Quantitative heterodonty in Crocodyliformes: assessing size and shape across modern and extinct taxa (#29741)

First revision

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Quantitative heterodonty in Crocodyliformes: assessing size and shape across modern and extinct taxa

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Heterodonty in Crocodylia and associated taxa has not been defined quantitatively, as the teeth rarely have been measured. This has resulted in a range of qualitative descriptors, with little consensus on the condition of dental morphology in the clade. The purpose of this study is to present a method for the quantification of both size- and shape-heterodonty in members of Crocodyliformes. Data were collected from dry skeletal and fossil specimens of 34 crown crocodylians and one crocodyliform. Digital photographs were taken of each tooth and the skull, and the margins of both were converted into both landmarks and semilandmarks. We expressed heterodonty through Foote's morphological disparity, and a Principal Components Analysis visualized shape variance. This analysis reveals that all Crocodyliformes sampled are heterodont to varying degrees. The majority of the shape variance was represented by a 'caniniform' to 'molariform' transition. Heterodonty varied significantly between positions; size undulated whereas shape was significantly linear from mesial to distal. Size and shape, although significantly correlated, appear to be primarily decoupled. Skull shape correlated significantly with tooth shape. High size-heterodonty often correlated with very large caniniform teeth, reflecting a prioritization of securing prey. Large, highly molariform, distal teeth may be a consequence of high-frequency durophagy combined with prey size. The slender-snouted skull shape correlated with a caniniform arcade with low heterodonty. This was reminiscent of other underwater-feeding tetrapods, as they focus on small prey that requires minimal processing. Several extinct taxa were very molariform, which was associated with low heterodonty. *Hamadasuchus rebouli* may have dealt with vertebrate prey similar to large modern taxa, but prey processing may have been different due to its terrestrial habitat. Disparity measures can be inflated or deflated if numerous teeth are absent from the tooth row, and regression analysis may not best apply to strongly slender-snouted taxa. Nevertheless, when these methods are used in tandem they can give a

complete picture of crocodylian heterodonty. Future researchers may apply our proposed method to most crocodyliform specimens with an intact enough tooth row regardless of age, species, or rearing conditions, as this will add rigor to many life history studies of the clade.

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ABSTRACT

Heterodonty in Crocodylia and associated taxa has not been defined quantitatively, as the teeth rarely have been measured. This has resulted in a range of qualitative descriptors, with little consensus on the condition of dental morphology in the clade. The purpose of this study is to present a method for the quantification of both size- and shape-heterodonty in members of Crocodyliformes. Data were collected from dry skeletal and fossil specimens of 34 crown crocodylians and one crocodyliform. Digital photographs were taken of each tooth and the skull, and the margins of both were converted into both landmarks and semilandmarks. We expressed heterodonty through Foote's morphological disparity, and a Principal Components Analysis visualized shape variance. This analysis reveals that all Crocodyliformes sampled are heterodont to varying degrees. The majority of the shape variance was represented by a 'caniniform' to 'molariform' transition. Heterodonty varied significantly between positions; size undulated whereas shape was significantly linear from mesial to distal. Size and shape appeared to be primarily decoupled. Skull shape correlated significantly with tooth shape. High size-heterodonty often correlated with very large caniniform teeth, reflecting a prioritization of securing prey. Large, highly molariform, distal teeth may be a consequence of high-frequency durophagy combined with prey size. The slender-snouted skull shape correlated with a caniniform arcade with low heterodonty. This was reminiscent of other underwater-feeding tetrapods, as they focus on small prey that requires minimal processing. Several extinct taxa were very molariform, which was associated with low heterodonty. *Hamadasuchus rebouli* may have dealt with vertebrate prey similar to large modern taxa, but prey processing may have been different due to its terrestrial habitat. Disparity measures can be inflated or deflated if

numerous teeth are absent from the tooth row, and regression analysis may not best apply to strongly slender-snouted taxa. Nevertheless, when these methods are used in tandem they can give a complete picture of crocodylian heterodonty. Future researchers may apply our proposed method to most crocodyliform specimens with an intact enough tooth row regardless of age, species, or rearing conditions, as this will add rigor to many life history studies of the clade.

INTRODUCTION

What constitutes heterodonty often seems like a moving target, with different qualitative definitions in place depending on the clade being studied (Shimada, 2001). Kieser et al. (1993, p.195) referred to the definition of heterodonty as “a bone of contention,” and since then the issue never has been fully resolved. Arguably, this lack of clarity is most pronounced within members of Crocodylia. Researchers have often referred to crocodylians as homodont (Langston, 1973; Osborn, 1998; Larsson & Sidor, 1999; Zahradnicek et al., 2014). Peyer (1968 p.17) defined the term as lacking the discrete dental categories seen in mammals (incisors, canines, premolars, molars), even though he admitted, “a sharp distinction between homodont and heterodont is not possible.” Ferguson (1981) referred to *Alligator mississippiensis* as “pseudoheterodont,” because it showed a gradual, as opposed to punctuated, change in tooth shape along the tooth row (see also Grigg and Gans, 1993; Hendrickx, Mateus, & Araújo, 2015a). Size variability along the tooth row has motivated the term “heterometric homodonty”

for *Crocodylus niloticus* (Fruchard, 2012). Others have applied anisodonty to the clade, which is apparent size, but not shape, heterodonty (Vullo et al., 2016). Certain fossil crocodylians, often interpreted as herbivores or omnivores, exhibit multi-cusped and/or grinding teeth, and are specifically called "heterodont crocodylians" by researchers (e.g. Martin, 2007; Ősi, Clark, & Weishampel, 2007; Novas et al., 2009). Lastly, some researchers have argued certain modern crocodylians are heterodont, and argue dental categories do in fact exist (Aoki, 1989; Kieser et al., 1993).

Semantics aside, one reason for the lack of resolution concerning crocodylian heterodonty is that their teeth rarely have been measured. Few studies have performed quantitative shape analyses of crocodylian teeth. Of these, linear-distance measures have been used for fossil identification (Frey & Monninger, 2010), replacement rates (Bennett, 2012), and biomechanical analyses (Monfroy, 2017). Aside from a study evaluating two fossil notosuchians (Lecuona & Pol, 2008), and a preliminary geometric morphometric investigation of *Crocodylus niloticus* (Farrugia, Polly, & Njau, 2016), no studies have quantitatively investigated heterodonty either within or between species. Typically, crocodylian dentition is described qualitatively, with the goal of characterization for phylogenetic analysis, or paleoecological inference (e.g. Schwarz-Wings, Rees, & Lindgren, 2009; Young et al., 2012; Salas-Gismondi et al., 2015; Adams, Noto, & Drumheller, 2017). Qualitative descriptors of crocodylian tooth morphology are numerous, and include terms such as "blunt, bulbous, broadened, button-shaped, conical, globular, fang, kidney-shaped, lanceolate, needle-like, procumbent, pseudocanine, robust, short, slender, spike-like," and "thick" (e.g. Brazaitis, 1973; Groombridge, 1982; Aoki, 1989; Brochu, 1999; Erickson, Lappin, & Vliet, 2003; Ősi, Clark, & Weishampel, 2007; Schwarz-Wings,

Rees, & Lindgren, 2009; Fruchard, 2012; Gignac & Erickson, 2014; Salas-Gismondi et al., 2015; Berkovitz and Shellis, 2017). There is clearly a gap in our knowledge concerning the nature of dental morphology in this clade, and closing this gap may be crucial for a more complete understanding of performance, behavior, and trophic ecology within Crocodylia, as well as more distantly related, crocodylian-line archosaurs.

The lack of quantitative studies on heterodonty in crocodylians and associated taxa is not due to a lack of applicable methodology, as there has been a burst of morphometric research in non-mammalian teeth in the past decade. Dinosaur teeth have probably received the most attention, with multiple studies using linear-distance measures for the identification of loose fossil crowns or to infer functional paleoecology (D'Amore, 2009; Larson & Currie, 2013; Buckley and Currie, 2014; Hendrickx and Mateus, 2014; Torices, Reichel, & Currie, 2014; Hendrickx, Mateus, & Araújo, 2015b, Gerke and Wings, 2016; Larson, Brown, & Evans, 2016). Extant reptiles have been investigated quantitatively as well, including colubrid snakes (Britt, Clark, & Bennett, 2009) and varanid lizards (D'Amore, 2015). Prior to this, lamniform sharks were studied heavily (Shimada, 2002b, 2004; Shimada and Seigel, 2005). These morphometric analyses have shed light on the nature of heterodonty, dental allometry, and ecomorphology in these vertebrates, and similar methods may be applied to Crocodyliformes in the hopes to elaborate upon the state of heterodonty in this taxon.

The purpose of this study is to present a method for the quantification of both size- and shape-heterodonty in members of Crocodyliformes. Data were collected from a multispecific sample of both extant and extinct specimens housed in museum collections, and their tooth

morphology was assessed through two-dimensional geometric morphometrics. In addition to this major goal, we also 1) outline and describe dental morphology within the specimens sampled; 2) report any morphological consistencies found within the members of our sample; and 3) present the advantages, limitations, and potential future uses of the method. Our intention is to put forward a method for assessing heterodonty that may be applicable to most crocodyliform specimens.

MATERIALS AND METHODS

Institutional abbreviations

American Museum of Natural History, New York, NY (AMNH); Royal Ontario Museum, Toronto, ON (ROM); University of California Museum of Paleontology, Berkeley, CA (UCMP)

Nomenclature

Crocodyliform teeth have very few discrete homologous anatomical loci, but, because they exhibit thecodont dentition (sensu Edmund, 1962, 1969), we defined them as having a crown with an apex, a neck, and a root within an alveolus. Nomenclature for tooth morphology used here was proposed by Smith & Dodson (2003; Figure 1A-B): mesial, towards the central premaxilla and mandibular symphysis; distal, away from the central premaxilla and mandibular symphysis; lingual, towards the tongue; labial, towards the lips; basal, towards the base of the tooth or alveolus; apical, away from the alveolus or towards the apex. An ‘enlarged’ tooth is the largest tooth in a given section of the jaw independent of shape. This type of tooth is typically referred to as a procumbent tooth (Gignac & Erickson, 2014) or a pseudocanine (Brochu, 1999).

