed centroid size. The resulting residuals contain the nonallometric component of shape variation within the data set (Drake 2011). Because the data set contains two groups (females and males), it is further worthwhile to consider group structure for size correction by repeating the analyses with a pooled within-group regression. For that, the deviations of the observations of the group averages of the variables are used instead of the deviations from the grand mean making a correction by subtracting the differences between the group means (Klingenberg 2009). If a significant difference remains in the NPMANOVA, one can conclude that males and females show sexual dimorphism in cranial shape that is not related to size.

#### *Shape versus function*

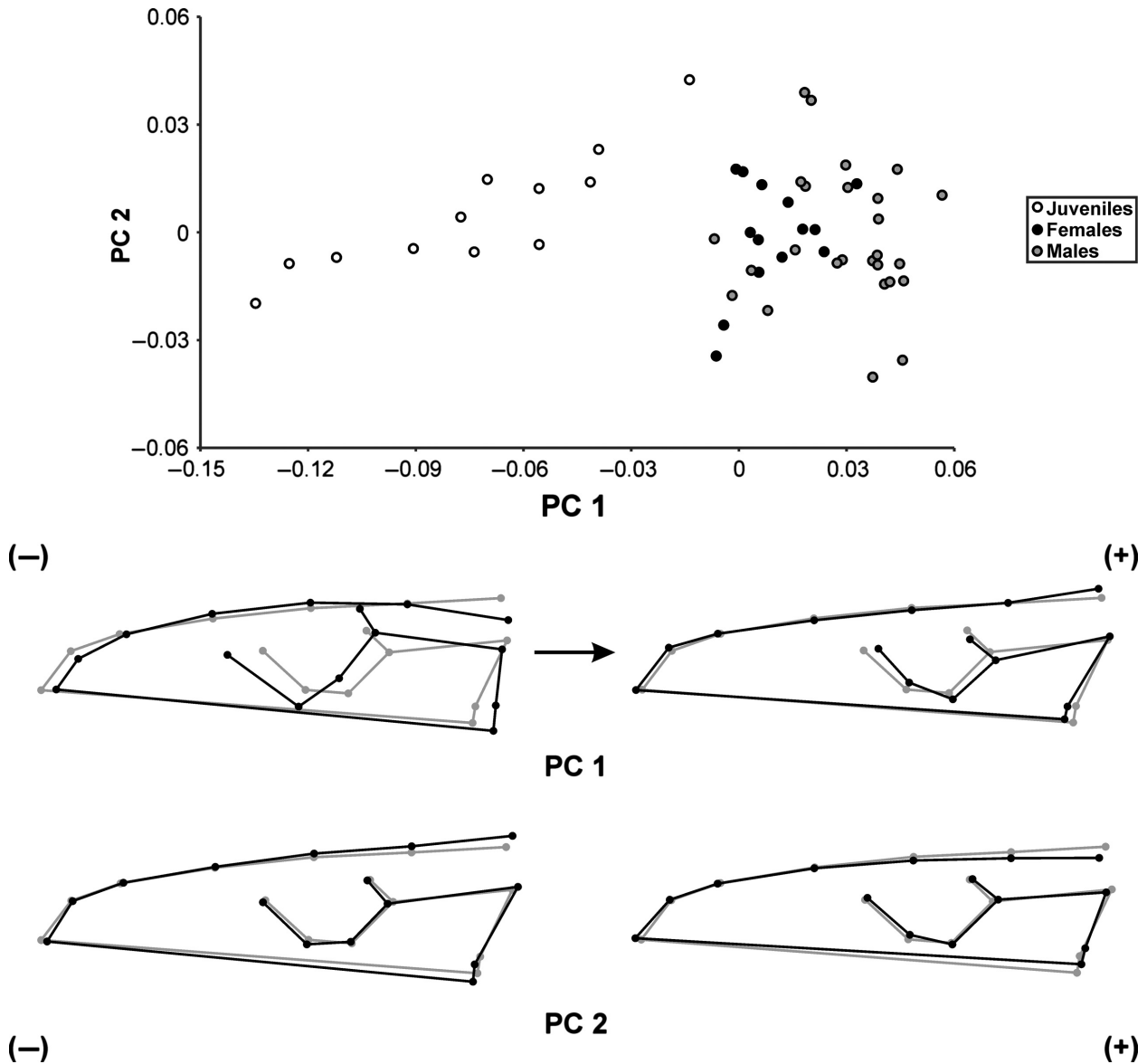
To test whether function is correlated with shape variation in the cranium, we follow Erickson *et al.* (2003), who propose an allometric relationship between bite force and skull length. We used the bite force performance of *A. mississippiensis* in relation to skull length as functional proxy. The bite force was estimated for every specimen and log-transformed. We performed a 2B-PLS in MorphoJ to determine the degree of covariation of bite force with cranial shape. Furthermore, we performed regression analyses between bite force and Procrustes coordinates. Both, the 2B-PLS and the regression analyses were performed as explained above (see Ontogenetic and Ontogenetic patterns section). To test whether bite force is only correlated with allometric shape changes, we additionally performed all analyses with nonallometric residuals. As described above, we excluded all specimens represented by X-ray images in further data set to verify whether the results are falsified by the usage of two different sources of samples.

