Zoological Journal of the Linnean Society, 2020, **188**, 507–521. With 4 figures.

A synthetic approach for assessing the interplay of form and function in the crocodyliform snout

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Received 28 February 2019; revised 12 June 2019; accepted for publication 30 July 2019

Existing classifications of snout shape within Crocodylia are supported by functional studies, but ecological surveys often reveal a higher than expected diversity of prey items within putatively specialist groups, and research into bite force and predation behaviour does not always reveal significant differences between snout shape groups. The addition of more distantly related crocodyliforms complicates the ecomorphological signal, because these groups often occupy a larger area of morphospace than the crown group alone. Here, we present an expanded classification of snout shapes and diets across Crocodyliformes, bringing together geometric morphometrics, non-hierarchical cluster analyses, phylogenetic analyses, ancestral state reconstructions, ecological surveys of diet, and feeding traces from the fossil record to build and test predictive models for linking snout shape and function across the clade. When applied to living members of the group, these new classifications partition out based on differences in predator body mass and maximal prey size. When applied to fossils, these classifications predict potential prey items and identify possible examples of scavenging. In a phylogenetic context, these ecomorphs reveal differences in dietary strategies and diversity within major crocodyliform clades. Taken together, these patterns suggest that crocodyliform diversity, in terms of both morphology and diet, has been underestimated.

ADDITIONAL KEYWORDS: behaviour – Crocodylia – Crocodyliformes – feeding adaptation – morphometrics – palaeoecology – palaeontology – prey capture – vertebrate palaeontology.

INTRODUCTION

The evolution of crocodylian snout shape is often presented as an elegant, straightforward case study of the interplay of form and function in the fossil record. Slender-snouted forms ate fish (Iordansky, 1973; Langston, 1973; Pooley, 1989; Busbey, 1995), boxy-headed forms ate hard prey (Carpenter & Lindsey, 1980; Salas-Gismondi *et al.*, 2015), and broad, triangular-shaped forms did not specialize and ate almost anything, depending on their size and ontogeny (Brochu, 2001). The addition of fossil forms, which exhibit snout morphologies no longer represented in the present (Brochu, 2001; Wilberg, 2017), adds more ecomorphs to this story. Ziphodont crocodyliforms were more terrestrial, as were their prey items (Brochu, 2001, 2012). Duck-faced crocodyliforms might have had a gular pouch and, possibly, exhibited filter feeding (Langston, 1965; Salas-Gismondi *et al.*, 2015; Cidade *et al.*, 2017). These interpretations have been bolstered by observations that sympatric crocodyliform species often separate out into different snout shape classes and body sizes, presumably to minimize competition for resources (Brochu, 2001; Marioni *et al.*, 2008; Irmis, 2013; Salas-Gismondi *et al.*, 2015; Adams *et al.*, 2017b). These ecomorphs are so widely accepted that they are used as analogues for interpreting the diet of distantly related groups, including phytosaurs (e.g. Hunt, 1989; Murry, 1989; Drumheller *et al.*, 2014), choristoderes (e.g. Katsura, 2004) and dinosaurs (e.g. Rayfield *et al.*, 2007; Cuff & Rayfield, 2013).

The recognition of this pattern has spurred increased research into crocodyliform snout shape in morphological, functional and phylogenetic contexts to gain a better understanding of the major ecological trends in the clade (Busbey, 1995; Brochu, 2001; Gignac

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& Erickson, 2016; Gignac & O'Brien, 2016; Pierce *et al.*, 2008; Sadleir & Makovicky, 2008). However, some unexpected results complicate the direct causal link between feeding strategy and snout shape. Surveys of modern crocodylian diets have revealed more diversity of prey items among members of specialist snout ecomorphs than previously thought (e.g. Webb & Manolis, 1983; Tucker *et al.*, 1996; Selvaraj, 2012). Both snout shape and diet change greatly during crocodylian ontogeny, further complicating this observed pattern (e.g. McIlhenny, 1935; Erickson *et al.*, 2014; Gignac & Erickson, 2015; Iijima, 2017). Recent morphometric analyses that sample only within the crown group do find similar snout shape groupings (Pierce *et al.*, 2008; Sadleir, 2009), but expanding sampling further into Crocodyliformes reveals a wider diversity of rostral morphologies, some of which do not fit nicely into existing ecomorphs (Wilberg, 2017). Although some aspects of cranial shape do not always reflect dietary preferences in other reptilian groups (e.g. Foth *et al.*, 2017), finite element analyses find real differences between how the snout ecomorphs react to forces associated with prey acquisition and consumption, suggesting different preferences for prey size, if not prey taxon (McHenry *et al.*, 2006; Pierce *et al.*, 2008, 2009). However, in vivo bite force data do not differentiate between these ecomorphs. Instead of partitioning into higher bite forces for durophagous and macrocarnivorous taxa and lower bite forces for putatively piscivorous taxa, crocodylian bite forces scale in a tight, linear nature with body mass, resulting in a seeming overperformance within the niches of several species (Erickson *et al.*, 2012; Gignac & Erickson, 2016; Gignac & O'Brien, 2016). Additionally, a survey of crocodylian death roll behaviour, long associated with large-bodied generalist groups, found that nearly all extant members of the group, including all slender-snouted and most small-bodied, boxy-headed species, perform this behaviour (Drumheller *et al.*, 2019). These results pose interesting complications to previous associations between snout shape and function, especially when applied to extinct taxa.

Here, we revisit patterns of crocodyliform snout shape and inferred diet throughout the history of the clade (Brochu, 2001), building upon the most recent phylogenies (Brochu, 2012; Brochu *et al.*, 2012; Pol *et al.*, 2014; Wilberg, 2017; Adams *et al.*, 2017b), and applying new morphometric analyses and a meta-analysis of published surveys of modern crocodylian body sizes and diets (e.g. Webb & Manolis, 1983; Tucker *et al.*, 1996; Selvaraj, 2012), supplemented with direct and indirect evidence of trophic interactions in the fossil record (e.g. Drumheller & Brochu, 2014, 2016 and references therein), in order to constrain the relationship between form and function of crocodyliform cranial shape during the evolution of this group more realistically.