Tooth position was indicated by either the presence of a tooth or an empty alveolus in the host bone (Figure 1A). Teeth were lettered based on the host bone (premaxilla = P, maxilla = M, dentary = D), and numbered in ascending order from mesial to distal positions (the mesial-most dentary tooth was D1, followed by D2, D3, etc.). For consistency, all specimens were assumed to have 5 premaxillary positions (P1–P5) (Berkovitz & Shellis, 2017). Members of *Paleosuchus* and *Osteolaemus* have only 4 premaxillary teeth during early stages of ontogeny (Brochu and Storrs, 2012; Narvaez et al., 2015), and an alveolus may atrophy in certain species (usually P2) as they grow (Webb & Messel, 1978; Brown et al., 2015; DC D'Amore, personal observation). If only four premaxillary positions were present, position P2 was assumed absent, and skipped over during numbering. In one case, a specimen had 6 premaxillary teeth (*Alligator mississippiensis*, ROM 4408). This tooth position was omitted for consistency. Our *Alligator prenasalis* specimen (ROM 1375) had its distal-most cranial positions obscured by poor preservation and matrix. We therefore based its maxillary tooth count on previous osteological accounts (a total of 15 maxillary teeth based on Harvard Museum of Comparative Zoology specimen #1015, Mook, 1932).

Specimens

Data were collected from 27 extant, and 8 extinct, crocodyliform specimens (Supplemental Information Table S1). This resulted in a total of 21 species. Although *Caiman crocodilus* is an extant species, a fossil specimen was also included. From these we measured 1,263 teeth in total. Although we did not use any distinct criteria to distinguish juveniles from adults, larger specimens were selected when possible. Specimens with the most complete tooth rows in the

collections were selected, in that they had the most of their tooth positions represented by measurable teeth on at least one side of the mouth. Certain fossil specimens only had cranial (*Alligator prenasalis* ROM 1375, *Borealosuchus sternbergii* UCMP 126099, "*Crocodylus*" *affinis* UCMP 131090, *Hamadasuchus rebouli* ROM 52620, *Leidyosuchus canadensis* ROM 1903) or dentary (*Borealosuchus sternbergii* UCMP 131769) material to sample.

Tooth data collection

Methods were similar to those proposed by D'Amore (2015). We photographed each tooth using either an Olympus Stylus or a Canon Rebel T3 EOS camera with a non-zoom lens. Skulls were positioned on a flat surface with a dark background such as a tabletop or camera stand, and held stationary by an available prop such as a box or sandbag if necessary. A scale was positioned at the same distance from the camera as the tooth. The camera was either mounted on a camera stand, or was held stationary by a researcher (for larger specimens). Digital photographs were taken from the labial perspective (Figure 1B). For each tooth, we positioned the specimen so the camera lens was parallel to the host bone adjacent to the tooth. This resulted in both carinae being visible in the shot (if present). We simultaneously positioned the lens parallel to the apical-basal long axis, determined qualitatively as when the tooth looked its tallest to the photographer regardless of any labio-lingual curvature. Each tooth was photographed separately, and teeth from both sides were photographed if available. Only fully erupted teeth with the neck visible were included (Figure 1B). Tooth quality was variable in extant specimens. Teeth with slightly worn apices were included. As the outline of the tooth margin was our basis of measurement, we omitted any teeth with large wear facets or chips

that largely interrupted this margin. Cracks down the long axis of the teeth were common, and were omitted if the crack distorted the shape of the tooth or resulted in a space where light could be seen from the other side.

We used a sliding semilandmark analysis (Bookstein, 1997; Sheets, Kim, & Mitchell 2004; Zelditch et al., 2004; Mitteroecker et al., 2013) to derive shape measurements from each tooth's outline. Photographs were entered in TpsDig 2.16, and the margin of the tooth was traced using the curve drawing tool (Rohlf, 2010) (Figure 1B). Because the enamel margin was not always clear, each tooth was traced from apex to the point where the tooth ceased to taper on the neck for both the mesial and distal side. TpsDig then transformed each of the two traced margins into 30 equidistant coordinates, and we combined the apical-most coordinates. This resulted in 3 discrete landmarks (two at the base and one at the apex) and 56 semilandmarks (Figure 1C). This number of coordinates has been used in previous studies of both dinosaur (Smith, Vann, & Dodson, 2005) and monitor lizard (D'Amore, 2015) dentition, as well as claw morphology (Tinius and Russel, 2016), in which it has been shown to accurately represent the totality of two-dimensional shape (Tinius and Russel, 2016). We performed a generalized least squares Procrustes (GLSP) superimposition on the data, calculated centroid size (CS), and slid the semilandmarks to minimize the total bending energy (Perez, Bernal, & Gonzalez, 2006; Gunz & Mitteroecker, 2013) using the program TpsRelw 1.53 (Rohlf, 2013).

Skull data collection

The shape of the skull, and particularly the rostrum, has long been considered both an important phylogenetic and ecomorphological feature in crocodylians (Busbey, 1995; Daniel &

McHenry, 2001; Brochu, 2001; Sadleir & Makovicky, 2008; Salas-Gismondi et al., 2016; Drumheller, Wilberg, & Sadlier, 2016; Wilberg, 2017). We attempted to determine if there was a correlation between tooth morphology and head shape, as these traits may be linked. All specimens' skulls were photographed from the dorsal perspective using the same cameras as above (Figure 1E). Each skull was positioned so the palate was parallel with the tabletop, and the camera was positioned with a camera stand and leveled. A scale was included. We derived skull shape data using a modified version of our technique for tooth outlines. Using TpsDig again, we traced the skull margin from the rostral-most point of contact between the premaxillae to the caudal-most quadratojugal along the margin on each side. We chose this margin because it outlined head-shape as close to as it would have appeared in life as possible, but avoided internal structures such as the jaw articulations or occipital condyles. Each margin was broken into 50 equidistant coordinates, and the rostral-most coordinates were combined. This resulted in 3 landmarks (two at the quadratojugals and one at the premaxillary junction) and 97 semilandmarks (Figure 1E). These also underwent a GLSP superimposition and the semilandmarks were slid to minimize the total bending energy using TpsRelw 1.53. In specimens with damaged or missing bones on one side, bilateral symmetry was assumed and the coordinates on the intact side were mirrored.

A body-size metric was needed for several of the following analyses, but unfortunately few were available for all specimens. Commonly used metrics such as snout-vent length and mass were not recorded for most dry skeletons prior to cataloging, and many specimens (especially fossils) lacked femora (see Farlow et al., 2005). Therefore, the length of the skull was used as a body size metric (see Fukuda et al. 2013 for potential influences on this

204 measurement). We derived skull length from the same landmarks outlining the skull above; it
205 was the linear distance from the rostral-most landmark to the posterior-most landmarks along
206 the mid-sagittal plane (Figure 1D). (Note: *Borealosuchus sternbergii* UCMP 131769 and
207 *Crocodylus niloticus* AMNH 142494 did not have intact skulls, and were therefore omitted from
208 all analyses involving skull data.)

209 **Statistical approaches**

210 All analyses were conducted in MorphoJ v. 106d (Klingenberg 2011), SPSS Version 19.0 [IBM
211 Corp, Armonk, NY], and PAST (Hammer, Harper, & Ryan, 2001). If both left and right teeth were
212 available at a given position, we averaged them. For size, CS values were simply averaged
213 together. For shape, each *x*-*y* coordinate of the GLSP superimposed landmarks and
214 semilandmarks was averaged with its counterpart for both teeth. To ensure that the left and
215 right sides were not significantly different, we ran a 10,000 permutations test on the Procrustes
216 distances between left and right teeth at positions that had both. The null hypothesis of
217 bilateral symmetry was confirmed (p = 0.6785). If only one tooth was available for a given
218 position, that tooth alone represented said position. We also tested the null hypothesis that
219 there was no statistical difference between tooth rows in Crocodyliformes, by running a 10,000
220 permutations test on the Procrustes distance between cranial (premaxilla and maxilla) and
221 dentary teeth. The specimens that only had one tooth row available were excluded from this.
222 No significant difference was found (p = 0.2455).

223 A singular measure of heterodonty was derived for each specimen in the form of
224 Foote's morphological disparity [$MD = (\sum_{i=1}^{m} D_i^2)/(m-1)$] (Foote, 1993; Zelditch, Sheets, &

Fink, 2003; Sheets & Zelditch, 2013). Disparity (*MD*) was the sum of the differences of the values of a given tooth (*i*) from the mean for all teeth from that specimen (*Di*, also known as the grand mean) squared, with the number of tooth positions (*m*) factored in. We calculated disparity for all tooth positions for each specimen. For size-heterodonty, *Di* was simply the difference in CS of a tooth from the mean of the specimen (Zelditch et al., 2004). For shape-heterodonty *Di* was the Procrustes distance between the tooth and the mean, and was calculated using DisparityBox7 (Sheets, 2012). Heterodonty then was regressed with a reduced major axis against head length to determine if there was a significant allometric change in the clade.

We attempted to correlate skull shape to tooth shape between individuals by using a two-block partial least squares (PLS) analysis in MorphoJ. Skull shape represented one block, and average tooth shape represented the other. Average tooth shape was constructed by averaging the corresponding GLSP superimposed landmarks and semilandmarks of every tooth from an individual. The scores for the first PLS of each shape block were plotted against one another and regressed with a reduced major axis. Visualization of variation along each PLS axis was depicted through vector diagrams (Figure 1F).

To determine if size and shape were coupled in Crocodyliformes, shape coefficients generated by MorphoJ were regressed against CS using a reduced major axes. Significance and a high goodness of fit would be indicative of strong coupling between size and shape. A Principal Components Analysis (PCA) was then conducted to visualize the degree of shape

variance within all cranial and dentary teeth. We only considered any PC representing over 5% of the shape variance, which we then visualized using vector diagrams (Figure 1D).

We plotted shape and size against tooth position to visualize heterodonty along the tooth row. For size CS was normalized by dividing it by head length, and then was plotted against tooth position in a series of box plots. For shape, PC scores of PCs over 5% were plotted against tooth position in a similar fashion. Each box represented a position. Note that we did not do any adjustments to these positions, so specimens with more tooth positions will be the only occupants of the distal-most categories. To determine if significant differences in these size and shape metrics existed between these positions, we used separate analyses of variance (ANOVA) for each superfamily. Both metrics had unequal variances according to Levene's test, so we specifically ran Welch's ANOVAs in SPSS. Any positions represented by less than 7 teeth were excluded from the ANOVAs.

Preliminary quantitative work has suggested a linear transition in tooth shape along the arcade (Farrugia, Polly, & Njau, 2016). We test this by regressing shape data against tooth position using ordinary least squares regressions for each individual. To standardize these regressions, we normalized tooth position into a percentage. We numbered the positions along the tooth row starting with 1 at the mesial-most position, divided each by the total number of positions along the arcade, and then subtracted 0.5 (this subtraction placed the *y*-intercept halfway along the arcade). PCs for each tooth were then regressed against this, and regression statistics were collected. Several factors may be implied by a significantly linear crocodyliform tooth row. Slope may be linked to heterodonty, as a steeper slope would imply more shape

266 change along the PC1 scores at *y*-axis and, consequently, greater shape-heterodonty. The *y*-
267 intercept would represent shape value for the median position, as the intercept is located half-
268 way along the tooth row. To visualize these coefficients, we plotted both slope and *y*-intercept
269 for each regression in scatterplots for both the cranium and the dentary.