**Results**

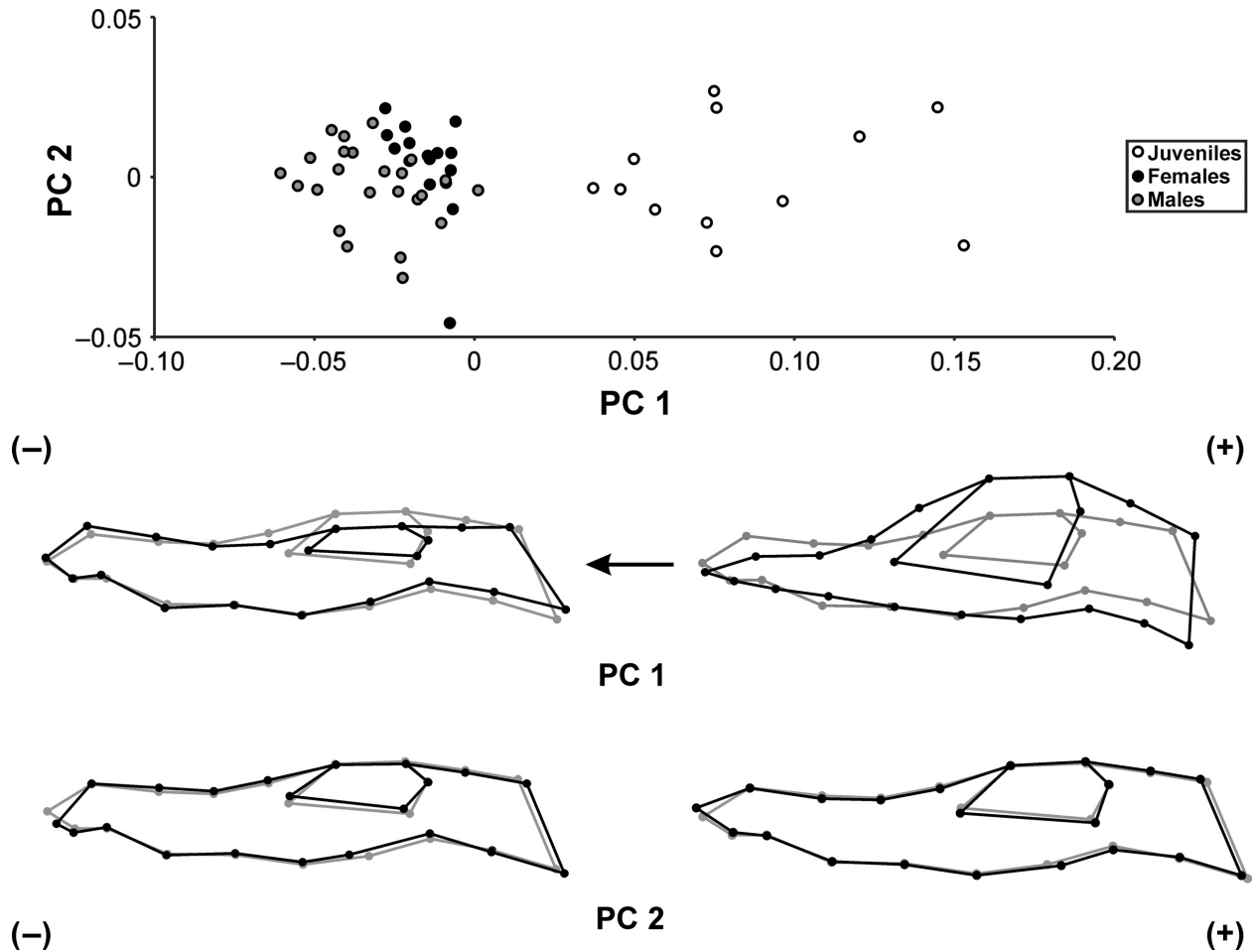
In dorsal view, the first two axes account for more than 80% of total variance (PC 1: 71.07% and PC 2: 9.90%). The first PC axis mainly accounts for the relative length of the snout, the relative size and position of the orbit influencing the relative width of the jugal region and the interorbital width, the relative length and width of the skull roof table and the position of the jaw angle in anterolateral–posteromedial direction. The second PC axis is primarily associated with the shape of the snout tip, the position of the orbit

influencing the length of the snout and the postorbital region inversely and the overall width of the postrostrum influencing the relative width of the occipital region and the position of the jaw joint in anteromedial–posterolateral direction (Fig. 2).

In lateral view, the first two PC axes account for almost 80% of total variance (PC 1: 74.96% and PC 2: 5.97%). The first PC accounts for mainly the depth of the tip of the rostrum, the relative size of the subnarial gap, the shape and length of the ventral margin of the maxilla, the relative size of the orbit influencing the overall depth of the jugal and the



**Fig. 2**—Two-dimensional cranial morphospace and major shape changes (black outlines) of *Melanosuchus* with respect to the consensus shape (grey outline) for the dorsal view. The arrows indicate shape changes along the first principal component axis (PC1) that is highly correlated with skull size.



**Fig. 3**—Two-dimensional cranial morphospace and major shape changes (black outlines) of *Melanosuchus* with respect to the consensus shape (grey outline) for the lateral view. The arrows indicate shape changes along the first principal component axis (PC1) that is highly correlated with skull size.

orbital and postorbital region and the relative position of the jaw joint in anteroventral–posterodorsal direction. The second PC accounts for the shape and the relative length of the premaxilla, the relative length of the maxilla and the length of the postorbital region (Fig. 3).

Based on the 2B-PLS and the regression test, skull shape (in both views) is strongly correlated with centroid size (log-transformed), indicating that the observed skull shape variation contains a linear allometric relationship between shape and size (log-transformed). This relationship only holds for the first PC, however (Table 1), with the remaining PCs not correlated with centroid size. This indicates that PC1 largely accounts for shape changes associated with size. Males and females possessing similar centroid sizes are not separated from each other (Fig. 4A,B). The exclusion of those specimens represented by X-ray images from the data sets has no significant impact on the general results, but the estimated correlations are slightly weaker. Skull shape is still correlated

with centroid size when only adult specimens are considered. However, these correlations are noticeably weaker than in the two previous cases.

Based on the Procrustes coordinates, a significant difference was found between males and females for both dorsal and lateral views (dorsal view:  $F = 4.31$ ,  $P = 0.002$ ; lateral view:  $F = 4.62$ ,  $P < 0.001$ ). Based on nonallometric residuals (nonpooled), both sexes cannot be distinguished from each other on a significant level (dorsal view:  $F = 1.66$ ,  $P = 0.139$ ; lateral view:  $F = 1.22$ ,  $P = 0.271$ ). However, using nonallometric residuals from a pooled within-group regression, a significant difference between both sexes remains as for the Procrustes coordinates, but at a lower level (dorsal view:  $F = 2.18$ ,  $P = 0.020$ ; lateral view:  $F = 2.33$ ,  $P = 0.033$ ).