MATERIAL AND METHODS

Morphometric analysis

Taxa were sampled across the temporal range of Crocodyliformes. Included taxa were represented by at least one skull possessing at least a complete right or left half ($N = 99$). To increase sample size, additional specimens showing obvious postmortem deformation impacting their shape in dorsal view or those represented by less complete material were represented by reconstructions ($N = 31$). This yielded a total sample size of 130 (for specimen information and references used, see Supporting Information, Table S1). Specimens were digitized from photographs in dorsal view using tpsDIG2 v.2.18 (Rohlf, 2010). Landmarks and semilandmarks were placed on the right side only (when only the left side was preserved, the photographs were mirrored). Six landmarks were chosen to characterize important aspects of cranial shape, and 24 sliding semilandmarks were used to capture the shape of the snout (18 sliding semilandmarks) and supratemporal fossa (six sliding semilandmarks; for landmark scheme, see Fig. 1). Digitization of all specimens was performed by E.W.W. All further analyses were performed in R (R Core Team, 2017).

To analyse shape variation of the cranium and avoid potential error introduced by the superimposition of unilateral landmarks on bilaterally symmetrical organisms, we followed the suggestion of Cardini (2016, 2017) and mirrored the right-side landmarks onto the left side to generate fully symmetrical 'total skulls'. Mirroring was performed using the mirrorfill function in the R package *paleomorph* (Lucas & Goswami, 2017). Given that this package was designed for three-dimensional data, some additional manipulation of our data was required before mirroring. First, 28 additional landmarks were added to correspond to the unsampled left-side landmarks and semilandmarks. These were given initial values of 'NA' to be replaced by the mirrored coordinates. An artificial third dimension (Z-coordinate) was then added to the two-dimensional data. To identify accurately the midline plane across which to mirror, we added an additional five evenly spaced points to the midline between landmarks 1 and 2. Z-Coordinate values for the midline landmarks were randomly sampled from a normal distribution (mean = 0; $\sigma = 50$) based on recommendations from the package author (T. Lucas, pers. comm.). The Z-coordinates of the remaining left-side landmarks were assigned a value of zero. After

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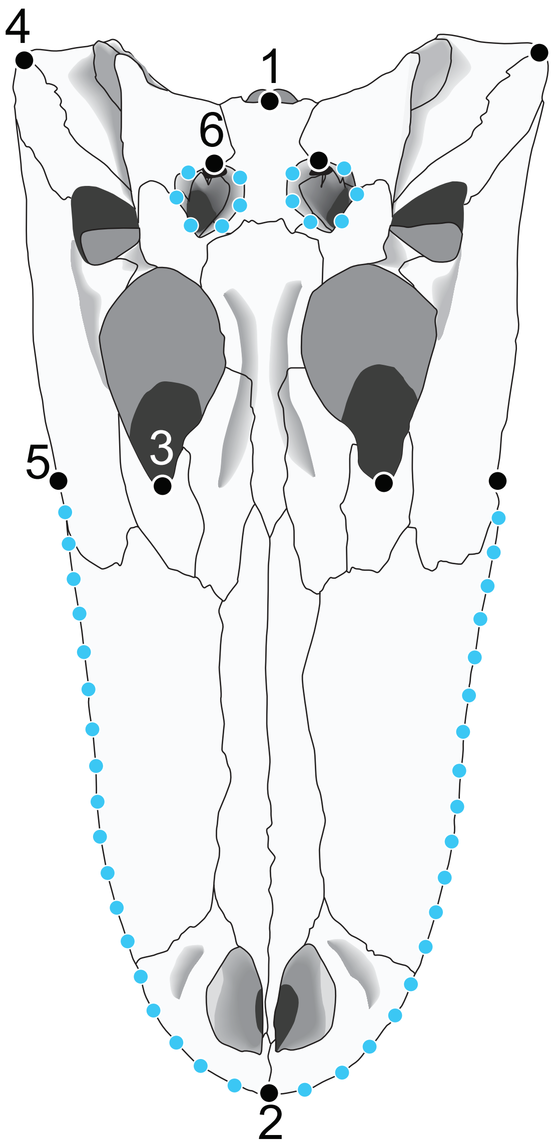

Figure 1. Landmark scheme for the morphometric analysis. Black circles represent landmarks; blue circles represent sliding semilandmarks. Numbered landmarks are as follows: 1, posterior midline of skull table; 2, anterior midline; 3, anterior-most point of orbit; 4, posterior-most point of quadrate–quadratojugal suture in dorsal view; 5, point on cranial margin where snout begins (directly lateral to landmark 3); 6, anterior-most point of parietal–squamosal suture on the margin of the supratemporal fenestra. All landmarks and semilandmarks on the left side are reflections of landmarks on the right side.

mirroring, each landmark configuration was inspected visually to ensure that mirroring worked properly. The *Z*-coordinates and extra five midline landmarks were removed from the data file, yielding symmetrical two-dimensional landmark configurations of the 'total skulls', with ten landmarks and 48 semilandmarks (Fig. 1).

Landmark configurations were superimposed by generalized Procrustes superimposition (Gower, 1975; Rohlf & Slice, 1990) in the R package *geomorph* (Adams & Otárola-Castillo, 2013; Adams *et al.*, 2017a) to remove variation attributable to position, orientation and scale. Semilandmarks were allowed to slide along lines tangent to the curve during superimposition to minimize bending energy (Bookstein, 1997). The aligned Procrustes shape configurations were subjected to a principal components analysis (PCA) of the covariance matrix to explore shape variation in the dataset.