270 **Results:**

271 **Shape variability in the sample**

272 There was statistically significant coupling between size and shape in Crocodyliformes, but to a
273 very weak degree overall. When shape coefficients were plotted against CS, they formed a
274 regression with a goodness of fit accounting for less than 10% of the variance (y=0.313x-0.981;
275 r^2=0.09; p<0.0001; 95% =0.296,0.328).

276 Most of the shape variance in Crocodyliformes was along a single axis. The only PC
277 accounting for over 5% of the shape variance was the first (PC1). It accounted for over 92.11%
278 of the variance, and is the only PC considered further [see supplemental information for
279 Eigenvalues and variances (Table S2), as well as a discussion on PC2 and PC3 (Figure S1)]. ~~PC1~~
280 ~~scores ranged from -0.3173 to 0.3715 within our sample.~~ The negative-most condition involved
281 apical-basal elongation, narrowing at the base, and a gentle concavity on the distal margin
282 (Figure 2). For simplicity, we will refer to this extreme as 'caniniform' (Erickson et al., 2012;
283 2014; Gignac & Erickson, 2014). The positive-most values depicted an apical-basal shortening
284 and mesial-distal broadening, and we will refer to the extreme as 'molariform' (Figure 2)
285 (Erickson et al., 2012; 2014; Gignac & Erickson, 2014).

286 **Skull vs. tooth morphology**

287 Skull and average tooth shape were significantly correlated. For the two-block test, PLS1
288 encompassed 99.96% of shape covariance. Shape variability within the skull shape block
289 showed the snout transitioning from narrow to broad (Figure 3). Taxa that occur below a PLS1
290 score of -0.15 are the slender-snouted taxa as defined by Brochu (2001), including *Gavialis*,
291 *Mecistops*, and *Tomistoma*. The remainder of the species, defined as either generalized or
292 blunt-snouted (also by Brochu, 2001), occurred around the mean and positive half mixed
293 together. Shape variability within the tooth shape block was similar to the above PCA of tooth
294 shape, displaying a transition from caniniform to molariform with increasing values. These
295 blocks regressed significantly against one another, with slender-snouted taxa separating out
296 with the most caniniform teeth. Scatter increased around the means, indicating the correlation
297 was not as strong among the generalized-to-blunt snouted taxa. *Alligator prenasalis*,
298 *Brachychampsa* sp., and "*Crocodylus*" *affinis* were all relatively blunt-snouted, but rose
299 noticeable above the regression. This indicated they possessed much more molariform teeth
300 on average than their counterparts of similar skull shape.

301 **Foote's disparity and heterodonty**

302 Size heterodonty was significantly correlated with head length, with an r^2 of ~0.76. The largest
303 individuals according to head length (members of *Crocodylus niloticus* and *Crocodylus porosus*)
304 possessing the greatest unadjusted size heterodonty (Figure 4A). The slope indicated that
305 heterodonty increased at over double the rate of size within the clade. Alligatoroids occur on
306 both sides of the regression. Members of *Alligator* had negative residual size heterodonty, with

307 *Alligator prenasalis* as the lowest. On the other side of the regression, caimanine (*Caiman*,
308 *Paleosuchus*) residuals were all positive with the exception of one individual. Several members
309 of *Crocodylus* had values around zero, but one *Crocodylus porosus* specimen had a high residual
310 and a *Crocodylus palustris* had a low residual. One *Osteolaemus tetraspis* individual had the
311 highest size-heterodonty residual, with the other around zero. *Hamadasuchus rebouli* had
312 positive residuals, similar to the greater *Crocodylus porosus* and the caimanines. The slender-
313 snouted taxa (*Gavialis*, *Mecistops*, *Tomistoma*) had some of the most negative residuals.

314 Shape heterodonty was highly variable, and correlated significantly, albeit rather poorly
315 (r^2 ~0.16), with head length (Figure 4B). Because of this poor correlation, we do not consider
316 residuals as very biologically meaningful. Similar to size heterodonty, the slender-snouted taxa
317 had some of the lowest shape heterodonty, although *Tomistoma* was relatively greater than
318 the others. In addition, members of *Brachychampsa* sp. and *Alligator prenasalis* also had some
319 of the lowest shape heterodonty in our sample. *Crocodylus siamensis* specimens were more
320 shape heterodont than their congenerics, with one individual being the most shape heterodont
321 in our sample. Several caimanine individuals, and both *Osteolaemus tetraspis* specimens, also
322 had relatively high shape heterodonty.

323 **Heterodonty along the tooth row**

324 Tooth position count varied between species (see Supplemental Information Table S3). Most
325 alligatoroids had between 19-20 positions on the cranial tooth row. Many had a similar number
326 on the dentary, except members of *Paleosuchus* had 22 positions. *Leidyosuchus canadensis* had
327 the most (23) cranial positions of the alligatoroids. *Hamadasuchus* (20 cranial) and

328 *Borealosuchus* (23 cranial and 20 dentary) specimens fit within ranges of alligatoroids.
329 Members of *Crocodylus* and *Mecistops* had between 18-19 cranial and 15 dentary positions.
330 *Osteolaemus* specimens had the least tooth positions for any crocodyloid (17 cranial and 14
331 dentary), and *Tomistoma* had the most (21 cranial and 19 dentary). The *Gavialis* specimen had
332 more positions than any other species sampled (28 cranial and 26 dentary). These tooth counts
333 are similar to previous published accounts (Brown et al., 2015; Berkovitz & Shellis, 2017). The
334 vast majority of the modern taxa tooth rows had over 60% their tooth positions represented by
335 measureable teeth (Supplemental Information Table S3). Fossil taxa ranged from having ~30%
336 to ~78% of their tooth row represented.

337 In both extant members of Alligatoroidea and Crocodyloidea, size varied significantly
338 between positions (Figure 5A-B). Size undulated three times along the dental arcade resulting in
339 significant differences between positions for both the cranium and mandible. Each undulation
340 peaked with an enlarged tooth. These were typically represented by P4 for both clades, and M4
341 for alligatoroid and M5 for crocodyloid specimens (sensu Brochu and Storrs, 2012). In addition,
342 members of *Paleosuchus* had very large P3 and M3. "*Crocodylus*" *affinis* also had a large P3.
343 Unlike other alligatoroid specimens, the *Leidyosuchus* specimen had both M4 and M5 enlarged,
344 and the *Brachychampsa* sp. had an enlarged M5 like crocodyloids (sensu Norell, Clark, &
345 Hutchison, 1994). A final undulation resulted in an enlarged tooth at M9-11 (Figure 5A-B).
346 Interspersed between these were smaller teeth, with the distal-most tooth often the smallest.
347 The dentary was similar to the cranium, with three undulations in size. Enlarged teeth were
348 found at positions D1 and D4, with a third size-peak between D11 and D14. Note that the
349 position of the enlarged teeth along the cranial tooth row tended to align with smaller teeth

along the dentary tooth row, and vice versa. This resulted in an 'interlocking' pattern between the size peaks of one arcade and the valleys of the other. The gavialoid specimen differed markedly by having the two mesial-most teeth enlarged, and the remainder showed a gradual decease in size distally (Figure 5C). *Hamadasuchus rebouli* had some of the largest teeth for its head length with a dramatic variation in size.

Alligatoroids and crocodyloids both showed a similar trend concerning tooth shape. Mesial teeth are typically the most caniniform in the mouth and distal teeth the most molariform, resulting in positions being significantly different (Figure 5D-E). In cranial teeth P1-M4 tend to exist primarily between PC scores and -0.25 and 0.00, followed by a gradual increase in score values as positions become more distal. Dentary teeth represented a more uniformly gradual caniniform-to-molariform transition. Both superfamilies were highly variable. Alligatoroid had teeth generally more molariform, with upper outliers almost entirely represented by *Alligator prenasalis*, *Alligator sinensis*, and *Brachychampsa* sp. (Figure 5D). Crocodyloids were generally more caniniform, with mesial upper outliers represented by "*Crocodylus*" *affinis* and lower outliers represented primarily by *Tomistoma* (Figure 5E). Both *Borealosuchus* tooth rows had PC1 scores between -0.22 and 0.20, and *Hamadasuchus* ranged between -0.19 and 0.23 (Figure 5F). Both taxa showed a similar progression from caniniformy to molariformy as the alligatoroids and crocodyloids. *Gavialis* deviated from the others the most, where most teeth had scores of < -0.20 with a steep increase towards the average in the distal-most fifth of the arcade (Figure 5F).

Shape heterodonty was found to be strongly linear. When each modern individual's PC1 values were regressed against position, all regressions were significant (Supplemental Information Table S3). The vast majority of tooth row regressions had r^2 values above 80%. *Gavialis* had the lowest r^2 values (cranium=0.495, mandible=0.616), followed by the crania of the fossil *Caiman crocodilus* (r^2=0.728) and *Tomistoma* (r^2=0.747). Both cranial and dentary tooth rows typically had slopes between 0.25-0.55 (Figure 6). More shape heterodont taxa typically had greater slopes, with *Crocodylus siamensis* specimens having some of the steepest slopes (0.39-0.68). All the slender-snouted specimens had the *y*-intercepts between -0.25 and -0.14, indicating strong caniniformy at the median position. The *Gavialis* specimen also had very shallow slopes (<0.25). Living members of *Alligator* had *y*-intercepts between 0.029 and 0.085, indicating molariformy at the median (Figure 6). *Alligator prenasalis, Brachychampsa* sp., and *"Crocodilus" affinis* had the shallowest slopes (0.22-0.32) and the greatest *y*-intercepts (0.15-0.24) in our sample, indicating molariform teeth consistent along the tooth row. *Hamadasuchus rebouli*'s regression characteristics are similar to members of *Caiman* and *Osteolaemus*. The slope of the fossil *Caiman crocodilus* differed from modern members of *Caiman* by being much shallower (Figure 6).

DISCUSSION

Defining heterodonty within Crocodyliformes

The methods proposed here offer a multi-faceted approach to quantifying heterodonty in Crocodyliformes. Foote's morphological disparity allows for a discrete measure of heterodonty that may be used for comparison, or normalized with other variables (as was done here with a

body size metric). This is not limited to Crocodyliformes, and may be used to compare distantly related taxa and/or a wide variety of dental morphotypes. This measure is ideal if one is interested in *how much* heterodonty is apparent. Alternatively, if one is interested in what characteristics make up tooth heterodonty, more traditional geometric morphometrics suffice in describing shape variability. It is opportune that only PC1 accounted for over 90% of the variance, allowing for us to use it as the sole measure of shape here. If more PCs accounted for over 5% of the shape variance, it would be appropriate to depict those other PCs in the same manner as PC1 for a comprehensive understanding of shape.