Both the 2B-PLS and the regression test indicate that Procrustes shape variation in *M. niger* is significantly correlated with bite force (log-transformed) (Table 1). This relationship

**Table 1** Relationship between skull shape, centroid size and bite force in *Melanosuchus niger* based on regression test (proportion of total variation in percentage/*P* value) and the two-block partial least squares analysis (2B-PLS; RV coefficient/*P* value)

	Dorsal view		Lateral view	
	Regression	2B-PLS	Regression	2B-PLS
<b>Centroid size</b>				
Procrustes coordinates (all)	65.28/<0.001	0.905/<0.001	68.97/<0.001	0.913/<0.001
PC 1 (all)	91.53/<0.001	0.955/<0.001	91.79/<0.001	0.918/<0.001
PC 2 (all)	1.25/0.437	0.013/0.430	0.90/0.510	0.009/0.500
Procrustes coordinates (no X-ray)	48.44/<0.001	0.816/<0.001	51.58/<0.001	0.844/<0.001
PC 1 (no X-ray)	87.05/<0.001	0.871/<0.001	86.19/<0.001	0.862/<0.001
PC 2 (no X-ray)	0.92/0.527	0.009/0.533	5.82/0.108	0.058/0.109
Procrustes coordinates (adults)	20.07/<0.001	0.430/<0.001	22.54/<0.001	0.528/<0.001
Procrustes coordinates (adults) <sup>a</sup>	15.83/<0.001	0.345/<0.001	16.83/<0.001	0.399/<0.001
<b>Bite force</b>				
Procrustes coordinates (all)	66.36/<0.001	0.920/<0.001	69.34/<0.001	0.918/<0.001
PC 1 (all)	93.07/<0.001	0.931/<0.001	92.27/<0.001	0.923/<0.001
PC 2 (all)	1.64/0.364	0.016/0.372	1.69/0.353	0.017/0.365
Procrustes coordinates (no X-ray)	50.57/<0.001	0.852/<0.001	51.08/<0.001	0.836/<0.001
PC 1 (no X-ray)	91.15/<0.001	0.912/<0.001	84.93/<0.001	0.849/<0.001
PC 2 (no X-ray)	1.41/0.443	0.014/0.431	7.53/0.068	0.075/0.068
Res. coordinates (all)	0.08/1.000	0.002/1.000	0.09/1.000	0.002/1.000
Res. coordinates (no X-ray)	0.29/0.999	0.006/0.100	0.06/1.000	0.001/1.000

<sup>a</sup>Pooled analyses.

is mainly influenced by PC 1, which is also strongly correlated with centroid size. By contrast, after excluding allometric information from shape, no significant correlation remains. These results remain if all specimens represented by X-ray images are excluded from the data set.

## Discussion

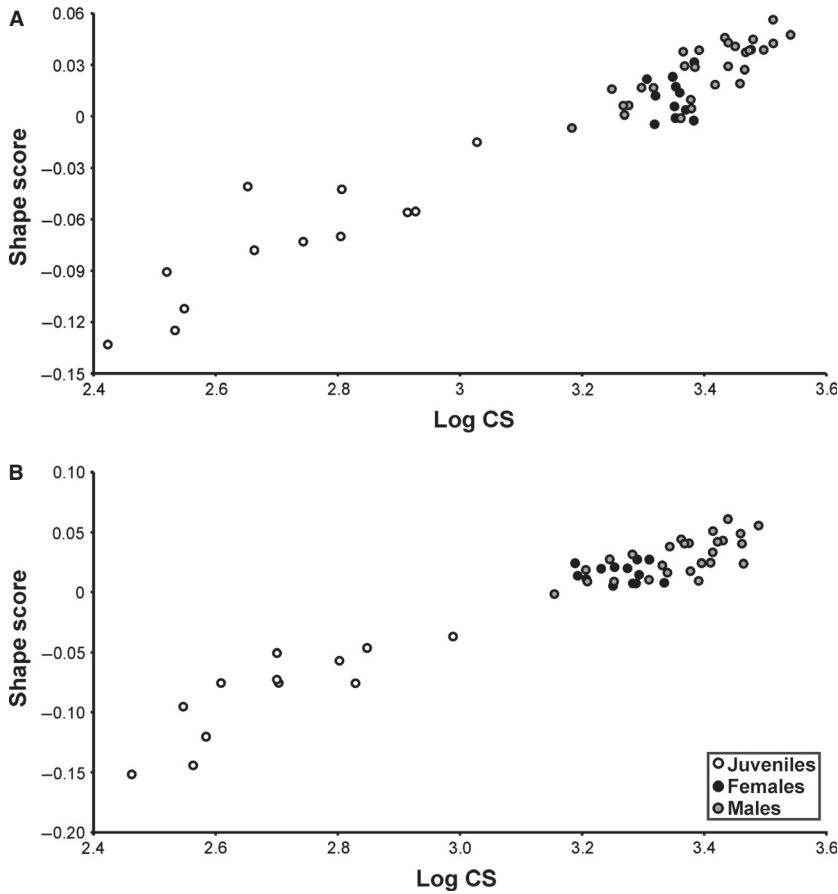
### Ontogenetic patterns

The correlation between overall shape and centroid size (log-transformed) in *M. niger* may represent an ontogenetic pattern, which is characterized by the shape change captured by the first PC. Skulls of young juveniles have a very short snout, which is wide in dorsal view, but dorsoventrally pointed, and the ventral margin is straight. The orbit is very large, the jugal region is slender in both dorsal and lateral views, and the postorbital region is elongated in anterior–posterior direction. The broad skull roof table is posteriorly inclined in lateral view. The posterior end of the skull is relatively narrow, and the jaw joint lies substantially anterior to the posterior end of the skull roof table. During ontogeny, the snout becomes longer due to the elongation of the maxilla, but also narrower (in dorsal view) and deeper (in lateral view). The tip of the snout becomes blunter, and a subnasal gap is developed between premaxilla and maxilla. The ventral margin of the maxilla becomes anteriorly convex in lateral view. The postrostrum becomes flattened, and the relative size of the orbit decreases. In contrast, the jugal region becomes broader and deeper. The postorbital region becomes shorter,

but expands posterolaterally. Due to the overall flattening of the postrostrum, the skull roof table becomes straight in lateral view, and the jaw joint moves substantially posterior to this.