DEFINING GROUPS

To determine the number of cranial shape groups present in the data, we used the non-hierarchical clustering algorithm partitioning around medoids (PAM; Kaufman & Rousseeuw, 1990). Given that these groups are meant to reflect feeding strategies, we included data on the major morphological variance within the skull and information related to dentition. Scores from the first two principal component (PC) axes were used as an approximation of overall skull shape. These axes were selected as significant based on the broken stick method (Frontier, 1976; Jackson, 1993) as implemented in the R package PCDimension (Coombes & Wang, 2018) and account for the overwhelming majority of cranial variation (88%). The dentition of most crocodyliforms consists of widely spaced, conical, monocuspid teeth. However, a number of lineages or taxa developed dentition that deviates from this trend and is likely to indicate feeding strategies functionally different from those of modern crocodylians (Ősi, 2014), including mediolaterally compressed, serrated teeth (ziphodont dentition) and complex, multicusped and/or heterodont dentition. To incorporate dental characteristics into our groupings, we scored each taxon for three binary dental characters: (1) heterodonty; (2) ziphodonty; and (3) numerous small, peg-like teeth of uniform size, referred to afterwards as isodonty. Heterodonty was scored based on characterizations by Ősi (2014 for taxa exhibiting functional heterodonty-with or without occlusion). We chose to exclude taxa he deemed heterodont owing to the presence of bulbous posterior teeth (globidonty), because this tooth shape shows continuous variation among living and extinct crocodylians, and determining the cut-off between blunt and anvil-like is highly subjective (Brochu, 1999; D'Amore *et al.*, 2019). Isodonty is known in a few extinct taxa that deviate from living crocodylians in a number of ways. Possession of isodont dentition is associated with broad, elongate, flat skulls and gracile, U-shaped mandibles, which has led researchers to

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propose a method of bulk feeding followed by straining or filtering prey from the water (e.g. Nopcsa, 1926; Langston, 1965; Riff *et al.*, 2010; Cidade *et al.*, 2017).

Given that our data included both continuous and discrete variables, we transformed our data into a Gower dissimilarity matrix (Gower, 1971) using the *daisy* function of the R package *cluster* (Maechler *et al.*, 2017). This dissimilarity matrix was then subjected to PAM clustering using the *pamk* function of the R package *fpc* (Hennig, 2018), using the Calinski–Harabasz (CH) index (Calinski & Harabasz, 1974) simultaneously to determine the optimal number of clusters. Although the use of an optimality criterion to determine the number of clusters is often treated as an 'objective' method for finding groups within data, different optimality criteria identify different numbers of clusters and/or differing cluster membership. Consequently, the choice of optimality criterion, in a way, implicitly defines the number of clusters found (Hennig & Liao, 2010). We therefore explored different treatments of our data (e.g. PAM clustering of PC scores only) and an alternative optimality criterion [average silhouette width (ASW); Kaufman & Rousseeuw, 1990], with the ultimate aim of defining groups with reasonable morphological differentiation.

To test the effects of allometry on our shape groups, we performed an additional regression of the Procrustes shape scores on the logarithm of centroid size in the R package *geomorph*. We then performed a PCA on the residuals of this regression. We reran the PAM cluster analysis on the first two PC axes from the non-allometric residuals plus the dentition characters.

Ancestral state reconstruction

To evaluate the evolution of crocodyliform cranial shape in a phylogenetic context, we first reconstructed ancestral states. We assembled an informal supertree based on several recently published topologies (Brochu, 2001, 2012; Brochu *et al.*, 2012; Pol *et al.*, 2014; Adams *et al.*, 2017b; Wilberg, 2017). To provide a time scale for the tree, we compiled stratigraphic ranges of all taxa (Supporting Information, Table S1) from the Paleobiology Database (http://paleobiodb.org) accessed via FossilWorks (http://fossilworks.org) on 26 November 2018. Trees were scaled using methods described by Wilberg *et al.* (2019). The time-calibrated tree file is available as Supporting Information (Nexus tree file). Ancestral states for internal nodes were reconstructed in Mesquite v.3.51 (Maddison & Maddison, 2015) using maximum likelihood under a Markov k model.

Feeding ecology/palaeoecology

The assignation of dietary classifications to extant and extinct species within this dataset required common ground to be found between ecological and palaeoecological studies. Surveys of diet among the living members of Crocodylia are heavily biased towards large-bodied groups that interact regularly with humans, related either to conflict (attacks on humans) or to economics (the skin and meat trade). This has resulted in *Alligator mississippiensis* [Daudin, 1801 (1802); Rowe *et al.*, 1999], *Crocodylus niloticus* (Laurenti, 1768) and *Crocodylus porosus* (Schneider, 1801; Tzika & Milinkovitch, 2008) often being treated as the de facto model organisms for the clade as a whole. This tends to mask dietary and behavioural diversity within the clade, because in addition to being large-bodied species, all three also exhibit snout shapes and behaviours associated with a generalist lifestyle. Other species have not enjoyed the same intensity of research, but efforts are being made to remedy this, especially given that several members of other snout ecomorphs are threatened or endangered, and understanding the ecology of these groups is crucial for conservation efforts (e.g. Webb & Manolis, 1983; Tucker *et al.*, 1996; Thorbjarnarson & Wang, 2010; Selvaraj, 2012).

When possible, we assessed the diet of modern groups based on large-scale surveys of diet across different ages and geographical ranges (e.g. Santos *et al.*, 1996; Antelo *et al.*, 2008; Borteiro *et al.*, 2009; Thorbjarnarson & Wang, 2010; Platt *et al.*, 2013; Sam *et al.*, 2015). Those studies drew from direct observations of gut contents, trophic interactions and droppings, and ranged in scope from new data collected from 22 animals (Pauwels *et al.*, 2007) to a meta-analysis of studies covering a total of 1369 animals (Nifong & Silliman, 2013). Large-scale dietary surveys were available for 15 of the 23 extant species of crocodylian included in this analysis, and the remaining eight represent some of the most critically endangered species and/or species only recognized recently as distinct species rather than subspecies (e.g. Ross & Magnusson, 1989; Thorbjarnarson & Wang, 2010; De Silva *et al.*, 2011). To capture the full spectrum of diet, especially within more poorly studied groups, smaller-scale case studies and observations recorded in the grey literature were also included (e.g. McIlhenny, 1935; CrocBITE, 2013). Finally, only studies documenting predation rather than scavenging were included, because scavenged remains do not necessarily reflect the animals a predator could take (e.g. gharials scavenging humans, described by Pooley *et al.*, 1989). Details and citations for all referenced analyses have been gathered into the Supporting Information (Table S2).