Regression analysis of shape is appropriate based on significance and high r^2 values, and the coefficients associated with it are useful characters for comparison. Certain caveats should be considered though. Regression may be more appropriate for the dentary than the cranium, as the premaxillary teeth do not appear to differ from one another as much as the maxillary. In most crocodylians this effect is mild, and r^2 values are still high. The effect is very pronounced in *Gavialis* though, as both the premaxillary and the mesial maxillary teeth are similar in shape. It is also interesting that this happens in the dentary as well. Future studies should consider this when applying this method to Gavialoidea or dentally analogous taxa.

Although the task of assigning a singular dental morphotype to any one species of crocodyliform is beyond the scope of the study, our data suggests that it would be potentially difficult. Heterodonty seems to vary within species, making the assignment of a singular heterodonty measure to an entire species dubious. As far as biological explanations for this, tooth form is almost certainly influenced by allometry. Ontogenetic shifts in feeding niche have

been documented in modern crocodylian species (e.g. Groombridge, 1982; Webb, Manolis, & Buckworth, 1982; Pooley & Gans, 1976; Pooley, 1989; Delany, 1990; Santos et al., 1996; Da Silveira and Magnusson, 1999; Subalusky, A. L., Fitzgerald, L. A., & Smith, 2009 Wallace and Leslie, 2008; Borteiro et al., 2009; Hanson et al., 2014), and allometric changes in the feeding apparatus with size are often explained as a structural consequence of this (e.g. Dodson, 1975; Webb and Messel, 1978; Hutton, 1987; Erickson, Lappin, & Vliet, 2003; Verdade, 2000; Wu et al., 2006; Watanabe & Slice, 2014; Gignac and Erickson, 2016; Gignac & O'Brien, 2016). Concerning teeth, a qualitative increase in overall molariformy was observed in *Alligator mississippiensis*, and functioned to meet the mechanical demands of increased durophagy (Erickson, Lappin, & Vliet, 2003; Gignac & Erickson, 2014). Although our sample size is too low to confidently assess dental ontogeny within each species, we did see a similar general trend in conspecifics of different sizes. In particular, the larger of our two *Crocodylus porosus* had a greater *y*-intercepts indicating greater molariformy. In addition to allometry, phenotypic changes due to environmental factors may also influence teeth. Skull shape and tooth orientation are irregularly influenced by captive rearing (Erickson et al., 2004; Drumheller, Wilberg, & Sadleir, 2016), and how this may also influence tooth shape has yet to be determined. Many of our specimens had 'no data' concerning their rearing, so we do not know if captivity influenced either tooth or skull morphology.

Morphological trends within Crocodyliformes

All crocodyliform specimens measured here were heterodont to varying degrees, and these data showed significant variability of morphotypes along the dental arcade for all specimens

(Figure 7). Although dentition varied between species, certain consistencies were seen throughout the clade:

1. Similar teeth occurred on both the cranial and dentary dental arcades.
2. As body size increased, size-heterodonty increased reliably with it. Shape-heterodonty shows a much less reliable negative correlation with body size.
3. The vast majority of shape variance from the labial perspective occurred along a single shape axis, representing the transition from caniniform to molariform. Only minor distal curvature was apparent in very caniniform crowns.
4. There was serial homology in tooth shape from-mesial-to-distal along the tooth row, and molariformy increased in this direction. The transition was significantly linear for both dental arcades for all specimens.
5. Size variability consisted of an undulating pattern with three peaks that interlock with the opposing row, with enlarged crowns interspersed within smaller crowns. This corresponded with the festooning pattern seen in the tooth bearing bones, and was less apparent in slender-snouted taxa.

Shape- and size-heterodonty were very loosely coupled in Crocodyliformes as they changed in dramatically different, and primarily independent, fashions along the arcade. Some correlation did occur; the regression's significance was probably the result of the fact that the distal-most crowns were typically both the smallest crowns as well as the most molariform. Nevertheless, the undulating pattern of tooth size did not align with linear shape heterodonty for the vast majority of the tooth row, as indicated by the very low r^2.

The low degree of coupling begs the question; do developmental agents influence size and shape separately? Although quite a bit of research has looked at how crocodylian teeth grow and replace themselves (Edmund, 1962; Westergaard and Ferguson, 1986, 1987, 1990; LeBlanc et al., 2017), surprisingly little has been done on what developmental influences affect tooth size and shape. Modern crocodylians replace their teeth in waves, or Zahnreihe (Edmund, 1962; Westergaard and Ferguson, 1990; Osborn, 1998), but it is unclear how the nature of these waves relate to the morphological variables investigated here. Keiser et al., (1993) compartmentalized the dentition along the tooth row for *Crocodylus niloticus*, grouping teeth into 'incisor,' 'premolar,' and 'molar' regions. These designations attempted to account for both size and shape heterodonty; each was defined by an enlarged tooth, and each become progressively more molariform. They did not offer a developmental mechanism that differentiates these categories though. Fruchard (2012, p.7) suggested that the only difference between enlarged teeth and their smaller counterparts was that the former was "programmed to be bigger," suggesting some sort of additional developmental signaling to enlarge teeth. More research is needed on how tooth shape and size are established developmentally in order to truly understand what generates heterodonty.

Adaptive explanations for morphological variability in modern taxa

There is a wide range of tooth morphologies present in modern Crocodylia, and, as teeth are anatomical units used for feeding and aggression, functional inferences may be drawn based on our present understanding of behavior and performance. Bite force in crocodylians is primarily influenced by size (Erickson et al., 2012, 2014), and our data set shows that similarly sized

crocodylians may have very different tooth dimensions. This rules out maximum bite force as the sole limiting factor dictating tooth form. Although we are reluctant to associate specific prey items with specific tooth forms, size and shape will influence how a tooth interacts with food items possessing certain physical properties. We therefore suggest that a biomechanical link should exist between the structural limits imposed by tooth form and the material properties of the substrates with which it interacts.

As with all jawed vertebrates, crocodylian teeth will succumb to different speeds and stresses based on their respective position along the arcade. Caniniform mesial teeth are ideal for the initial acquisition of prey. Pointed apices reduce surface area to puncture compliant foods that deform under pressure, such as muscle, fat, and fibrous connective tissue (Frazetta, 1988). Being farther from the hinge, these teeth move faster during a strike and are more likely to contact prey trying to escape (Busbey, 1989). They will also will endure less force based on their position, and can afford to be relatively elongate and gracile. On the other end, distal teeth need to withstand greater forces due to their close proximity to the hinge (Cleuren, Aerts, & Vree, 1995; Erickson, Lappin, & Vliet, 2003; McHenry et al., 2006; Erickson et al., 2012). This explains why these teeth are typically on the molariform half of the shape spectrum; the larger base-to-height ratio gives them greater relative bending strengths (Van Valkenburgh and Ruff, 1987; Gignac & Erickson, 2014; Monfroy, 2017). Because force is highest in this region, it is ideal for processing food items after they are acquired (Busbey, 1989; Davenport et al., 1990; Cleurens and de Vree, 2000). The reduced height of these teeth also ensures they do not impede jaw closure. This necessity is very apparent in our representative member of *Gavialis*, and provides a functional explanation for the poor linear shape relationship along the tooth

497 row in this individual. Having all the teeth be highly caniniform except for the distal-most region
498 may be interpreted as an attempt to reduce heterodonty as much as possible (Grigg and Gans,
499 1993), while ensuring the distal crowns do not impede jaw closure or break when processing
500 food.

501 Particular attention should be paid to the relative size of the distal-most crowns, as they
502 vary considerably within our sample. Most modern alligatoroids and crocodyloids have a single
503 enlarged tooth followed distally by several smaller teeth. These typically were represented by
504 positive PC1 scores, especially concerning *Alligator mississippiensis* and *Crocodylus siamensis*,
505 and were also some of the smallest teeth in its arcade (Figure 7A). Both members of *Alligator*
506 *sinensis* differed from this though, in that they had a row of 4-5 relatively large, high-
507 molariform crowns (followed by only one crown reduced in size). Probably the most extreme
508 condition, *Osteolaemus tetraspis* specimens had distal crowns that were exceptionally large;
509 the largest relative crowns at positions M10-12 and D11-13 for modern taxa all belonged to
510 members of this species. These two species also have the lowest number of teeth for modern
511 alligatoroids and crocodyloids respectively, a reduction potentially based on the need to fit
512 these enlarged teeth. Aoki (1989) qualitatively noted these unique conditions, and suggested
513 they facilitated durophagy. All alligatoroids and crocodyloids sampled here have been recorded
514 to consume at least some hard prey items though (e.g. Brazaitis, 1973; McIlhenny, 1976; Taylor,
515 1979; Groombridge, 1982; Ross and Magnusson, 1989; Santos et al., 1996; Selvaraj, 2012;
516 Nifong & Silliman, 2013), so it is unclear what selection pressure resulted in these particular
517 morphologies. It may be a result of body size. Bite force tests of *Alligator mississippiensis*
518 showed the pressure produced at its enlarged M11 to be adequate to crush its harder prey

519 items (Erickson, Lappin, & Vliet, 2003; Gignac & Erickson, 2014). If this is the case in most of the
520 large crocodylians, enlarging the distal-most crowns would be unnecessary. *Alligator sinensis*
521 and *Osteolaemus tetraspis,* on the other hand, may need more extreme dentition closer to the
522 hinge; their smaller size would make it more difficult to process foods with similar mechanical
523 properties. Another explanation for this may be the frequency of consuming hard prey.
524 Although both these species have broad diets, studies have shown certain (but not all)
525 populations to consume disproportionately large numbers of shelled mollusks and crustaceans
526 (Cheng-Kuan, 1957; Groombridge, 1982; Ross and Magnusson, 1989; Luiselli, Akani, & Capizzi,
527 1999; Pauwels et al., 2007).