As was mentioned in the introduction, the numbers of studies investigating the cranial shape variation of crocodylians using geometric morphometric are rare. This is especially true for ontogenetic studies (Monteiro *et al.* 1997; Piras *et al.* 2010). On the other hand, in the past, ontogenetic variation of crocodylian skulls was studied multiple times by traditional morphometrics (Dodson 1975; Webb and Messel 1978; Hall and Portier 1994; Monteiro and Soares 1997; Wu *et al.* 2006). As no standardized samplings and analyses do exist so far, we compared the ontogenetic shape variation of *M. niger* with that of other crocodylian species taken from literature (Table 2). However, due to differences in the sampling of skull measurements, landmark configurations and statistical analyses in the studies mentioned above, the current comparison is limited to whether certain skull regions growth is allometric (positive or negative) or isometric during ontogeny.

*Melanosuchus niger* shares a relative increase in snout length with all extant crocodylians except *Tomistoma schlegelii* and *G. gangeticus* (Piras *et al.* 2010). A relative increase in the width of the snout during ontogeny occurs also in *Alligator sinensis* (Wu *et al.* 2006), *Crocodylus acutus*, *Mecistops cataphractus* and *T. schlegelii* (Piras *et al.* 2010), whereas *Caiman crocodilus* and *Caiman yacare* (Monteiro and Soares 1997) show a relative narrowing of the rostral width. In *A. mississippiensis*, the posterior part of the snout grows isometrically, but the snout tip increases in width (Dodson



**Fig. 4**—Relationship between skull shape and log-transformed centroid size (Log CS). —**A.** Dorsal view. —**B.** Lateral view.

**Table 2** Ontogenetic patterns in the skull of *Melanosuchus* and other extant crocodylian species. (+) Positive allometric growth, (–) negative allometric growth, (=) isometric growth, (?) unknown; (1) Monteiro and Soares (1997); (2) Dodson (1975); (3) Wu *et al.* (2006); (4) Piras *et al.* (2010); (5) Hall and Portier (1994); (6) Monteiro *et al.* (1997); (7) Webb and Messel (1978)

Species	Reference	Snout (= rostrum)			Orbital region		Postorbital region	
		Length	Width	Depth	Orbit size	Interorbital width	Length (skull roof)	Posterior width
<i>Melanosuchus niger</i>		+	+	+	–	+	–	+
<i>Caiman crocodilus</i>	1, 6	+	–	?	–	+	–	=
<i>Caiman latirostris</i>	1, 6	+	=	?	–	+	–	+
<i>Caiman yacare</i>	1, 6	+	–	?	–	+	–	=
<i>Alligator mississippiensis</i>	2	+	+/=	?	–	+	?	=
<i>Alligator sinensis</i>	3	+	+	?	–	–	–	=
<i>Crocodylus acutus</i>	4	+	+	+	–	?	–	+
<i>Crocodylus novaeguineae</i>	5	+	+/-	?	–	+	+	+
<i>Crocodylus porosus</i>	7	+	?	?	?	+	?	+
<i>Mecistops cataphractus</i>	4	+	+	+	–	?	–	+
<i>Tomistoma schlegelii</i>	4	=	+	+	–	?	=	+
<i>Gavialis gangeticus</i>	4	=	=	=	–	?	=	=

1975), whereas in *Crocodylus novaeguineae* snout, width decreases from early juveniles to small adults, but increases again in later ontogenetic stages (Hall and Portier 1994). In *C. latirostris*, snout width grows isometrically (Monteiro and Soares 1997). A relative ontogenetic increase in the depth of

the snout occurs in *C. acutus*, *M. cataphractus* and *T. schlegelii*. The relative decrease in the orbit size is the only common ontogenetic pattern that is present in all taxa used for comparison. A further common ontogenetic pattern in crocodylians is the relative increase in the interorbital width,

which is only absent in *A. sinensis*. Another common pattern is the relative decrease in length of the postorbital skull roof, which is probably related to the relative increase in the snout length mentioned above (Marugán-Lobón and Buscalioni 2003). However, in *T. schlegelii* and *G. gangeticus*, the postorbital skull roof grows almost isometrically. Finally, most taxa show a relative increase in the posterior width of the postorbital region during ontogeny with the exception of *A. mississippiensis*, *A. sinensis*, *C. crocodilus*, *C. yacare* and *G. gangeticus*, which show isometric growth.

Based on this simplified comparison, most crocodylian taxa share similar ontogenetic patterns in skull shape, and some ontogenetic trajectories seem to be relatively constrained (e.g. the relative increase in the snout length together with relative decrease in the postorbital length, the relative decrease in the orbit size together with the relative increase in the interorbital width). The only exception is the long-snouted *G. gangeticus*, which shows an almost isometric growth of the skull during ontogeny (Piras et al. 2010). However, the current comparison of ontogenetic trends in crocodylian skulls is very limited, as the available ontogenetic studies on crocodylian skulls are not standardized in sampling and methods. Thus, with the data on hand, it is not possible to compare the growth of certain skull regions relative to others or how ontogenetic patterns in the cranium differ within different taxa in detail. To improve our understanding of cranial ontogeny in crocodylians also with respect to heterochronic events within their evolution, it would be worthwhile to investigate ontogenetic shape variation in the future with broader taxon and specimen sampling and with standardized methods.

#### Sexual dimorphism

Sexual dimorphism in crocodylians is described for both Caimaninae (Verdade 2000, 2003) and Crocodylinae (Hall and Portier 1994; Platt et al. 2009) and mainly size-related. The larger size in male crocodylians has been found to be the result of generally faster and longer growth (Chabreck and Joanen 1979; Rootes et al. 1991; Wilkinson and Rhodes 1997), probably resulting from different selective pressures faced by females and males (see Shine 1989; Platt et al. 2009). Female growth trajectories probably slow upon reaching sexual maturity as energy is shifted from growth to reproduction (Andrews 1982), whereas males are subjected to sexual selection favouring large body size in male-to-male interactions (Anderson and Vitt 1990; Cooper and Vitt 1993). A size-related sexual dimorphism is also present in *M. niger*, in which the skull length of the largest males is about 30 per cent longer than that of the largest females.