In the fossil record, dietary preferences almost always have to be observed indirectly, through functional studies of anatomy (e.g. Gignac & Erickson, 2016; Gignac & O'Brien, 2016) and inferences drawn from bite marks, gut contents and coprolites (e.g. Drumheller & Brochu, 2014, 2016). Among crocodyliforms, gut contents and coprolites are usually uninformative, owing to the highly

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destructive nature of the digestive process within this clade (Fisher, 1981), leaving bite marks as the primary type of usable trace fossil evidence, with a few notable exceptions (e.g. Langston & Rose, 1978; Alexander & Burger, 2001). Although initially thought to be uncommon (Carpenter, 1998; Jacobsen, 2001), vertebrate bite marks are becoming more well documented, stemming from the availability of modern surveys to aid in initial identification and interpretation (e.g. Njau & Blumenschine, 2006; Milàn *et al.*, 2010; Westaway *et al.*, 2011; Baquedano *et al.*, 2012; Drumheller & Brochu, 2014, 2016) and increasing numbers of case studies documenting patterns of bite mark preservation in the fossil record (e.g. Noto *et al.*, 2012; Boyd *et al.*, 2013; Botfalvai *et al.*, 2014, 2015; Hastings *et al.*, 2015; Scheyer *et al.*, 2018; Gônet *et al.*, 2019).

Data on diet in the fossil record have obvious limitations in comparison to modern surveys. The crocodyliform feeding process itself is a strong taphonomic filter, and only larger, more durable or discarded portions of prey skeletons would be expected to survive (e.g. Davidson & Solomon, 1990; Njau & Blumenschine, 2006; Noto *et al.*, 2012). When available, we include other indirect sources of trophic information (Alexander & Burger, 2001), but the palaeontological dataset remains heavily biased. Nevertheless, these feeding traces provide key insights into the feeding behaviours of crocodyliforms with morphotypes no longer represented among extant groups.

Across both extant and extinct clades, ontogeny is another complicating factor when characterizing diet within species. Changes in snout morphology and diet during growth and development are well documented among modern crocodylians (e.g. McIlhenny, 1935; Erickson *et al.*, 2014; Foth *et al.*, 2015; Gignac & Erickson, 2015). In order to limit the effects of ontogeny in the present study, we characterized crocodyliform dietary preferences by exploring patterns of maximal predator and prey body mass within and across snout ecomorphs in order to assess prey size specialization among adult animals only. Crocodyliform and prey maximal body masses were taken from the literature (e.g. Trutnau & Sommerlad, 2006; Jones *et al.*, 2009) or, if they were not available, were predicted using a regression of body length to body mass based on measurements reported by Drumheller & Brochu (2016). These values and their sources are presented in the Supporting Information (Table S2). To address the biased nature of the fossil dataset, initial analyses were performed using the extant species only. Ensuing patterns and their statistical significance were explored using ordinary least squares regressions and an analysis of covariance (ANCOVA) in the software package PAST v.3.20 (Hammer *et al.*, 2001). The resulting predictive models provided a basis of comparison for the fossil dataset.

RESULTS

MORPHOMETRIC ANALYSIS

The first five PC axes collectively summarized > 95% of the variance (Supporting Information, Table S3), although only the first two were deemed significant based on the broken stick method. These two axes defined a lower-dimensional subspace used to describe the cranial morphospace qualitatively (Fig. 2). The first PC axis primarily involved relative snout length, with a component of snout width and supratemporal fossa size and shape. The second PC axis included aspects of snout width, supratemporal fossa size, mediolateral position of the orbits, and festooning of the snout margin.

The PAM cluster analysis yielded seven cranial shape categories: macro-generalist, generalist, slender longirostrine, stenorostrine with large supratemporal fenestrae (STF), ziphodont, duck-faced and brevirostrine heterodont (Fig. 2). See Table 1 for qualitative descriptions of each category. Justifications for these names are discussed below, in the 'Feeding ecology/palaeoecology' section. See the Supporting Information (Table S1) for an exhaustive list of group assignment. Cluster analysis of PC scores from the first two PC axes (without dentition characters) resulted in only two groups (essentially long, slender-snouted taxa vs. all others). The PAM cluster analysis of the PC scores plus dental characters, but using the ASW optimality criterion, likewise divided the data into only two groups based primarily on snout length. Both these grouping schemes placed taxa from disparate ends of the morphospace into the same group [e.g. the tiny herbivorous notosuchian *Simosuchus* (Buckley et al., 2000) grouped with the giant, duck-faced, potentially bulk-feeding caiman *Mourasuchus* (Price, 1964)] and thus seemed unhelpful for parsing diet.

Results of the allometrically corrected analyses were highly congruent with those of the primary analysis. The effect of allometry was significant ($r^2 = 0.2649$; $P = 0.001$), but the primary aspects of morphology described by the first two PC axes were very similar (accounting for 84.7% of the variance). The PAM cluster analysis of these allometrically corrected data resulted in eight cranial shape categories. Most matched exactly with those defined in the primary analysis. However, the allometry-corrected analysis subdivided the generalist and macro-generalist categories into three groups: long-snouted generalists; a group of moderate snout-length generalists and narrower/longer-snouted macro-generalists; and broad-snouted macro-generalists. These results suggest that our PAM categories are not strongly affected by allometry (for an exhaustive list of group assignments from the allometrically corrected analyses, see the Supporting Information, Table S4).

For the remainder of this work, we focus on the non-allometrically corrected cranial ecomorph groups.