528 All taxa measured here also have two sets of enlarged mesial teeth on both arcades.
529 These teeth are well built for puncturing, likely make first contact with prey during jaw closure,
530 and are resilient against struggling prey (Iordansky, 1964). An apparent trade-off to enlarging
531 these teeth is the need to reduce the size of teeth on the opposing tooth row. This character
532 played a large role in size-heterodonty, with different crocodylians undulating their tooth sizes
533 to different degrees. High relative size-heterodonty in caimanine specimens was typically a
534 consequence of the dramatic size difference between the enlarged teeth and the small
535 remaining crowns, (Figure 7B). Their dentary crowns in particular became so large they often
536 grew entirely through the cranial rostrum in adults (as mentioned in Brazaitis, 1973), which
537 suggests securing prey takes priority. The remaining crowns were rather small by comparison,
538 including the distal crowns: the teeth with the greatest mechanical advantage when processing
539 hard prey. This arrangement may be a specialization for hunting more mobile and/or compliant
540 prey (Sampaio et al., 2013), as insects and fish can make up a large portion of the caimanine

diet (Santos et al., 1996). The *Crocodylus porosus* specimens had the largest M5 crowns in our sample, which may also show a prioritization for puncturing and securing soft-bodied prey in a larger context (Figure 7B). This species is notorious for actively hunting large vertebrates such as sharks, cattle, horses, and humans (e.g. Taylor, 1979; Kar & Bustard, 1981; Groombridge, 1982; Doody, 2009; Hanson et al., 2015), and these teeth are ideal for puncturing and securing such prey. Similar to caimanines, this species atrophies position P2 to make room for its enlarged D1 crowns (Brown at al., 2015)

The slender-snouted species possessed generally more caniniform teeth, which may be a consequence of feeding habitat and prey preference. These taxa have a reputation for eating small, aquatic prey with a focus on fish (Peyer, 1968; Webb, Manolis, & Buckworth, 1982), and multiple lines of evidence suggest the feeding apparatus is well suited for this function. The slender shape reduces resistance during both lateral motion and jaw adduction when feeding underwater, and the increased snout length allows for a faster strike (Taylor, 1987; Pooley, 1989; Thorbjarnarson, 1990; McHenry et al., 2006; Pierce et al., 2008). Highly caniniform teeth can quickly puncture fast-moving, compliant prey, and their elongate shape may also lower their mechanical resistance (Figure 7C). The longirostrine condition, defined as a snout that is both slender and elongate (Brochu, 2001), resulted in increased tooth positions; *Tomistoma* had more teeth than any other crocodyloid, and *Gavialis* has the most teeth out of all crocodylians sampled. This cranio-dental morphotype may be prey-size prohibitive though, as larger prey could damage the slender rostrum while struggling. Their elongate mandibular symphysis results in a mechanical disadvantage against the forces produced by shaking and twisting prey (Walmsley et al., 2013). The gracile nature of the dentition means a lower bending

strength, making them more susceptible to breakage from larger and/or harder prey as well. On rare occasions, large individuals have been known to take land-based, vertebrate prey (Thorbjarnarson, 1990; Selvaraj, 2012). This is most likely because the overwhelming size of these crocodylians allows their feeding apparatus to withstand the forces exerted by said prey.

The slender-snouted taxa had some of the lowest size- and shape-heterodonty of modern crocodylians, which is reminiscent of several other clades of aquatic predators. They share certain traits with the anisodont plesiosauromorphs (Sassoon et al., 2015; Kear et al., 2017). Although these crocodylians are not anisodont in the strict sense (they all have some shape heterodonty), both taxa have elongate mesial crowns transitioning to smaller distal ones. These taxa also reflect similarities with the 'homodont' condition apparent in odontocete whales (Rommel, 1990), where all the teeth in the arcade possess a similar, peg-like shape. This condition is believed to be ideal for catching and holding, but not processing, small aquatic prey (MacLeod et al., 2007), as most prey items consumed are under 10% of their body length (MacLeod et al., 2006). A convergent reduction in size- and shape-heterodonty within these independently aquatic groups may indicate a transition from a multi-functional dental arcade to one almost exclusively for prey capture. This is clearly the condition in members of *Gavialis,* as it is almost entirely caniniform along its tooth row and eats primarily fish (Groombridge, 1982, Figure 7C). Members of *Mecistops* and *Tomistoma*, although also primarily caniniform, still displayed the linear shape change typical of other crocodyloids. These species may consume prey that require relatively more processing with their distal crowns, and there are numerous reports of them eating prey such as crustaceans, turtles, and immature primates (Brazaitis, 1973; Groombridge, 1982; Galdikas and Yeager, 1984; Selvaraj, 2012).

585 Tooth shape may indicate differences in feeding behavior and processing ability, even
586 though overlap exists in prey selection. *Alligator mississippiensis* and *Crocodilus niloticus* both
587 consume a wide variety of prey, including both large and small mammals, crustaceans, fish,
588 water fowl, snakes, turtles, and conspecifics (McIlenny, 1976; Pooley & Gans, 1976;
589 Groombridge, 1982; Delany and Abercrombie, 1986; Hutton, 1987; Shoop & Ruckdeschel, 1990;
590 Rootes & Chabreck, 1993; Elsey, Trosclair III, & Linscombe, 2004; Wallace and Leslie, 2008;
591 Gabrey, 2010). A comparison of controlled feedings of each of these species showed *Alligator*
592 *mississippiensis* to fracture and consume noticeably more bovine skeletal elements than
593 *Crocodylus niloticus* (Njau & Blumenschine, 2006; Drumheller & Brochu, 2014; 2016). Our
594 *Alligator mississippiensis* specimens was generally more molariform than *Crocodylus niloticus.*
595 These teeth would have greater bending strengths to resist breakage when processing hard
596 material such as bone.

597 **Fossil taxa and the appropriateness of analogues**

598 Certain fossil taxa were reminiscent of modern counterparts. We expected the fossil *Caiman*
599 *crocodilus* to be similar to its congenerics, due to the fact that these specimens are closely
600 related and all consume insects, crustaceans, and fish (Brazaitis, 1973; Groombridge, 1982; Da
601 Silveira and Magnusson, 1999). Any differences in size and shape ranges appear to simply be a
602 consequence of the former's incomplete arcades; no distal maxillary or any dentary crowns
603 were available (see **Limitations** below). *Alligator mississippiensis* specimens have similar shape
604 regression statistics to our *Leidyosuchus* specimen, but, unlike members of *Alligator*, this
605 specimen lacked enlarged distal teeth (Figure 7D). This caused size heterodonty to differ

606 noticeably, and may be indicative of a difference in the degree these taxa process hard
607 materials (although no taphonomic evidence for this currently exists associated with
608 *Leidyosuchus*). The two specimens of *Borealosuchus* differed from one another in median shape
609 as indicated by *y*-intercepts, which may due to an allometric increase in molariformy. The best
610 analogue for this species may be a member of *Crocodylus* with similar slopes, but more data is
611 necessary to confirm this (Figure 7D).

612 The inclusion of *Hamadasuchus*, and the fact that it showed similar trends in
613 heterodonty to crown crocodylians, was particularly revealing. Peirosaurids are believed to be
614 primarily terrestrial crocodyliforms (Tavares et al., 2017), and they most likely did not occupy
615 the semi-aquatic, sit-and-wait predator niche dominated by modern crocodylians (Larsson &
616 Sues, 2007). Nevertheless, the nature of size- and shape-heterodonty is similar between the
617 two groups, indicating the methods proposed here are transferable outside of Crocodylia. The
618 fact that the *Hamadasuchus* specimen had similar relative size heterodonty and relative
619 maximum tooth size to the larger *Crocodylus porosus* specimen indicates that it may have dealt
620 with similar prey from a mechanical standpoint (Figure 7E). Its greatly enlarged mesial teeth
621 would puncture vertebrate tissue with similar effectiveness to those of a large *Crocodylus*
622 *porosus* (Figure 7B). The *Hamadasuchus* specimen differed in that it had very large distal
623 crowns, which, unlike members of *Osteolaemus*, are laterally flattened and considered
624 ziphodont (Larsson & Sidor, 1999). This suggests potential differences in prey processing. It
625 may have used these for either sheering soft tissue or breaking bone similar to modern
626 mammalian carnassials, as rolling on land is not an effective means of dismemberment (Fish et
627 al., 2007).

Several authors have stated that modern taxa do not have, or have secondarily lost, an extreme degree of molariformy commonly found in extinct representatives. 'Globidonty' describes the enlarged, highly molariform crowns in fossil taxa potentially used for durophagy (Norell, Clark, & Hutchison, 1994; Brochu, 1999; 2001; Ősi & Barrett, 2011). Species of *Brachychampsa* are textbook examples of a globidont taxon (Case, 1925; Carpenter and Lindsey, 1980, Figure 7F), and our specimen is the only one in the sample with distal teeth so molariform their PC1 scores exceed 0.349. Although we agree with Brochu (2001, 2004) that *Osteolaemus tetraspis* is not as extreme, the PC1 scores of its enlarged distal teeth are closer to our *Brachychampsa* than another other taxon sampled (0.322-0.341). *Alligator prenasalis* and *"Crocodylus" affinis* distal crowns are similar to *Alligator sinensis* in shape, and also create a ridge of robust teeth (Mook, 1932). The mechanical capabilities of these particular crowns in modern taxa should be similar to the extinct, which suggests similar processing abilities in the distal regions of the skull. The similarities break down when the rest of the jaw is considered though. In addition to these highly molariform teeth, modern taxa also possess caniniform mesial teeth suggesting a division of labor along the tooth row. Contrarily, almost all teeth of members of *Alligator prenasalis, Brachychampsa* sp.*,* and *"Crocodylus" affinis* are on the molariform half of the shape-spectrum (Figure 7F), making both their size- and shape-heterodonty rather low. These extinct taxa probably did not need to do as much puncturing of compliant substrate, which supports the argument that they may have foraged for mollusks and slow moving turtles (Carpenter and Lindsey, 1980; similar to Salas-Gismondi et al., 2015) rather than being ambush predators.

Limitations and future work

Foote's morphological disparity is a reliable method for assessing heterodonty if the tooth row is near complete, but some of the variability in heterodonty seen here is the result of incompleteness. This measure of disparity relies on, among other things, the grand mean and the sample size. Size heterodonty may be underrepresented if, for example, an enlarged tooth is missing. This tooth would deviate greatly from the grand mean if present, so its exclusion would deflate size heterodonty. As shape is linear in Crocodyliformes, missing the mesial- or distal-most teeth would deflate size heterodonty. This was apparent in the fossil *Caiman crocodilus*; even though it shared almost identical tooth morphology with modern congenerics when positions were compared, its shape heterodonty was much lower because the distal 30% of its teeth were missing. This also affected the shape regression, as the fossil specimen's cranium slope was much shallower than the modern members of *Caiman*.

We did not consider all three dimensions here. Living crocodylian teeth are often discussed as conical (Edmund, 1969) or conidont (Hendrickx, Mateus, & Araújo, 2015b). Studies of bending strengths show variation between mesial-distal and labial-lingual axes (Monfrey, 2017), indicating that functional information may be drawn from the dimension not measured here. This is especially important concerning fossil taxa, as pronounced lateral compression is commonplace. *Hamadasuchus* distal teeth have been referred to as ziphodont (Larsson & Sidor, 1999), but, as this is defined by lateral flattening, our method did not register this character. Future studies should consider this third dimension at least qualitatively, in order to avoid conflating disparate tooth morphotypes such as these.

Principal component scores as shape measurements are very much dependent on the nature of the sample. Although they are very revealing concerning shape variability, they are not transferable between different data sets. A potential method for creating transferable shape metrics is using our PC1 axis as a guide to derive linear distance measures that would account for the serial shape homology seen in Crocodyliformes. Since PC1 essentially represents molariformy vs. caniniformy from the labial perspective, it could possibly be simplified into a comparison of linear distance measures such as maximum mesial-distal widths and apical-basal heights. These metrics would be not only easy to collect, but also transferable between data sets.