In contrast, non-size-related sexual variation seems to be less common in crocodylians. It is only documented for the shape of the external naris in *G. gangeticus* (Hall and Portier 1994) and *C. latirostris* (Verdade 2000). Furthermore, Webb and Messel (1978) describe a non-size-related sexual dimor-

phism in the interorbital width and width of the skull roof table in *Crocodylus porosus*. Thus, non-size-related sexual dimorphism documented in these crocodylian taxa is only restricted to certain skull regions. Using nonpooled regression for computing nonallometric residuals, no difference can be detected between males and females, rejecting the presence of a non-size-related sexual dimorphism for *M. niger*. In contrast, taking within-group variation between females and males into account, overall skull shape of males and females shows a non-size-related sexual dimorphism. Thus, these two contradicting results are primarily caused due to different methodological approaches considering within-group variation during the regression estimation or not. At this stage, the presence of a non-size-related sexual dimorphism in *M. niger* has to be seen with caution. This is further true because the sample size of females ( $n = 14$ ) is distinctively smaller than that of males ( $n = 26$ ). Additionally, it is possible that the large number of landmarks and semilandmarks compared with the sample size of both males and females could lead to wrong positive signals due an overestimation of the true degrees of freedom (Zelditch et al. 2004). Thus, the current findings should be tested in future examinations in greater detail with larger data sets for *M. niger*, different landmark configurations (also with a three-dimensional approach) as well as for other crocodylians.

#### Shape versus function

That allometric skull shape variation in *M. niger* is significantly correlated with bite force performance (log-transformed) is not surprising because the functional proxy used in this study is correlated with skull size (Erickson et al. 2003, 2004, 2012). Deleting allometric information from shape leads to a nonsignificant signal, showing that this correlation seems to be primarily related to allometric shape changes caused by ontogenetic growth. However, in recent crocodylians, stress distributions during biting do not distribute over the whole skull uniformly, but are largely concentrated in the postrostrum, peaking around the orbits and the temporal fenestrae during bilateral and unilateral biting, and laterally at the level of the jugal during lateral loading to the snout (Pierce et al. 2008). Thus, the strong correlation found between bite force performance and ontogenetic shape variation is probably an artefact of the allometric dependency of both parameters. Based on the biomechanical results of Pierce et al. (2008), only the shape changes seen in the postrostral region (including the expansion of the jugal, the relative decrease in the orbit size and the posterolateral expansion of the postorbital region) seem to be functionally related. In this context, the posterolateral expansion of the postorbital region might further correlate with the increase in the muscle system in the postorbital region to achieve higher bite performance (Schumacher 1973; van Drongelen and Dullemeijer 1982; Busbey 1989; Erickson et al. 2003, 2012; Bona and Desojo 2011).

Based on the results of recent studies on cranial function in several crocodylian species with different snout morphologies, snout shape is not strongly correlated with function, but instead with prey selection (McHenry *et al.* 2006; Pierce *et al.* 2008; Erickson *et al.* 2012). Thus, it is likely that the shape changes seen in the snout of *M. niger* (including the relative increase in the snout length and depth, the formation of a subnarial gap and the shape changes of the ventral margin of the maxilla) are rather related to changes in diet preferences and feeding behaviour through ontogeny. Hatchlings and small *M. niger* possessing skulls with a short pointed snout feed predominantly on aquatic and shoreline invertebrates (e.g. insects, beetles and snails) (Da Silveira and Magnusson 1999; Horna *et al.* 2001, 2003), whereas adults possessing deep and elongated snouts with a subnarial gap feed on medium-sized prey, such as capybaras (*Hydrochoerus hydrochaeris*), white-lipped peccaries (*Tayassu pecari*), long-whiskered catfishes (Pimelodidae) and piranhas (Trutnau 1994; Horna *et al.* 2001). Similar dietary shifts from small invertebrates to medium-sized vertebrates during ontogeny are also documented for other crocodylian species (Cott 1961; Webb and Messel 1978; Hutton 1987; Webb *et al.* 1991; Cleuren and de Vree 2000). Especially, the development of a convex shape of the anterior part of the ventral margin of the maxilla could be related to the development of a prominent upper caniniform tooth, which is used primarily for seizing larger prey (Erickson *et al.* 2012). In this context, the ontogenetic shape changes in the jugal and postorbital region provide the mechanical background for handling larger prey.

Finally, the usage of two different sample sources (i.e. photographs and X-ray images) affected only the selection of landmarks to capture skull shape, as many skull structures (e.g. bone sutures or the lateral temporal fenestra) were not visible in the X-ray images. However, the similar results regarding the relation between shape, centroid size and bite forces for both data sets with and without X-ray images (Table 1) as well as the minor error for plotting landmarks on both sample sources (Table S2, Supporting information) indicate that the usage of photographs and X-ray images together did not falsify the current results.

## Conclusions

The present study represents the first assessment of intraspecific variation of the skull of the caimanine crocodylian *M. niger* using a geometric morphometric approach. Skull shape variation is concentrated in the width and height of the postorbital region, the length and depth of the snout, the size of the orbit and the relative position of jaw joint. Similar patterns can be observed in the cranial ontogeny of other crocodylian taxa, but due to the lack of broad-scale examinations with standardized landmark configurations and statistical methods, the results of the current comparison are limited regarding the quality of change. The ontogenetic

shape changes in *M. niger* seem to be correlated with increased bite force performance, but are primarily restricted to the postrostral region. In contrast, shape variation seen in the snout is probably rather related to the changes in diet through ontogeny. Based on the current results, the skull shape of females and males differs on a significant level. Excluding allometric shape variation from the Procrustes coordinates leads to contradicting results based on the consideration of within-group variation while computing nonallometric residuals. Thus, the presence of a non-size-related sexual dimorphism in *M. niger* based on a pooled within-group regression has to be seen with caution and needs to be tested in more detail in future examinations. This is also true because of the small sample sizes in relation to the number of landmarks and semilandmarks and differences of sample sizes between males and females. Because knowledge of intraspecific variation is important for the systematics of extant, but also extinct taxa, it would be worthwhile investigating ontogenetic patterns in different crocodylian taxa with the help of standardized methods (Piras *et al.* 2010) to capture broad-scale patterns of intraspecific variation and specific trajectories in crocodylian ontogeny more precisely. This may in turn allow us to resolve the taxonomic status of problematic extinct species such as *M. fisheri*.