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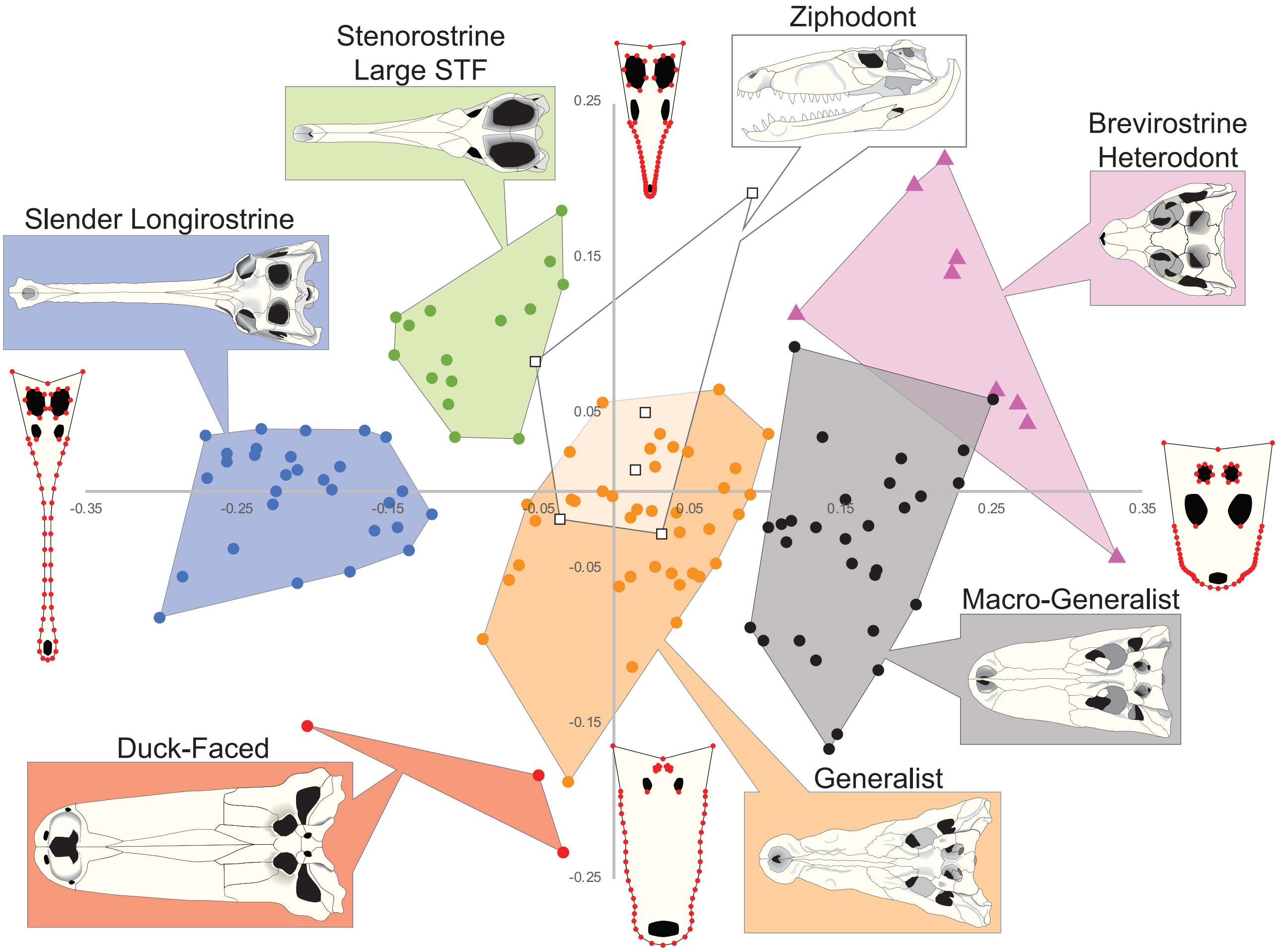

Figure 2. Comparative cranial morphospace on principal components (PC) 1 (69.8% of variance) and 2 (18.2% of variance). Polygons enclose groups as defined by partitioning around medoids (PAM) cluster analysis of morphometric and dental morphology data. Exemplar skulls are shown for each group, as follows: brevirostrine heterodont, *Mariliasuchus amarali* (Carvalho and Bertini, 1999); macro-generalist, *Alligator mississippiensis*; generalist, *Crocodylus niloticus*; duck-faced, *Mourasuchus atopus* (Langston, 1965); slender longirostrine, *Gavialis gangeticus* (Gmelin, 1789); stenorostrine large supratemporal fenestrae (STF), *Metriorhynchus superciliosus* (de Blainville, 1853); ziphodont, *Sebecus icaeorhinus* (Simpson, 1937).

We prefer this grouping scheme for two primary reasons: (1) given the large phylogenetic scope of our data, it is very likely that different allometric scaling relationships apply to different clades, and a single size–shape correction might be affecting some groups excessively (e.g. Notosuchia; some particularly small taxa possessing short, triangular snouts shift dramatically across the morphospace to areas representing highly elongate, slender snouts); and (2) size-related changes in shape are likely to be relevant to feeding.

FEEDING ECOLOGY/PALAEOECOLOGY

Of the cranial shape classifications defined in our geometric morphometric and cluster analyses, extant species occupied only three of the seven ecomorphs: macro-generalists, generalists and slender longirostrine. Ordinary least squares regressions revealed that significant overlap between groups occurred in smaller-bodied taxa, but that the ecomorphs did separate out as body size increased (ANCOVA, $P = 0.003319$). These linear regressions and their corresponding 95% confidence intervals and r^2 values are reported in Figure 3. We name the first group macro-generalists, because these species exhibit the 'generalist' morphotype (*sensu* Brochu, 2001) and are capable of taking prey species with a higher body mass than themselves. Species within the generalist morphotype can take prey items of roughly equal mass to themselves, whereas slender longirostrine taxa are small-prey specialists, which

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Table 1. Qualitative descriptions of each cranial shape ecomorph group derived from the PAM cluster analysis

Group name	Medoid taxon	Description
Brevirostrine heterodont	*Libycosuchus brevirostris* (Stromer, 1914)	Brevirostrine; relatively large STF; heterodont dentition
Macro-generalist	*Caiman crocodilus fuscus* (Linnaeus, 1758)	Brevirostrine to mesorostrine; generally, a more U-shaped snout
Generalist	*Brachyuranochampsa eversoli* (Zangerl, 1944)	Generally, mesorostrine, with a somewhat triangular snout
Stenorostrine, large STF	*Teleidosaurus calvadosii* (Eudes-Deslongchamps, 1866)	Mesorostrine to moderate longirostrine; enlarged supratemporal fenestrae; somewhat laterally positioned orbits
Slender longirostrine	*Tomistoma schlegelii* (Müller, 1838)	Moderate to extreme longirostrine slender snout
Ziphodont	*Hamadasuchus rebouli* (Buffetaut, 1994)	Mesorostrine, somewhat narrow snout; orbits more laterally positioned; ziphodont dentition
Duck-faced	*Mourasuchus pattersoni* (Cidade *et al.*, 2017)	Elongate, broad, flattened snout; tiny STF; isodont dentition

The medoid taxon is the specimen representing the centre of each cluster (ecomorph group).
Abbreviations: PAM, partitioning around medoids; STF, supratemporal fenestrae.

only eat prey items that are substantially smaller than themselves.