These limitations aside, future researchers may apply our proposed method to any crocodyliform specimen with an intact enough tooth row. We limit our evaluation of interspecific differences, and make no attempt to analyze other factors such as ontogenetic changes or the effect of captive rearing (Erickson, Lappin, & Vliet, 2003; Erickson et al., 2004; Gignac & Erickson, 2014; Drumheller, Wilberg, & Sadleir, 2016). All of these variables may be investigated in the future using our method, as there is nothing to suggest that crocodyliform individuals of most species, ages, and/or rearing conditions would not be able to be quantified in a similar manner. This method could be very useful in dealing with incomplete fossils. It is common for fossil crocodylian specimens to be lacking many, or even most, of their teeth. The linear nature of tooth shape can predict the shape of these missing teeth. A record of the ranges of slopes may be accumulated for fossil specimens with intact teeth. These slopes may then be used as a reference, and be applied to a fossil with the missing teeth. The preserved teeth can be plugged into the linear equation, and the shapes of missing teeth may be

692 predicted with a high degree of certainty. This would result in a more complete representation
693 of the extinct animal's anatomy, useful from the standpoint of both anatomical science and
694 paleontological reconstruction.

695 Quantifying the teeth of Crocodyliformes will add rigor to future life history studies of
696 the clade. First and foremost, values may be applied to the plethora of qualitative terms used
697 by researchers (see **Introduction**). This would allow for stricter definitions of the terms when
698 used in the future. As a quantifiable trait, both tooth shape in a single position and
699 heterodonty as a whole may be incorporated into character matrices for phylogenetic analyses.
700 Quantitative descriptors of dentition can describe a numerical range of morphology as opposed
701 to cherry-picking an average tooth or single position. The teeth of fossil taxa can be compared
702 statistically to modern taxa to determine the best analogue, and rigorous hypotheses about
703 paleobehavior and paleoecology may be drawn. Crocodyliformes, both living and extinct, may
704 be grouped into dental categories, allowing for species and specimens to be compared to one
705 another (similar to snouts in Brochu, 2001). Frequency, size, and hardness of food items may
706 be compared to these categories to determine if a link exists between dental morphotypes and
707 dietary patterns (similar to Aoki, 1989). Crocodylians are used in both performance and
708 actualistic taphonomy studies frequently (Njau & Blumenschine, 2006; Erickson et al., 2012,
709 2014; Drumheller & Brochu, 2014; 2016), and the output of these studies could be correlated
710 with tooth dimensions. Tooth shape may also be compared to bite-force, death-rolling, bone-
711 modification.

712 **CONCLUSION**

Multiple measures of morphology have allowed us to describe heterodonty in a thorough manner across a number of both extinct and extant crocodyliform specimens. Through a combination of Foote's morphological disparity and regression analysis along the tooth row, our data indicated that crocodylians are indeed heterodont non-mammals with a number of dental morphotypes available spanning from extreme cases of caniniform to molariform. This variability may be functional in nature, and relate to the size, frequency, and compliance of certain prey in their typically generalist diets. The methods used here should be applied in the future to most crocodylian specimens to investigate dental morphology in the context of a number of natural history related questions.

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FIGURE LEGENDS

Figure 1: Data collection methods. A) We numbered teeth based on position and host bone (only the left teeth are labeled). Teeth P4, M5, and M10 are defined as the enlarged teeth. B) We photographed each tooth individually, and traced the margins. C) The software converted each outline into 30 equidistant coordinates. Three coordinates were transformed into landmarks (magneta) and the rest into semilandmarks (green). D) We represented tooth shape variance through vector diagrams, with points representing the mean and vectors representing shape deviation. E) For skulls, we produced an outline from the dorsal perspective, with 50 coordinates on each margin that were transformed into landmarks (magenta) and semilandmarks (green). F) We represented shape variance with vector diagrams similar to above. (Specimen depicted: *Crocodylus palustris* AMNH 96134.) [Half page width]

Figure 2: Variability within the first Principal Component for teeth. Vector diagrams indicate the maximum range of variance (vectors) from the mean (points) for both cranial and dentary teeth. Landmarks are in magenta and semilandmarks are in green. [Half page width]

Figure 3: Partial Least Squared (PLS) two-block analysis of shape. A) Vector diagrams indicate shape variance of PLS1 for skull shape (Block 1) and average tooth shape (Block 2). B) PLS1 scores for both Blocks were regressed, with colors representing major taxonomic groups. Solid markers depict extant specimens, and hollow markers depict extinct. [Full page width]

Figure 4: Heterodonty represented by Foote's morphological disparity. Ln scaling of Morphological Disparity (MD) for size (A) and shape (B) are plotted against the ln of skull length.

Colors represent major taxonomic groups, solid markers depict extant specimens, and hollow markers depict extinct. [Half page width]

Figure 5: Heterodonty by tooth position. Centroid Size (CS) and Principal Component one (PC1) for extant Alligatoroidea, Crocodyloidea, and remaining taxa, plotted against position along the arcade. Welch's ANOVA output comparing positions is listed for each graph with multiple specimens. Colors represent major taxonomic groups. See Figure 2 for a visual representation of shape change depicted by PC1 scores. [Full page width]

Figure 6: Regression information for shape heterodonty. Slope (*m*) and y-intercept (*b*) data for regressions of the first Principal Component plotted against tooth position for individuals. Error bars indicate 95% confidence intervals. Colors represent major taxonomic groups, with solid markers depicting extant specimens and hollow markers depicting extinct. Regression statistics are available in Table S3. [Full page width]

Figure 7: Direct comparisons between selected extant and extinct taxa. The size axis represents normalized centroid size (ranging from 0.00-0.20), and the shape axis represents scores from the first principal component (ranging from -0.04-0.04). Taxa are grouped by A) specimens with high molariform distal teeth, B) modern taxa that display high size heterodonty, C) slender-snouted taxa, D) *Hamadasuchus rebouli*, E) *Borealosuchus sternbergii* and *Leidyosuchus canadensis*, and F) fossil globidont taxa. (Note: *B. sternbergii* teeth were not size normalized by its own skull length, as indicated by hollow bars.) Scale = 5 cm. [Full page width]

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Data collection methods

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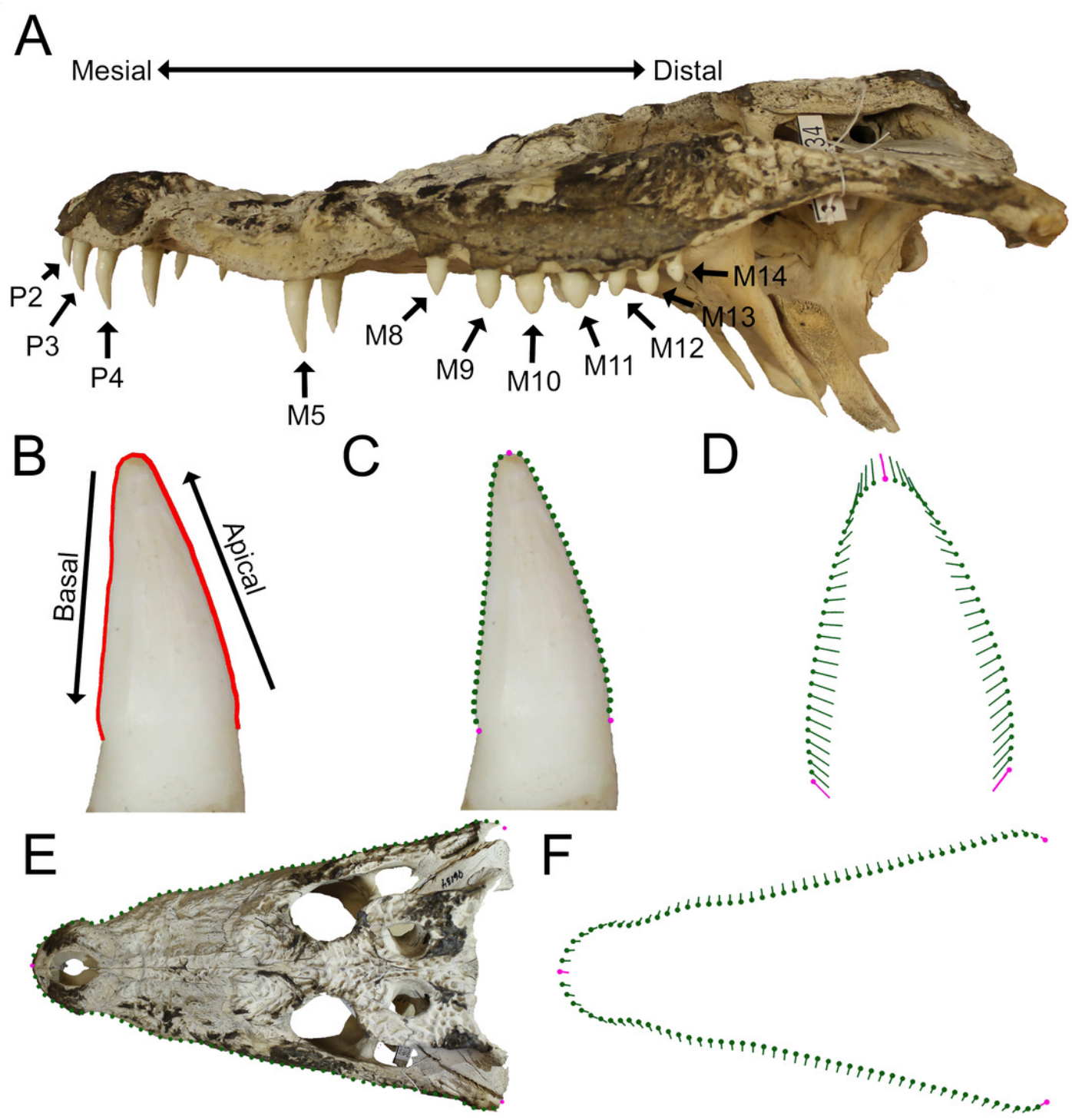

A
Mesial
Distal
34
P2
P3
P4
M5
M8
M9
M10
M11
M12
M13
M14
B
Basal
Apical
C
D
E
F

Figure 2

Variability within the first Principal Component for teeth

Vector diagrams indicate the maximum range of variance (vectors) from the mean (points) for both cranial and dentary teeth. Landmarks are in magenta and semilandmarks are in green.