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## References

- Adams, D. C., Rohlf, F. J. and Slice, D. E. 2004. Geometric morphometrics: Ten years of progress following the 'revolution'. *Italian Journal of Zoology* 71: 5–16.
- Aguilera, O. A., Riff, D. and Bocquentin-Villanueva, J. 2006. A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the Upper Miocene Urumaco Formation, Venezuela. *Journal of Systematic Palaeontology* 4: 221–232.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.
- Anderson, R. A. and Vitt, L. J. 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* 84: 145–157.
- Andrews, R. M. 1982. Patterns of growth in reptiles. In: Gans, C. and Pough, F. H. (Eds): *Biology of the Reptilia*, pp. 273–320. Academic Press, New York.
- Bona, P. 2007. Una nueva especie de *Eocaiman* Simpson (Crocodylia, Alligatoridae) del Paleoceno Inferior de Patagonia. *Ameghiniana* 44: 435–445.
- Bona, P. and Desojo, J. B. 2011. Osteology and cranial musculature of *Caiman latirostris* (Crocodylia: Alligatoridae). *Journal of Morphology* 272: 780–795.
- Bookstein, F. L. 1991. *Morphometric Tools for Landmark Data*. Cambridge University Press, Cambridge.
- Bookstein, F. L. 1997. Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. *Medical Image Analysis* 1: 225–243.
- Bookstein, F. L., Gunz, P., Mitteroecker, F., Prossinger, H., Schaefer, K. and Seidler, H. 2003. Cranial integration in *Homo*: Singular warps analysis of the midsagittal plane in ontogeny and evolution. *Journal of Human Evolution* 44: 167–187.
- Brazaitis, P. 1974. The identification of living crocodiles. *Zoologica* 58: 59–105.
- Brochu, C. A. 1999. Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Journal Vertebrate Paleontology* 19: 9–100.
- Brochu, C. A. 2001. Crocodylian snouts in space and time: Phylogenetic approaches toward adaptive radiation. *American Zoologist* 41: 564–585.
- Brochu, C. A. 2003. Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Sciences* 31: 357–397.
- Brochu, C. A. 2010. A new alligatorid from the lower Eocene Green River Formation of Wyoming and the origin of caimans. *Journal Vertebrate Paleontology* 30: 1109–1126.
- Brochu, C. A. 2011. Phylogenetic relationships of *Necrosuchus ionensis* Simpson, 1937 and the early history of caimanines. *Zoological Journal of the Linnean Society* 163: S228–S256.
- Busbey, A. B. 1989. Form and function of the feeding apparatus of *Alligator mississippiensis*. *Journal of Morphology* 202: 99–127.
- Carpenter, K. 2010. Variation in a population of Theropoda (Dinosauria): *Allosaurus* from the Cleveland-Lloyd Quarry (Upper Jurassic), Utah, USA. *Paleontological Research* 14: 250–259.
- Chabreck, R. H. 1963. Methods of capturing, marking and sexing alligators. *Southeastern Association of Game and Fish Commissioners* 17: 47–50.
- Chabreck, R. H. and Joanen, T. 1979. Growth rates of American Alligators in Louisiana. *Herpetologica* 35: 51–57.
- Cleuren, J. and de Vree, F. 2000. Feeding in crocodylians. In: Schwenk, K. (Ed.): *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*, pp. 337–358. Academic Press, New York.
- Cooper, W. E. and Vitt, L. J. 1993. Female mate choice of large male broad-headed skinks. *Animal Behaviour* 45: 683–693.
- Cott, H. B. 1926. Observations on the life habits of some batrachians and reptiles from the lower Amazon, and note on some mammals from Marajó. *Proceedings of the Zoological Society of London* 29: 211–256.
- Cott, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and northern Rhodesia. *Transactions of the Zoological Society of London* 29: 211–356.
- Da Silveira, R. and Magnusson, W. E. 1999. Diets of Spectacled and black caiman in the Anavilhanas Archipelago, Central Amazonia, Brazil. *Journal of Herpetology* 33: 181–192.
- Dodson, P. 1975. Functional and ecological significance of relative growth in *Alligator*. *Zoology* 1975: 315–355.
- Drake, A. G. 2011. Dispelling dog dogma: An investigation of heterochrony in dogs using 3D geometric morphometric analysis of skull shape. *Evolution & Development* 13: 204–213.
- Drake, A. G. and Klingenberg, C. P. 2008. The pace of morphological change: Historical transformation of skull shape in St Bernard dogs. *Proceedings of the Royal Society B* 275: 71–76.
- van Drongelen, W. and Dullemeijer, P. 1982. The feeding apparatus of *Caiman crocodilus*; a functional-morphological study. *Anatomischer Anzeiger* 151: 337–366.
- Elewa, A. M. T. 2004. *Morphometrics: Applications in Biology and Paleontology*. Springer-Verlag, Heidelberg.
- Erickson, G. M., Lappin, A. K. and Vliet, K. A. 2003. The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *Journal of Zoology* 260: 317–327.
- Erickson, G. M., Lappin, A. K., Parker, T. and Vliet, K. A. 2004. Comparison of bite-force performance between long-term captive and wild American alligators (*Alligator mississippiensis*). *Journal of Zoology* 262: 21–28.
- Erickson, G. M., Gignac, P. M., Stepan, S. J., Lappin, A. K., Villet, K. A., Brueggen, J. D., Inouye, B. D., Kledzik, D. and Webb, G. J. W. 2012. Insights into the ecology and evolutionary success of crocodylians revealed through bite-force and tooth-pressure experimentation. *PLoS One* 7: e31781.
- Farias, I. P., Silveira, R., de Thoisy, B., Monjeló, L. A., Thorbjarnarson, J. B. and Hrbek, T. 2004. Genetic diversity and population structure of Amazonian crocodylians. *Animal Conservation* 7: 265–272.
- Gower, J. C. 1975. Generalized Procrustes analysis. *Psychometrika* 40: 33–51.
- Hall, P. M. and Portier, K. M. 1994. Cranial morphometry of New Guinea Crocodiles (*Crocodylus novaeguineae*): Ontogenetic variation in relative growth of the skull and an assessment of its utility as a predictor of the sex and size of individuals. *Herpetological Monographs* 8: 203–225.
- Hammer, O. and Harper, D. A. T. 2006. *Paleontological Data Analysis*. Blackwell Publishing, Malden.
- Hammer, O., Harper, D. A. T. and Ryan, P. D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1–9.
- Herron, J. C. 1991. Growth rates of black caiman *Melanosuchus niger* and spectacled caiman *Caiman crocodilus* and the recruitment of breeders in hunted caiman populations. *Biological Conservation* 55: 103–113.
- Horna, J., Horna, V., Cintra, R. and Vásquez, P. 2001. Feeding ecology of black caiman *Melanosuchus niger* in a western Amazonian forest: The effects of ontogeny and seasonality on diet composition. *Ecotropica* 7: 1–11.
- Horna, V., Zimmermann, R., Cintra, R., Vásquez, P. and Horna, J. 2003. Feeding ecology of the black caiman (*Melanosuchus niger*) in Manu National Park, Peru. *Lyonia* 4: 65–72.