ANCESTRAL STATE RECONSTRUCTION

Results of the ancestral state reconstruction illuminated some general trends in the evolution of crocodyliform cranial morphotypes over time (for complete results, see Supporting Information, Fig. S1). Our analysis reconstructed slender longirostrine as the ancestral state for the basal node. However, we interpreted this result with some scepticism because this is almost certainly attributable to the lack of additional outgroup taxa (none of which possesses an elongate slender snout). The ancestral state for Neosuchia was reconstructed as generalist, and this remained the ancestral state for the nested clades Eusuchia and Crocodylia. Within Crocodylia, both Alligatoroidea and Crocodyloidea were ancestrally generalist. However, the evolution of cranial ecomorphs within these groups was markedly different (Fig. 4). There was a strong tendency within Alligatoroidea towards macro-generalist cranial shapes (with a shift to duck-faced in *Mourasuchus*, and numerous reversions to generalist morphotypes), whereas crocodyloids were predominantly generalists (with some excursions into slender longirostrine and macro-generalist morphotypes). The ziphodont morphotype, with the exception of *Dakosaurus* (von Quenstedt, 1856), occurred only in taxa inferred to be terrestrial. The stenorostrine large STF morphotype was restricted taxa inhabiting marine ecosystems (Wilberg *et al.*, 2019 and references therein).

DISCUSSION

PALAEODIET AND FEEDING BEHAVIOUR

Although several of the snout shape groupings recognized in the present study echo previous, qualitatively described groups (Brochu, 2001), the division of broad- and slender-snouted taxa into four separate groups suggests that we have been masking morphological diversity by lumping these groups together. The significant difference in prey size selection among the two generalist ecomorphs also suggests that these snout shapes reflect diverging feeding and prey selection strategies.

Within the fossil dataset, sample numbers of bite-marked bones are often extremely small, making it doubtful that the palaeoecological data accurately reflect maximal potential prey size. However, the predictions based on modern groups do provide a framework to gain a better understanding of these case studies in a broader context. When plotted against the extant dataset, the majority of fossil examples fall either within or below the 95% confidence interval of the mass vs. prey mass regression for each ecomorph (Fig. 3). This is the expected pattern for predatory behaviour and essentially reflects species eating within their expected weight class of prey items.

However, a few fossil case studies fall well above the maximal potential prey mass predicted by the corresponding regressions and 95% confidence intervals for their ecomorph (Fig. 3). Predation and scavenging can be difficult to differentiate in the fossil record (e.g. Bell & Currie, 2010; Longrich *et al.*, 2010; Mclain *et al.*, 2018). However, we argue that the predictive models based on extant crocodylian prey

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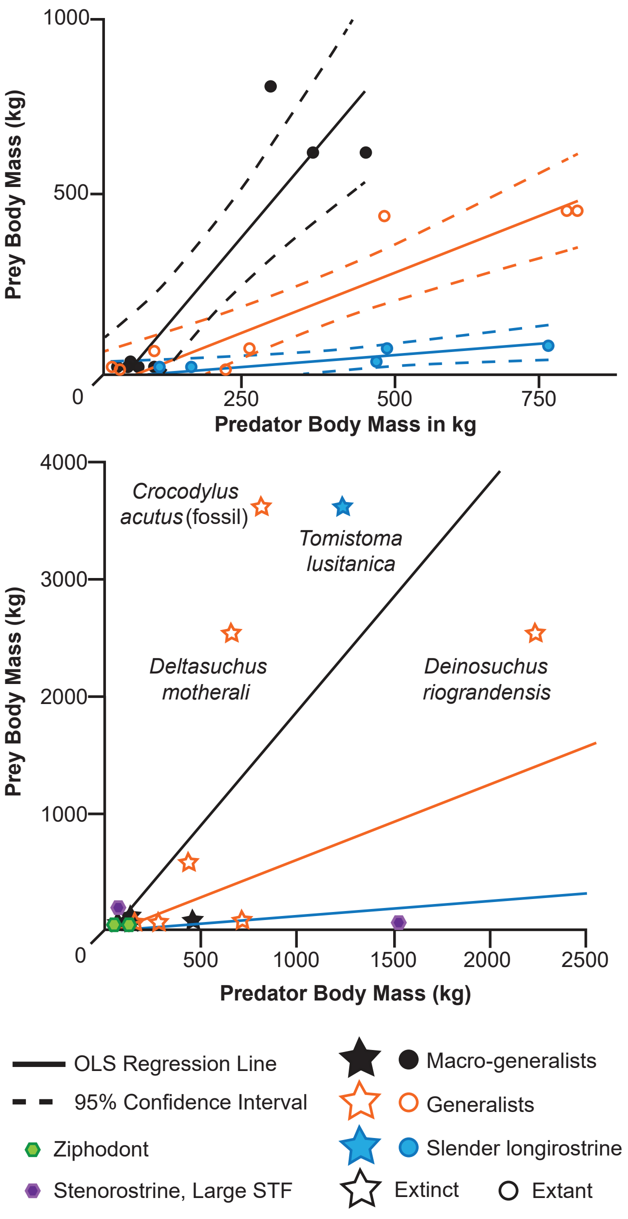