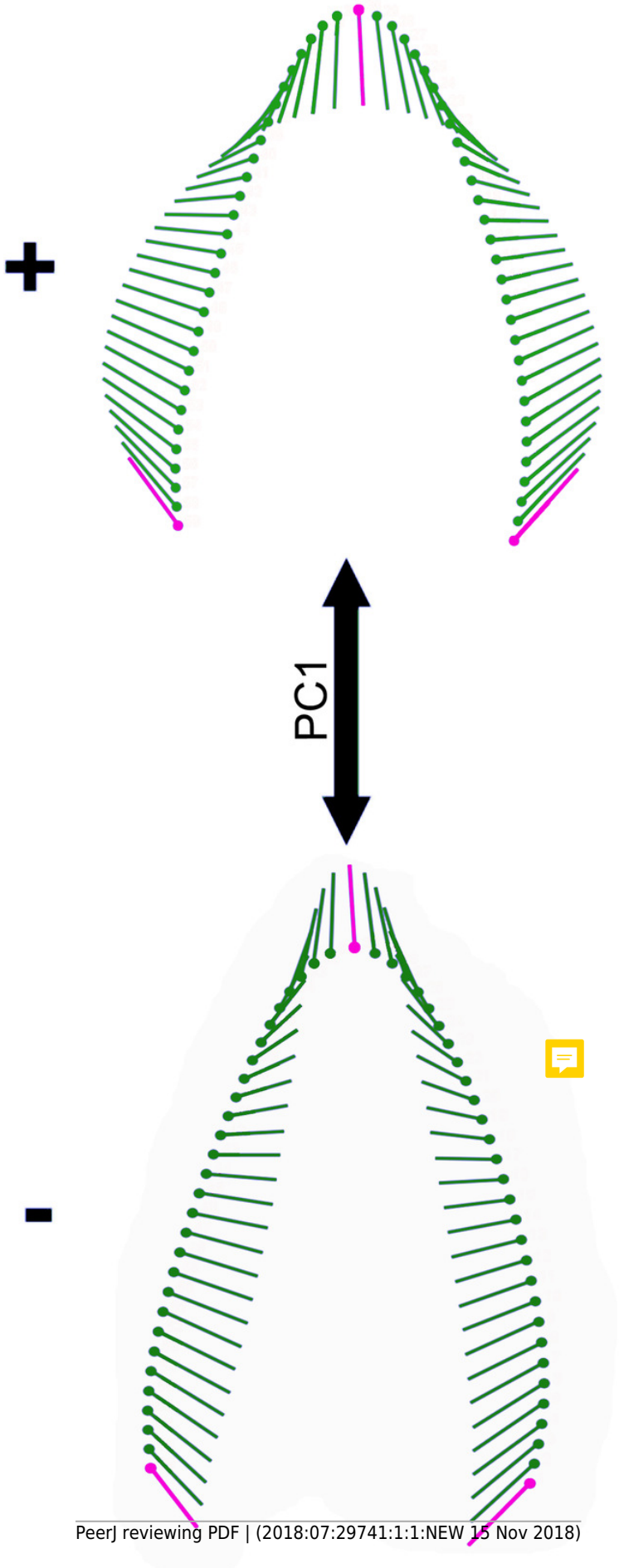

+
PC1
-

Figure 3

Partial Least Squared (PLS) two-block analysis of shape

A) Vector diagrams indicate shape variance of PLS1 for skull shape (Block 1) and average tooth shape (Block 2). B) PLS1 scores for both Blocks were regressed, with colors representing major taxonomic groups. Solid markers depict extant specimens, and hollow markers depict extinct.

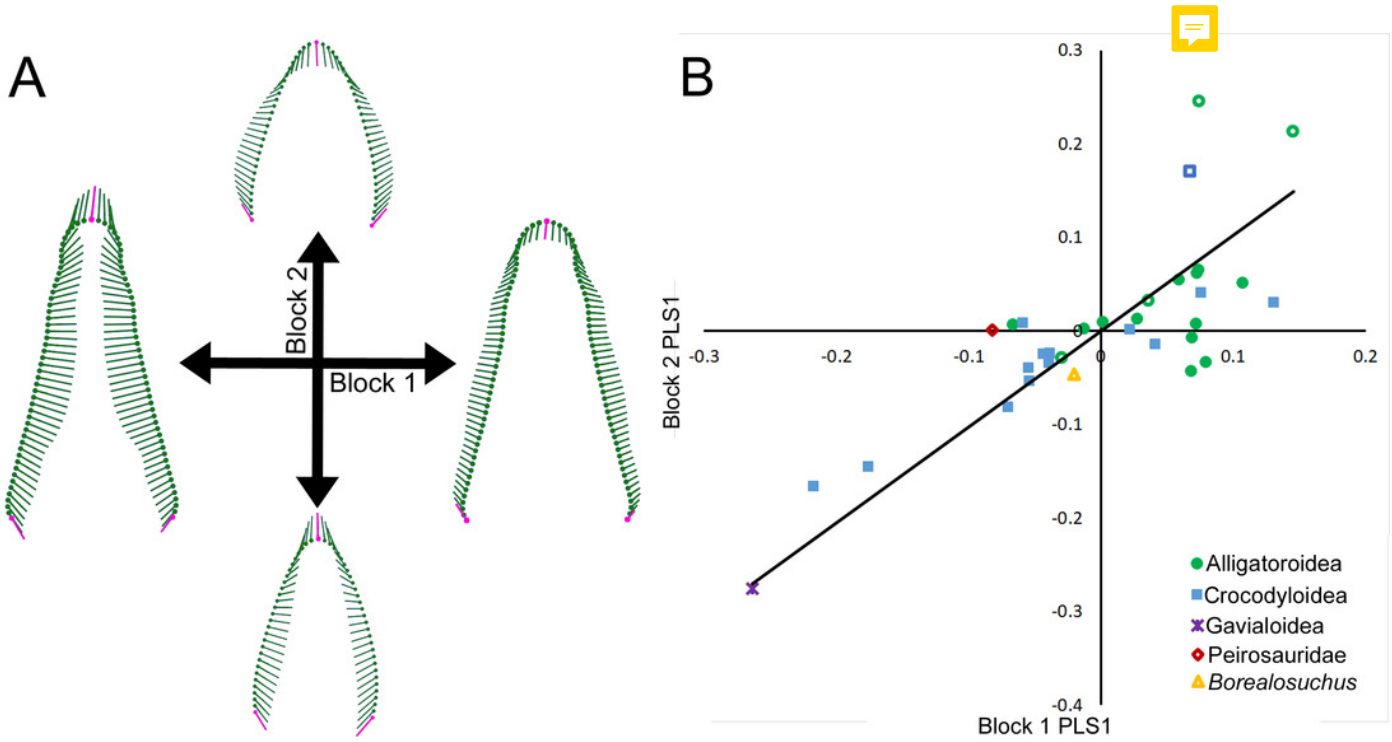
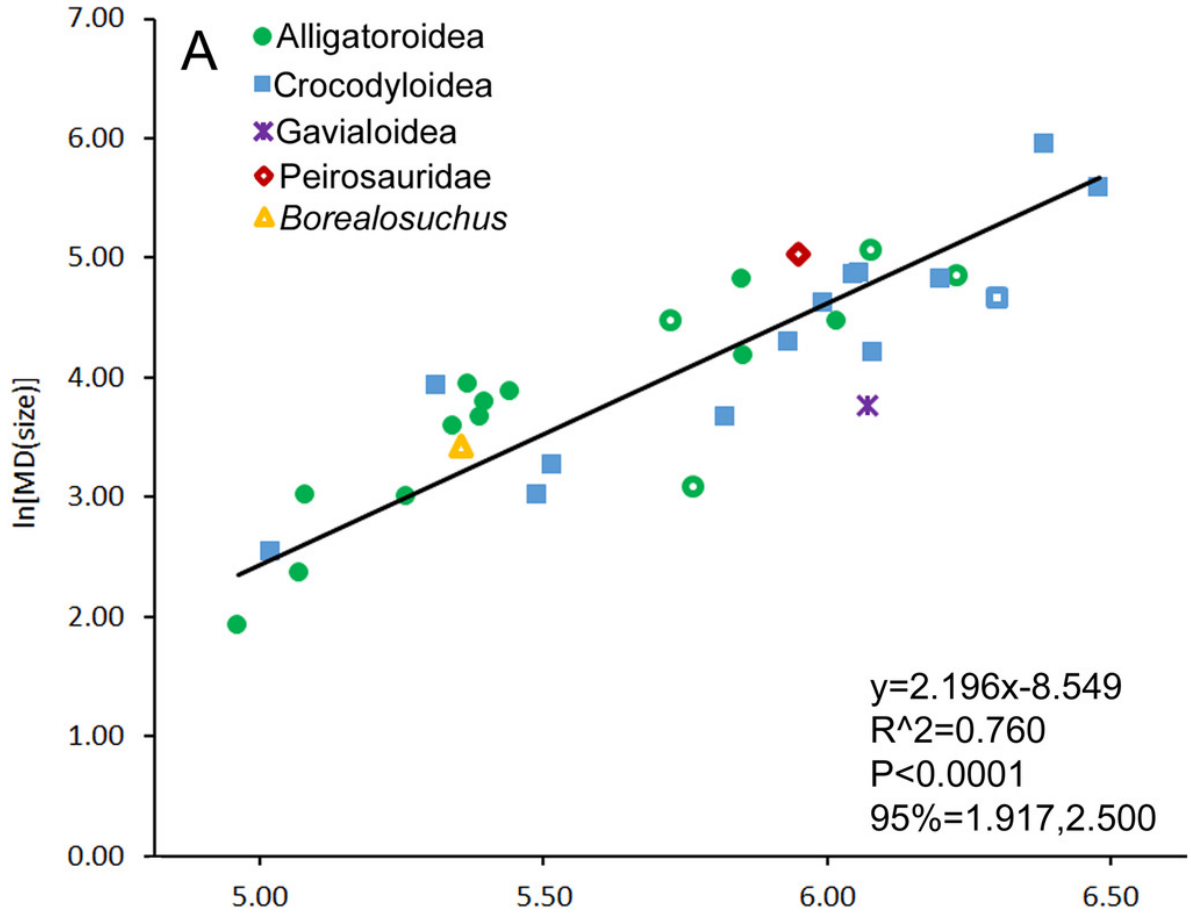


Figure 4

Heterodonty represented by Foote’s morphological disparity

Ln scaling of Morphological Disparity (MD) for size (A) and shape (B) are plotted against the ln of skull length. Colors represent major taxonomic groups, solid markers depict extant specimens, and hollow markers depict extinct.


