

# A morphometric analysis of crocodylian skull shapes

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This paper presents insights into the variety and variability in skull shapes of crocodiles using both traditional and nontraditional measurements within a landmark analysis. Using 159 adult crania of all 23 crocodylian species from the collections of five European museums, we found that the relationship between total skull width and length does not account for the majority of the variation between crocodylian species. We identified measurements between the orbit and premaxillary notch, explaining 90% of the variance, the distance from the orbit to the 5<sup>th</sup> maxillary tooth, and Kálin's number 12 (1933) as main focal areas for species differentiation. These measurements usefully define the shape of the crocodylian skull, differentiate between species with good precision, and allow reasonable inferences about function.

*Key words:* crocodiles, landmark analysis, morphology

## INTRODUCTION

Grouping and taxonomy of animals are large components of zoological studies and the cause of constant debate within *Crocodylia* (Norell, 1989; Brochu, 2000). Head shape constitutes a physical attribute that notably differs between crocodylian species, and is also relevant to crocodile ecology, behaviour, evolution and conservation (Ouboter, 1996; Brochu, 2001a; McHenry et al., 2005; Sadleir & Makovicky, 2008). To date, the most commonly used variables in skull morphology are maximum length and width. This current description of skull shapes is, however, insufficient to account for the noticeable diversity in crocodylian species (Pierce et al., 2008).

Crocodylians have previously been divided into two groups: longirostrine, with a long, thin rostrum, and brevirostrine, with a shortened rostrum (*sensu* Busbey, 1995). While these groups were reflective of obvious physical characteristics within the snout, subsequent research has shown these to be insufficient for describing the variety of rostral shapes. Busbey (1995) further divided crocodylian snouts based on both length and width, and on lateral profile (platyrostral, having a broad, flat snout, and oreinrostral, having a domed snout). Although these extended categories were useful for descriptions, Busbey (1995) stated that they are not taxonomically definitive, due to overlap in head shape between taxa. Brochu (2001a) added the groupings of ziphodonts (deep, laterally compressed snouts) and duck-faced crocodylians, based on the inclusion of fossil specimens within Archosauria. He also suggested minor changes within the existing groups, concluding that the skull was phylogenetically plastic and that similar snout shapes had arisen several times in disparate lineages. Marugán-Lobón & Buscalioni (2003) then suggested a return to three skull types (meso-, longi-, and brevirostral) based on lateral rather than dorsal views, using percentages of brain case vs orbit vs rostrum. Other studies define skull shape based on different rostral shape groups (Sadleir & Makovicky, 2008).

Traditional morphometrics, measuring distances and angles, may not capture the subtle shape variation between crocodylian skulls, whereas geometric morphometrics, using landmarks and eliminating bias through interdependence of variables within datasets, can draw more conclusions (Pierce et al., 2008). The present paper studies morphometric parameters of the crocodylian skull using consistent landmarks that reflect homologous points. The main goal of this study is to further characterize and quantify the differences in cranial morphology across crocodylian species.

## METHODS

We collected data on 159 adult crania of all 23 crocodylian species from the collections of five European museums (for a list of the specimens used, see the Electronic Appendix at [http://www.thebhs.org/pubs\\_journal\\_online\\_appendices.html](http://www.thebhs.org/pubs_journal_online_appendices.html)). We used sub-adult and adult skulls of wild individuals or, if necessary, from captive-bred animals with minimal deformation. We photographed the skulls in dorsal view for two-dimensional digital analysis. Placing each on a black cloth, we levelled them along the medial suture from the highest point on the cranial table to the highest point at the anterior end of the snout, exposing the skull surface in a uniform fashion. We preferred cranium only so that the skull rested on the pterygoid flanges evenly; where these were uneven, we levelled the skull width-wise along the cranial table. If the cranium and jaw could not be detached, we used the same levelling techniques, disregarding the lower jaw for analysis.