Figure 3. Top panel shows ordinary least squares regressions for modern macro-generalists (black), generalists (orange) and slender longirostrine (blue) crocodylians, shown with 95% confidence intervals (CI). Macro-generalist regression: $r^2 = 0.832$, slope = 1.9507 (95% CI = 0.56087; 3.877), y-intercept = –74.567 (95% CI = –161.48; 28.475). Generalist regression: $r^2 = 0.8557$, slope = 0.94327 (95% CI = 0.53439; 1.5444), y-intercept = –48.149 (95% CI = –121.18; 55.875). Slender longirostrine regression: $r^2 = 0.83924$, slope = 0.081023 (95% CI = 0.034489; 0.15188), y-intercept = –6.4329 (95% CI = –31.2; 4.4102). ANCOVA, $P = 0.003319$. Bottom panel shows macro-generalist (black), generalist (orange) and slender longirostrine (blue) regression lines charted with fossil bite mark case studies in corresponding colours [additional ziphodont examples in green; stenorostrine, large supratemporal fenestrae (STF) in purple]. Probable examples of scavenging are labelled with the species that made the trace (Schwimmer, 2002, 2010; Cisneros, 2005; Rivera-Sylva *et al.*, 2009; Noto *et al.*, 2012; Antunes, 2017).

selection provide strong justification for interpreting these specific case studies as incidences of scavenging rather than predation, because the crocodyliforms were feeding on prey far above their maximal predicted prey mass. *Deinosuchus* (Holland, 1909) and *Deltasuchus* (Adams *et al.*, 2017b) fall within the generalist ecomorph, and based on the regression for that group, we predict that neither would be expected to take adult hadrosauromorph prey successfully (e.g. Schwimmer, 2002, 2010; Rivera-Sylva *et al.*, 2009; Noto *et al.*, 2012; Adams *et al.*, 2017b). *Crocodylus acutus* (Cuvier, 1807) is another generalist, with modern maximal prey mass peaking at 613 kg (Supporting Information, Table S2), but fossil bite marks attributable to this species have been identified on a proboscidean (estimated mass ~3629 kg; Supporting Information, Table S2), another example of probable scavenging (Cisneros, 2005). *Tomistoma lusitanica* (Vianna and Moraes, 1945) falls within the slender longirostrine ecomorph, suggesting small-prey specialization, and yet its bite marks are recorded on gomphothere remains. The interpretation of this feeding trace as scavenging rather than predation was first proposed in the initial study of these traces (Antunes, 2017) and is supported by our analysis.

EVOLUTION OF CRANIAL SHAPE ACROSS CROCODYLIFORMES

The variation in crocodyliform cranial shape across their evolutionary history has been noted in previous qualitative and quantitative studies (e.g. Brochu, 2001; Wilberg, 2017). Our ancestral state reconstructions show a complex pattern of convergent evolution towards particular cranial shape ecomorphs. Few clades maintain a single cranial shape throughout their evolutionary history. The generalist ecomorph is reconstructed as the ancestral shape for Neosuchia. Members of this group span from the Late Jurassic to the Recent, and this long persistence of similar cranial shapes doubtlessly contributes to the fallacy that crocodylians are 'living fossils'. The pattern of cranial shape evolution within Alligatoroidea and Crocodyloidea suggests somewhat different responses to selective pressures during their evolution (Fig. 4). Although both groups contain numerous members of the two generalist shape categories, alligatoroids repeatedly evolved into the macro-generalist morphotype, allowing them to take prey larger than their own body mass. Crocodyloids, in contrast,

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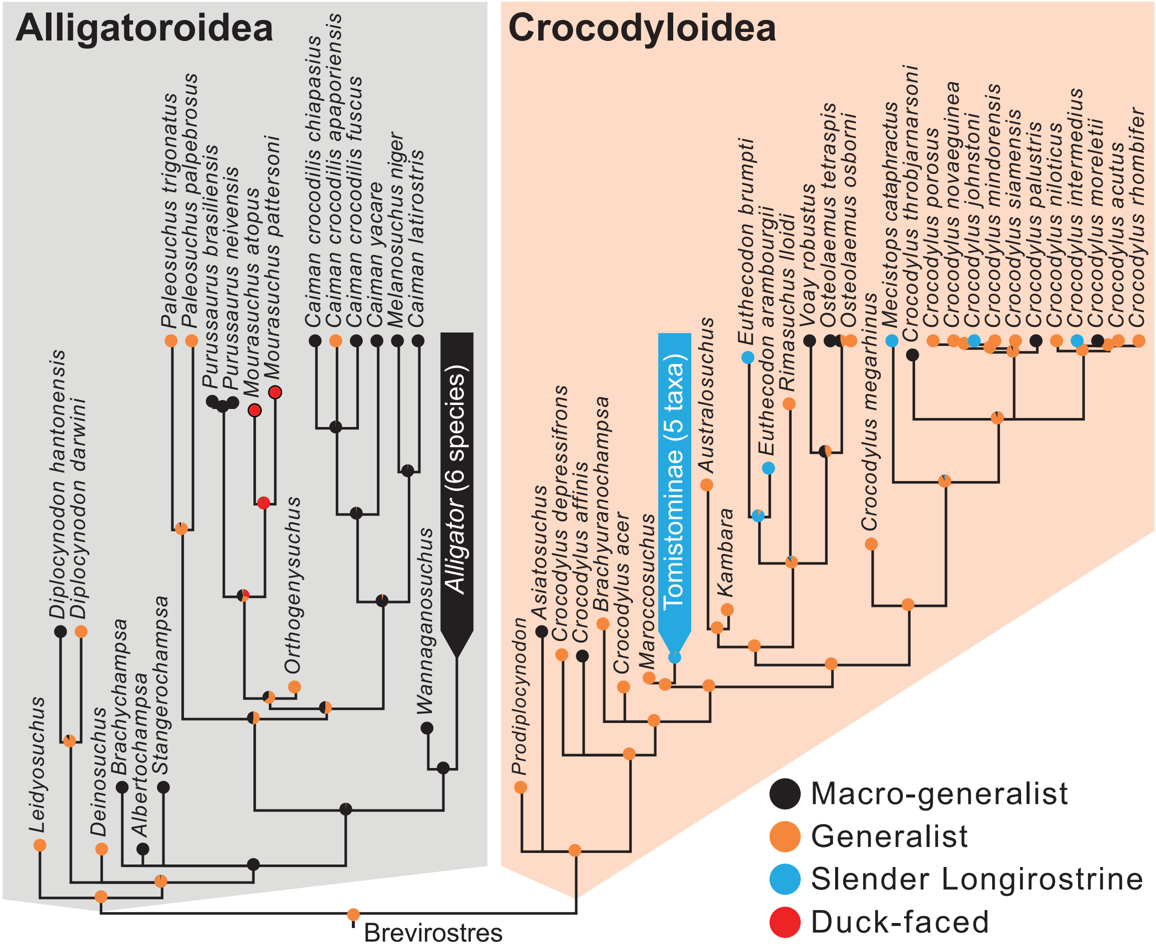