- Hutton, J. M. 1987. Growth and feeding ecology of the Nile crocodile *Crocodylus niloticus* at Ngezi, Zimbabwe. *Journal of Animal Ecology* 56: 25–38.
- Jordansky, N. N. 1973. The Skull of the Crocodilia. In: Gans, C. and Parson, T. S. (Eds): *Biology of the Reptilia*, pp. 201–262. Academic Press, New York.
- Kälin, J. A. 1933. Beiträge zur vergleichenden Osteologie des Crocodilidenschädels. *Zoologisches Jahrbuch* 57: 535–714.
- Klingenberg, C. P. 2009. Morphometric integration and modularity in configurations of landmarks: Tools for evaluating a priori hypotheses. *Evolution & Development* 11: 405–421.
- Klingenberg, C. P. 2010. Evolution and development of shape: Integrating quantitative approaches. *Nature Reviews Genetics* 11: 623–635.
- Klingenberg, C. P. 2011. MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources* 11: 353–357.
- Langston, W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University of California Publications in Geological Sciences* 52: 1–152.
- Marioni, B., Da Silveira, R., Magnusson, W. E. and Thorbjarnarson, J. B. 2008. Feeding behavior of two sympatric caiman species, *Melanosuchus niger* and *Caiman crocodilus*, in the Brazilian Amazon. *Journal of Herpetology* 42: 768–772.
- Marugán-Lobón, J. and Buscalioni, A. D. 2003. Disparity and geometry of the skull in Archosauria. *Biological Journal of Linnean Society* 80: 67–88.
- McHenry, C. R., Clausen, P. D., Daniel, W. J. T., Meers, M. B. and Pendharkar, A. 2006. Biomechanics of the rostrum in crocodilians: A comparative analysis using finite-element modeling. *The Anatomical Record* 288: 827–849.
- Medem, F. 1963. Osteología craneal, distribución geográfica y ecología de *Melanosuchus niger* (Spix), (Crocodylia, Alligatoridae). *Ibidem* 12: 5–19.
- Medem, F. 1981. Los Crocodylia de Sur América. Vol. I. Los Crocodylia de Colombia. Colciencias, Bogotá.
- Monteiro, L. R. and Soares, M. 1997. Allometric analysis of the ontogenetic variation and evolution of the skull in *Caiman* Spix, 1825 (Crocodylia: Alligatoridae). *Herpetologica*, 53: 62–69.
- Monteiro, L. R., Cavalcanti, M. J. and Sommer, H. S. J. 1997. Comparative ontogenetic shape changes in the skull of *Caiman* species (Crocodylia, Alligatoridae). *Journal of Morphology* 321: 53–62.
- Mook, C. C. 1921. Notes on the postcranial skeleton in the Crocodilia. *Bulletin of the American Museum of Natural History* 44: 67–100.
- Norell, M. A. 1988. Cladistics Approaches to Evolution and Paleobiology as Applied to the Phylogeny of Alligatorids. Yale University, New Haven, CT.
- O’Higgins, P. and Collard, M. 2002. Sexual dimorphism and facial growth in papionin monkeys. *Journal of Zoology* 257: 255–272.
- Otte, K. C. 1974. Research programme *Melanosuchus niger*, in the Manu National Park. *World Wildlife Yearbook 1973–1974* 25: 7–260.
- Pacheco, L. F. 1994. Estimating crocodilian abundance in forest lagoons. In: Group, Proceedings of the 12th Working Meeting of the IUCN-SSC Crocodile Specialist. Crocodiles, pp. 241–244. IUCN, Gland.
- Pierce, S. E., Angielczyk, K. D. and Rayfield, E. J. 2008. Patterns of morphospace occupation and mechanical performance in extant crocodilian skulls: A combined geometric morphometric and finite element modelling approach. *Journal of Morphology* 269: 840–864.
- Piña, C., Larriera, A., Siroski, P. and Verdade, L. M. 2007. Cranial sexual discrimination in hatchling broad-snouted caiman (*Caiman latirostris*). *Iheringia, Série Zoologia* 97: 17–20.
- Piras, P., Teresi, L., Buscalioni, A. D. and Cubo, J. 2009. The shadow of forgotten ancestors differently constrains the fate of Alligatoroidea and Crocodyloidea. *Global Ecology and Biogeography* 18: 30–40.
- Piras, P., Colangelo, P., Adams, D. C., Buscalioni, A. D., Cubo, J., Kotsakis, T., Meloro, C. and Raia, P. 2010. The *Gavialis-Tomistoma* debate: The contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships. *Evolution & Development* 12: 568–579.
- Platt, S. G., Rainwater, T. R., Thorbjarnarson, J. B., Finger, A. G., Anderson, T. A. and McMurry, S. T. 2009. Size estimation, morphometrics, sex ratio, sexual size dimorphism, and biomass of Morelet’s crocodile in northern Belize. *Caribbean Journal of Science* 45: 80–93.
- Plotkin, M. J., Medem, F., Mittermeier, R. A. and Constable, I. A. 1983. Distribution and conservation of the black caiman (*Melanosuchus niger*). In: Rhodin, A. and Mitaya, K. (Eds): *Advances in Herpetology and Evolutionary Biology*, pp. 695–705. Museum of Comparative Zoology, Cambridge.
- Poe, S. 1997. Data set incongruence and the phylogeny of crocodilians. *Systematic Biology* 45: 393–414.
- Porro, L. B., Holliday, C. M., Anapol, F., Ontiveros, L. C., Ontiveros, L. T. and Ross, C. F. 2011. Free body analysis, beam mechanics, and finite element modeling of the mandible of *Alligator mississippiensis*. *Journal of Morphology* 272: 910–937.
- Richtsmeier, J. T., Corner, B. D., Grausz, H. M., Cheverud, J. M. and Danahey, S. E. 1993. The role of postnatal growth pattern in the production of facial morphology. *Systematic Biology* 42: 307–330.
- Robert, P. and Escoufier, Y. 1976. A unifying tool for linear multivariate statistical methods: The RV-coefficient. *Applied Statistics* 25: 257–265.
- Rohlf, F. J. 2000. Statistical power comparisons among alternative morphometric methods. *American Journal of Physical Anthropology* 111: 463–478.
- Rohlf, F. J. 2003. TpsRelw, Relative Warps Analysis, Version 1.36. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.
- Rohlf, F. J. 2005. TpsDig2, Digitize Landmarks and Outlines, Version 2.05 Department of Ecology and Evolution, State University of New York, Stony Brook, NY.
- Rohlf, F. J. and Corti, M. 2000. Use of two-block partial least-squares to study covariation in shape. *Systematic Biology* 49: 740–753.
- Rohlf, F. J. and Marcus, L. F. 1993. A revolution in morphometrics. *Trends in Ecology and Evolution* 8: 129–132.
- Rohlf, F. J. and Slice, D. E. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 39: 40–59.
- Rootes, W. L., Chabreck, R. H., Wright, V. L., Brown, B. W. and Hess, T. J. 1991. Growth rates of American alligators in estuarine and palustrine wetlands in Louisiana. *Estuaries* 14: 489–494.
- Sadleir, R. W. and Makovicky, P. J. 2008. Cranial shape and correlated characters in crocodilian evolution. *Journal of Evolutionary Biology* 21: 1578–1596.
- Sánchez-Villagra, M. R. and Aguilera, O. A. 2006. Neogene vertebrates from Urumaco, Falcón State, Venezuela: Diversity and significance. *Journal of Systematic Palaeontology* 4: 213–220.
- Schumacher, G. H. 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodilians. In: Gans, C. and Parsons, T. S. (Eds): *Biology of the Reptilia*, pp. 101–199. Academic Press, London.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The Quarterly Review of Biology* 64: 419–461.