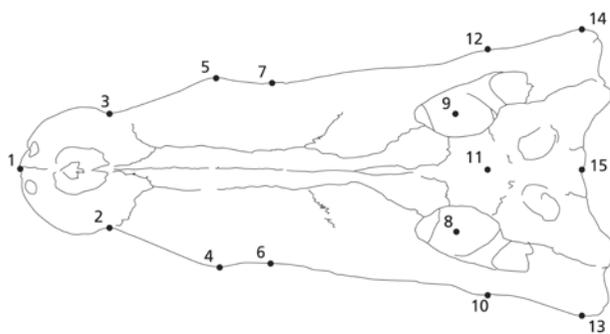
We photographed dorsal views of specimens following a method adapted from Pearcy & Wjitten (2010), using a Panasonic Lumix DMC-FX107 digital camera set to intelligent AUTO mode, 3072 by 2304 pixels, JPEG/Exif format. We set the camera perpendicular to the centre of the cranium along the midline axis using a tripod at a distance of 40–120 cm from the specimen, depending on its size. To light the skull, we used flash, natural light

**Table 1.** Location of landmarks used within the crocodylian skull.

Landmark	Point location
1	Anterior tip of premaxillae contact
2	Minimum width immediately posterior to premaxilla–maxilla contact (notch), left side
3	Minimum width immediately posterior to premaxilla–maxilla contact (notch), right side
4	Maximum preorbital width posterior to premaxilla–maxilla contact, left side
5	Maximum preorbital width posterior to premaxilla–maxilla contact, right side
6	Minimum preorbital width posterior to maximum preorbital width, left side
7	Minimum preorbital width posterior to maximum preorbital width, right side
8	Centre of left orbit
9	Centre of right orbit
10	Kälin 12 left side
11	Midline at Kälin 12
12	Kälin 12 right side
13	Maximum width quadratojugal bone, left side
14	Maximum width quadratojugal bone, right side
15	Posterior tip of supraoccipital (medial posterior margin of cranial table)

and ambient light against a black background. We plotted landmarks or homologous points on the crania (Fig. 1; Table 1) using the digital images in the program ImageJ (Rasband, 2009).

We chose landmarks at locations representing traditional measurements such as the anterior tip of the premaxilla, and other areas which have an obvious physical characteristic (Fig. 1, Table 1). Landmarks 4–9 are easily located on the dorsal view of a cranium. Landmarks 4 and 5 are

**Fig. 1.** General positions of the landmarks on the cranium corresponding to Table 1 (dorsal view).

often associated with the 5<sup>th</sup> maxillary tooth, while landmarks 6 and 7 associate with the 6<sup>th</sup> maxillary, which is variable between species. Landmarks 4–7 can be difficult to locate on longirostrine groups such as *Gavialis* and *Tomistoma*; however, they are apparent in most other species. We also adopted a measure of skull width described by Kälin (1933), consisting of the width of the skull measured at the anterior point of the postorbital bar suture (Kälin 12). We present Kälin 12–12 (the distance between landmarks 10 and 12 in this study) as a location for measuring size within Crocodylia (Percy, 2010). It is located across the width of the skull level with the anterior end of the postorbital bar suture. For validating the use of landmark analysis in this study, we took measurements using a caliper for total length, total width, width at Kälin 12–12 and length from midline of Kälin 12–12 to the anterior tip of the premaxillae contact (tip of the snout) along the long axis.

### Data analysis

We used a General Procrustes Analysis (GPA) to standardize the coordinate data, removing unwanted effects of size, rotation and position (Dryden & Mardia, 1998; Jolliffe, 2002). From the standardized data residuals, we ran several principal component analyses (PCA) to determine the amount of variability accounted for by each landmark. The first PCA considered all landmarks, the second removed highly variable landmarks (or landmarks not as easily definable on all species), and the third explored a noted area of variation. We used a cluster analysis with the same data to examine the differences between species (Ezard et al., 2010). Furthermore, we created a thin-plate spline warp picture for each species. We used PAST (Paleontological Statistics Software, Hammer et al., 2001) to conduct all analyses.

Using the coordinates of each landmark extracted from the digital pictures, we calculated the distances for total length, total width, width at Kälin 12–12 and length from Kälin 12–12 along to the tip of the snout. Using PAST, we conducted a Pearson correlation test between these measurements and the same measurements taken with a caliper.

## RESULTS

Pearson correlations between the ratios of 13–14:1–15 (cranial width to total skull length) determined using both digital and caliper measurements were 0.908 ( $P < 0.01$ ,  $\alpha = 0.01$ ). Figure 2 presents thin-plate splines for each species, showing the average skull shape warps formed. Differences in warps between species are reflected in landmarks that represent areas of difference among species. There is distinct warping around landmarks 4, 5, 6 and 7 along the length of the snout, and again around 10, 11 and 12 near the posterior end of the skull.