Figure 4. Results of cranial ecomorph ancestral state reconstruction among alligatoroids and crocodyloids (for comprehensive results, see Supporting Information, Fig. S1). Pie charts at internal nodes indicate the proportional likelihood for each ecomorph shape category.

generally retain the ancestral generalist morphotype, with numerous independent transitions to slender longirostrine morphologies. They also show a number of isolated transitions into the macro-generalist region of morphospace. Alligatoroids cover a much narrower range of morphospace along PC1 than crocodyloids (Supporting Information, Fig. S2). Throughout their evolutionary history, no alligatoroid ever evolved a truly slender elongate snout so common among crocodyloids (Brochu, 2001). In instances where they did develop elongate snouts, these remained very broad, resulting in the duck-faced ecomorphs. This raises the interesting idea that alligatoroids might be developmentally constrained to broader snout morphotypes. Recent studies investigating the ontogenetic trajectories of extant crocodylians (Watanabe & Slice, 2014; Foth *et al.*, 2018; Morris *et al.*, 2019) describe a greater range of developmental trajectories in crocodyloids (including a large number of heterochronic shifts) than alligatoroids. Perhaps this variation in developmental patterns has allowed for greater flexibility in the evolution of different snout shapes within this group.

Two of the seven cranial ecomorphs are absent from the crown group. Although some members of the crown group (some alligatoroids, in particular) possessed blunt snouts, none ever developed truly heterodont dentition, like members of the brevirostrine heterodont group. It should be reiterated here that some members of Alligatoroidea did develop globidont, anvil-like posterior dentition [e.g. *Allognathosuchus* (Mook, 1921)]. We were unable to include this dental character in our analysis because it shows continuous variation among extant and extinct taxa and would require an arbitrary cut-off (but for a more detailed discussion of crocodylian dental morphotypes, see D'Amore *et al.*, 2019). However, this type of dentition is not

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associated with the complex chewing behaviours inferred for other heterodont crocodyliforms (Ősi, 2014), and thus these taxa are likely not to be similar functionally to members of the brevirostrine heterodont group. The other cranial ecomorph absent from the crown group is the stenorostrine large STF group. No members of Crocodylia possess particularly large STF in comparison to some non-crown clades (e.g. Thalattosuchia, Dyrosauridae). Perhaps some developmental repatterning occurred along the lineage leading to Crocodylia that precludes the reacquisition of enlarged STF (e.g. shift in emphasis to a different group of jaw adductor muscles). This region of the tree corresponds to the inferred evolution of modern bite forces in the lineage (Gignac & O'Brien, 2016).

Conclusions

The relationship between form and function in an evolutionary context is rarely as straightforward or simple as we would like it to be. In the present study, we provide a more holistic approach to studying the interrelationship of cranial shape and dietary preference within Crocodyliformes by bringing together geometric morphometrics, ecological surveys, phylogenetics and ichnological/taphonomic case studies. This synthetic approach reveals more diversity in snout shape and feeding strategy than previously recognized. Furthermore, the pattern of evolution of cranial shape is complex. Some groups show little disparity, remaining within one or two cranial ecomorph categories, whereas others explore nearly all regions of morphospace. Crocodylia is reconstructed as ancestrally generalist, with crocodyloids exploring both macro-generalist and slender longirostrine morphotypes, but Alligatoroidea is restricted to the broad-snouted regions of morphospace (i.e. generalist, macro-generalist and duck-faced). This pattern is possibly related to differing developmental constraints within these groups.

ACKNOWLEDGEMENTS

We thank C. Brochu and A. Turner for access to photographs and line drawings of specimens. We thank T. Lucas for assistance with applying the 'paleomorph' package to two-dimensional data and A. Watanabe and E. Gold for general assistance with R. Valuable feedback by M. Stocker and an anonymous reviewer improved an earlier version of this work. This research was supported, in part, by a National Science Foundation, Division of Environmental Biology grant, #1754596.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Time-calibrated phylogeny of Crocodyliformes, showing cranial ecomorph ancestral state reconstructions. The time scale on the right of the plot is in millions of years before the present. The pie charts at internal nodes represent the proportional likelihood of the ancestral state.

Figure S2. Comparative cranial morphospace on principal component (PC) 1 (69.8% of variance) and 2 (18.2% of variance). Polygons enclose the clades Alligatoroidea and Crocodyloidea for comparison of morphospace occupation.

Table S1. Information on specimens used in the morphometric analyses and stratigraphic midpoint values used for the time scale tree. See main text for information on how time scaling was performed. *These taxa were represented by reconstructions.

Table S2. Dietary surveys and case studies across extant and extinct members of Crocodyliformes. Species column; extinct taxa indicated with an asterisk. Maximal length is reported in centimetres. Maximal mass is reported in kilograms. Mass estimates are based on a polynomial regression based on length and mass data presented by Drumheller & Brochu (2016) and performed in Microsoft Excel. The formula is as follows: $y = 0.0022x^2 - 0.2259x + 3.3506$, with an r^2 of 0.95627. Under published prey types, bold indicates the group used to estimate maximal prey mass, italics indicate fossil case studies, and parentheses indicate examples of scavenging. Maximal prey mass is reported in kilograms.

Table S3. Percentage of variance accounted for by each axis resulting from the principal components analysis.

Table S4. Results of the partitioning around medoids (PAM) cluster analysis of allometrically corrected morphometric data in comparison to results of non-allometrically corrected cluster analysis. Taxa recovered in different groups between analyses (except those resulting from the splitting of the generalist and macro-generalist categories into three) are highlighted in bold.

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