- Singleton, M. 2002. Patterns of cranial shape variation in the *Papio-nini* (Primates: Cercopithecinae). *Journal of Human Evolution* 42: 547–578.
- Sudhaus, W. and Rehfeld, K. 1992. Einführung in die Phylogenetik und Systematik. Gustav Fischer Verlag, Stuttgart.
- de Thoisy, B., Hrbek, T., Farias, I. P., Vasconcelos, W. R. and Laver-gne, A. 2006. Genetic structure, population dynamics, and conser-vation of black caiman (*Melanosuchus niger*). *Biological Conservation* 133: 474–482.
- Trutnau, L. 1994. Krokodile. Westarp Wissenschaften, Magdeburg.
- Vasconcelos, W. R., Hrbek, T., Da Silveira, R., de Thoisy, B., Marioni, B. and Farias, I. P. 2006. Population genetic analysis of *Caiman crocodilus* (Linnaeus, 1758) from South America. *Genetics and Molecular Biology* 29: 220–230.
- Verdade, L. M. 2000. Regression equations between body and head measurements in the broad-snouted Caiman (*Caiman latirostris*). *Revista Brasileira de Biologia* 60: 469–482.
- Verdade, L. M. 2003. Cranial sexual dimorphism in captive adult broad-snouted caiman (*Caiman latirostris*). *Amphibia-Reptilia* 24: 92–99.
- Villamarin-Jurado, F. and Suárez, E. 2007. Nesting of the black caiman (*Melanosuchus niger*) in northeastern Ecuador. *Journal of Herpetology* 41: 164–167.
- Webb, G. J. W. and Messel, H. 1978. Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, northern Australia. *Australian Journal of Zoology* 26: 1–27.
- Webb, G. J. W., Hollis, G. J. and Manolis, S. C. 1991. Feeding, growth, and food conversion rates of wild juvenile saltwater crocodiles (*Crocodylus porosus*). *Journal of Herpetology* 25: 462–473.
- Wiesemüller, B., Rothe, H. and Henke, W. 2003. Phylogenetische Systematik. Springer-Verlag, Berlin.
- Wilkinson, P. M. and Rhodes, W. E. 1997. Growth rates of American alligators in coastal South Carolina. *Journal of Wildlife Management* 61: 397–402.
- Wu, X. B., Xue, H., Wu, L. S., Zhu, J. L. and Wang, R. P. 2006. Regression analysis between body and head measurements of Chinese alligators (*Alligator sinensis*) in captive population. *Animal Biodiversity and Conservation* 29: 65–71.
- Young, M. T., Brusatte, S. L., Ruta, M. and Andrade, M. B. 2010. The evolution of Metriorhynchoidea (Mesoeucrocodylia, Thalatosuchia): An integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. *Zoological Journal of the Linnean Society* 158: 801–859.
- Zelditch, M. L., Swiderski, D. L., Sheets, H. D. and Fink, W. L. 2004. Geometric Morphometrics for Biologist: A Primer. Elsevier Academic Press, San Diego, CA.
- Ziegler, T. and Olbort, S. 2007. Genital structures and sex identification in crocodiles. *Crocodile Specialist Group Newsletter* 26: 16–17.

### Supporting Information

Additional supporting information may be found in the online version of this article:

**Table S1.** List of specimens of *Melanosuchus niger* used in the geometric morphometric analysis with information on sex, skull length SL, bite force, and data sets in which in was included (dorsal, ventral and lateral views).

**Table S2.** Percentage error for each landmark for both photographed (ZSM 2416/2006) and the X-rayed specimens (ZSM 3/1971) (in dorsal and lateral view) with  $n = 10$ .