An initial landmark analysis evaluated 15 landmarks in a PCA. The first three components explained the majority of the variance (81.6%), with PC1 accounting for 68.1%. PC1 is largely determined by landmarks representing the premaxillary–maxillary (pm) notch and landmarks 4–7, associated with preorbital minimum and maximum



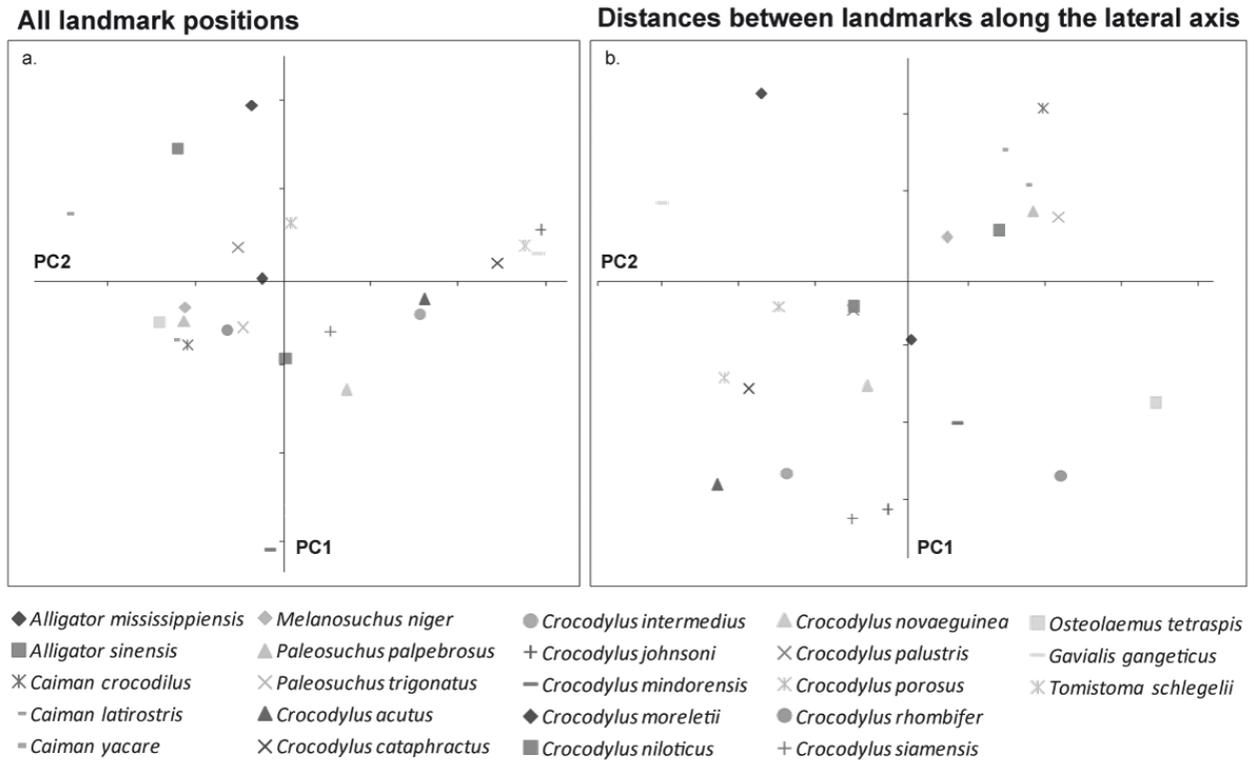
**Fig. 2.** Thin-plate spline warp graphs for all 23 crocodile species, with an estimated indication of average skull shape and size from our data set.

widths. We derived the first indication on the ability of our data to distinguish between species by performing a hierarchical cluster analysis (correlation coefficient = 0.773) on the Procrustes fit coordinates of each landmark by individual. Since the test demonstrated successful division, it legitimized further analysis of the data.

Figure 3a shows that PC1 is associated with relative rostrum length. All species to the far right expressed a longirostrine phenotype. *Gavialis gangeticus* and *Tomistoma schlegelii* were at the outer limits of the grouping.

However, species to the left of the PC1 axis overlap and represent all other variations from the extreme brevirostrine *Alligator mississippiensis* to the wide variety of *Crocodylus* snouts, excluding the extreme longirostrines (*Crocodylus cataphractus* and *C. johnsoni*).

We repeated the PCA omitting landmarks 4, 5, 6 and 7, since these are difficult to locate on some species. The first three components explain 80.6% of the variance, 62.9% of which is explained by component 1. The driving factor for the component was the pm notch, represented



**Fig. 3.** PCA with scores averaged for each species showing a) difference between landmark positions and b) all length measurements along the lateral margin between the orbit and the premaxillary notch.

by landmarks 2 and 3 (Table 2). Landmarks 10 and 12, representing Kälin 12–12, drove the second component (10.2%). A separate cluster analysis, again using landmarks of individual species, showed a correlation (0.75) similar to the previous analysis.

We used a further PCA to explore the noted area of variation between landmarks 2, 3 and 8, 9 (Fig. 3b). We calculated the distances between landmarks to generate multiple distances between the orbit and the pm notch (9–7, 7–5, 5–3, 7–3 and 9–5). PC1, which is predominantly associated with distances between the orbit and maximum preorbital width, explained 90.0% of the variance. When we compared these landmarks in a cluster analysis, there was notable clustering (correlation coefficient 0.76) similar to the previous analyses.

Figure 3a mimics the gradient of Figure 3b along rostral shape, with the extremes (*C. latirostris* and *T. schlegelii*) being present to the far sides of the cluster. However, there is a slight deviation as *A. mississippiensis* skull shape expression moves closer to the cluster of other species. PC2 might be driven by a size gradient, with smaller species along the negative axis and sturdier animals on the positive axis, which would explain this effect.

## DISCUSSION

Although only dorsal views were considered, we are able to draw conclusions about general areas of importance pertaining to variation in snout shape. We found that the area between the pm notch and the orbit (landmarks 2–8, 3–9), the distance between the orbit and maximum preorbital width (4–8, 5–9), and the width of the skull at Kälin 12 (10–12) each have an obvious significance in crocodile species delimitation using skull characters.

By broadening the scope and integrating obvious areas of variation around the orbit and lateral line, we confirm that the measurements of total length and width considered previously are not the factors that are most variable between species (Pierce et al., 2008; Sadleir & Makovicky, 2008). Points along the lateral margin, however, are difficult to locate in extreme longirostrine species such as *G. gangeticus* and *T. schlegelii*, and might create unwanted artefacts. We therefore further investigated the relevance of our findings by removing landmarks susceptible to dissimilarity and found our hypothesis still validated. Since skull shape is an important physical attribute in distinguishing crocodile species, this informa-

**Table 2.** Changes in case loadings for principal component 1 for the PCA inclusive of all landmarks and for the PCA with landmarks 4, 5, 6, and 7 removed.

		All landmarks	Without 4,5,6,7
Notch	x1	-0.20	0.15
	y1	0.00	0.02
	x2	-0.20	0.20
	y2	-0.26	0.33
	x3	-0.21	0.21
Orbits	y3	0.27	-0.34
	x8	0.14	-0.18
	y8	-0.07	0.11
	x9	0.13	-0.17
Kälin 12	y9	0.01	-0.11
	x10	0.12	-0.16
	y10	-0.27	0.41
	x11	0.06	-0.06
	y11	0.00	-0.01
	x12	0.06	-0.07
	y12	0.26	-0.41
	x13	0.00	-0.01
	y13	-0.23	0.33
	x14	0.03	0.01
y14	0.21	-0.31	
x15	-0.03	0.09	
y15	0.02	-0.03	

tion is useful in crocodile ecomorphology with relation to ontogeny, suitability of habitat, and hunting and fighting techniques. However, it must be noted that some physical characteristics are subject to variability due to ontogenetic parameters (see Pearcy, 2010, for Kälin 12–12).

Within the region between the pm notch and the orbit, the distance between the centre of the orbit and the maximum preorbital width was an important variable of variation. Different locations within this area were already subject to consideration as marked variants between crocodylian species. The skull growth of New Guinea crocodiles (*C. novaeguineae*), showing ontogenetic variation in relative growth mainly in this area, was hypothesized to be related to functional foraging responses (Hall, 1994). The area distinguishes extinct crocodylians (Joffe, 1967), and sexual dimorphism in allometric growth was hypothesized to be related to visual sex recognition when only the top of the head extends above the water surface.

We were able to assign Kälin 12–12 within both PCAs as a driving force of variation between species (see also Pearcy, 2010). The three skull-type morphology system of Marugán-Lobón & Buscalioni (2003) implies that the structural design of craniofacial morphology can deviate

from species-specific adaptive explanations. This is supported by our results regarding pm notch to orbital shape characteristics. Our results are also in line with Brochu's (2001a) hypothesis of phylogenetic plasticity in orbital to pm notch snout shape in disparate archosaur lineages (Brochu, 2001b).

In summary, we confirm that Kälin 12–12 and maxillary length measurements are better traits for differentiating between species than total skull width and length. We identified the orbital to pm notch area, Kälin 12–12 and the distance between the centre of the orbit and the maximum preorbital width as main focus areas for species differentiation. These measurements usefully define the shape of the crocodylian skull, and allow reasonable inferences about function.

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