A
Alligatoroidea
Crocodyloidea
Gavialoidea
Peirosauridae
Borealosuchus
ln[MD(size)]
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
5.00
5.50
6.00
6.50
y=2.196x-8.549
R^2=0.760
P<0.0001
95%=1.917,2.500

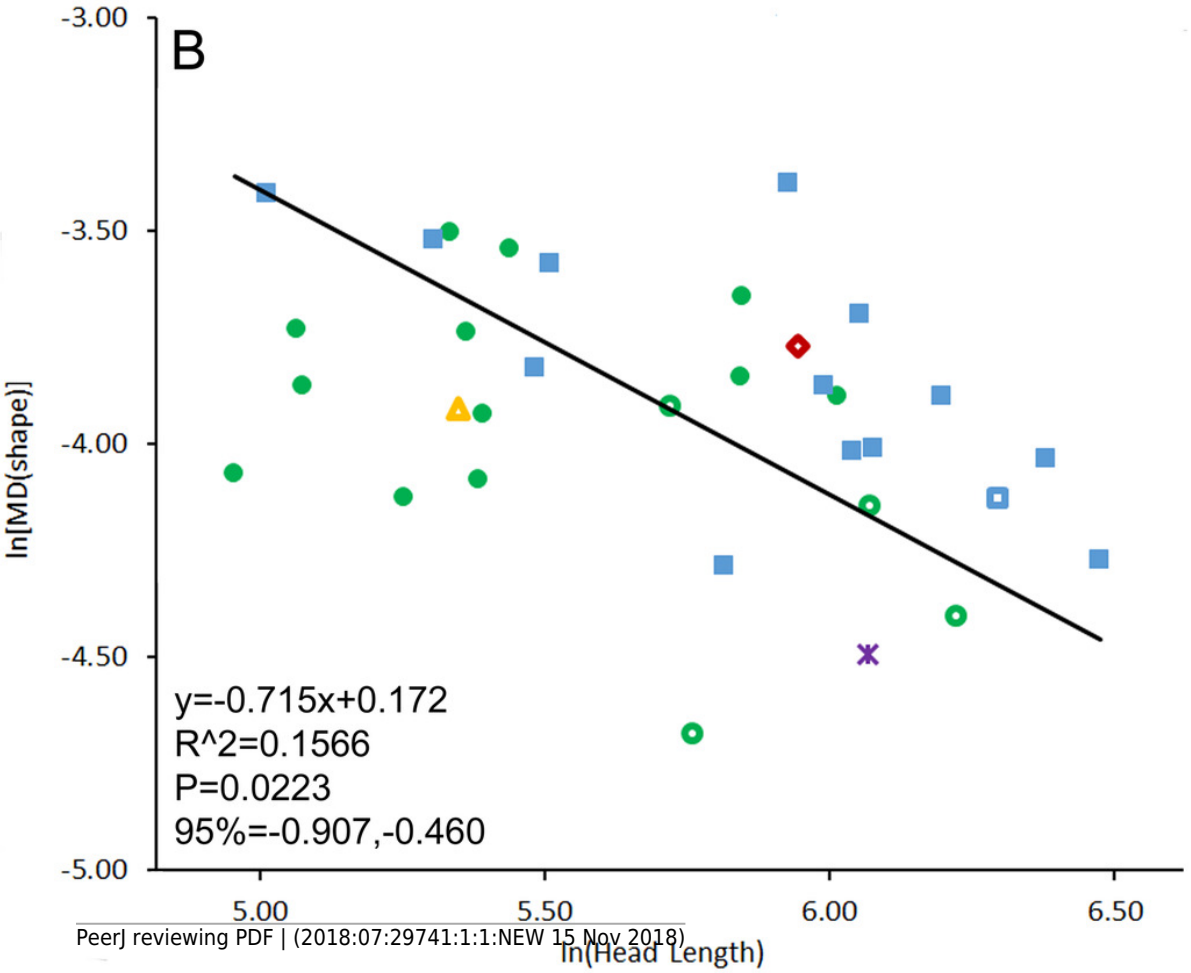
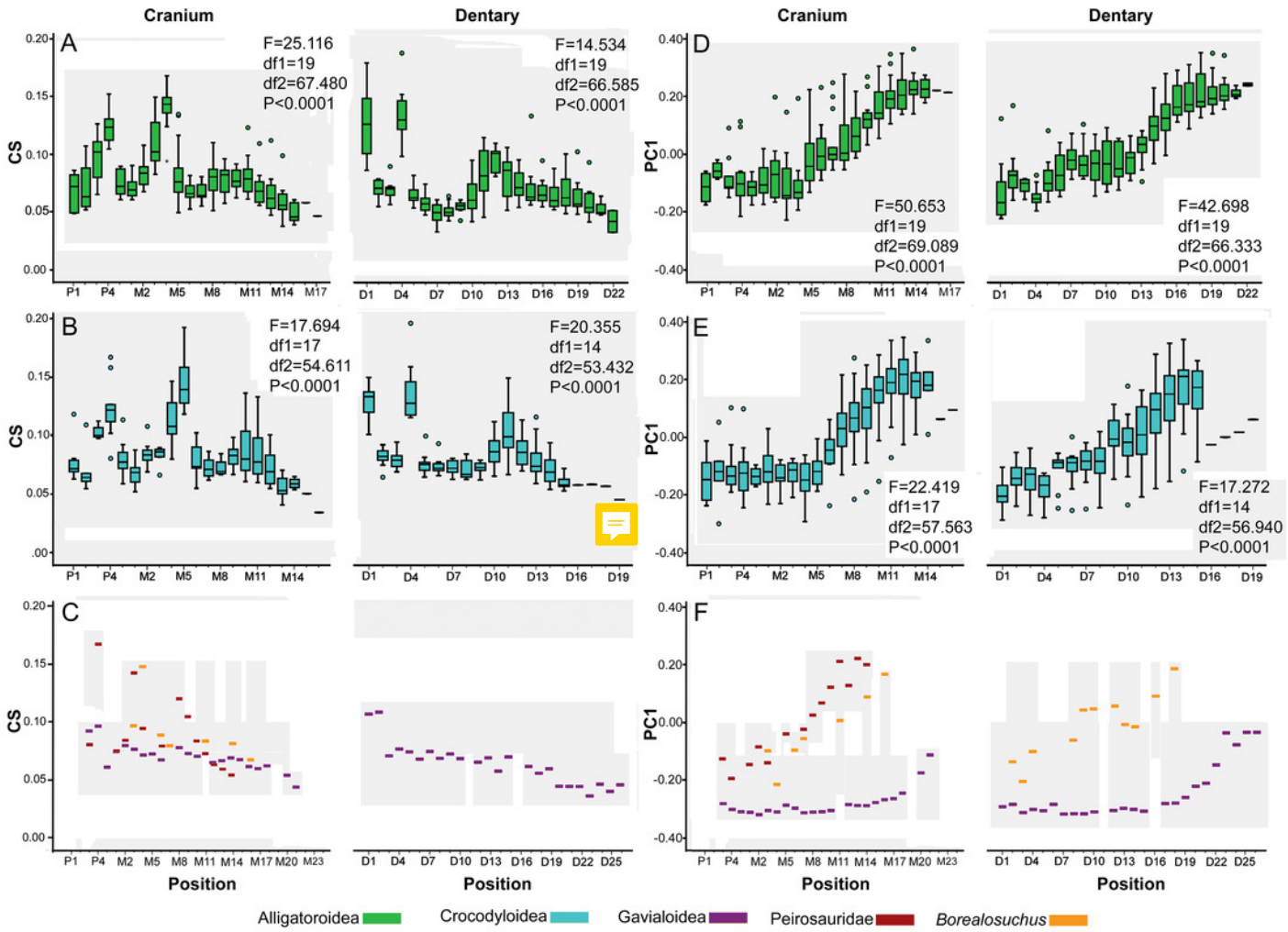

B
ln[MD(shape)]
-3.00
-3.50
-4.00
-4.50
-5.00
5.00
5.50
6.00
6.50
ln(Head Length)
y=-0.715x+0.172
R^2=0.1566
P=0.0223
95%=-0.907,-0.460

Figure 5

Heterodonty by tooth position

Centroid Size (CS) and Principal Component one (PC1) for extant Alligatoroidea, Crocodyloidea, and remaining taxa, plotted against position along the arcade. Welch's ANOVA output comparing positions is listed for each graph with multiple specimens. Colors represent major taxonomic groups. See Figure 2 for a visual representation of shape change depicted by PC1 scores.



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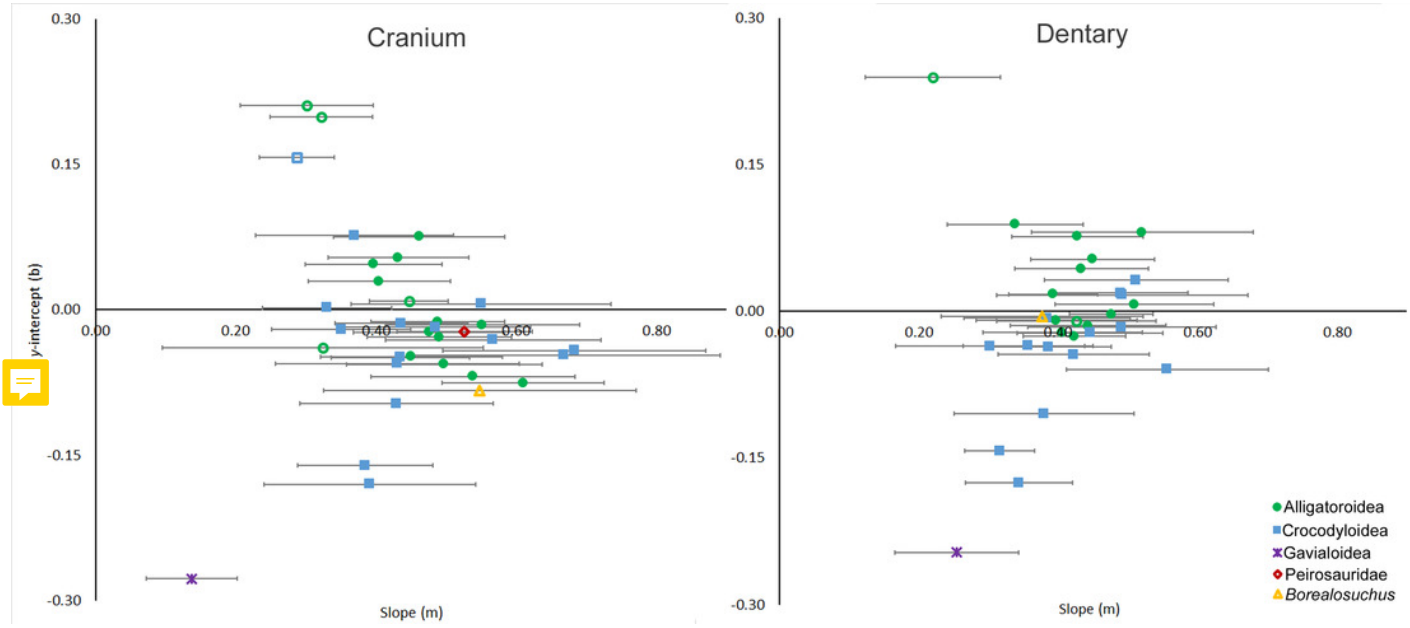

Figure 7

Direct comparisons between selected extant and extinct taxa

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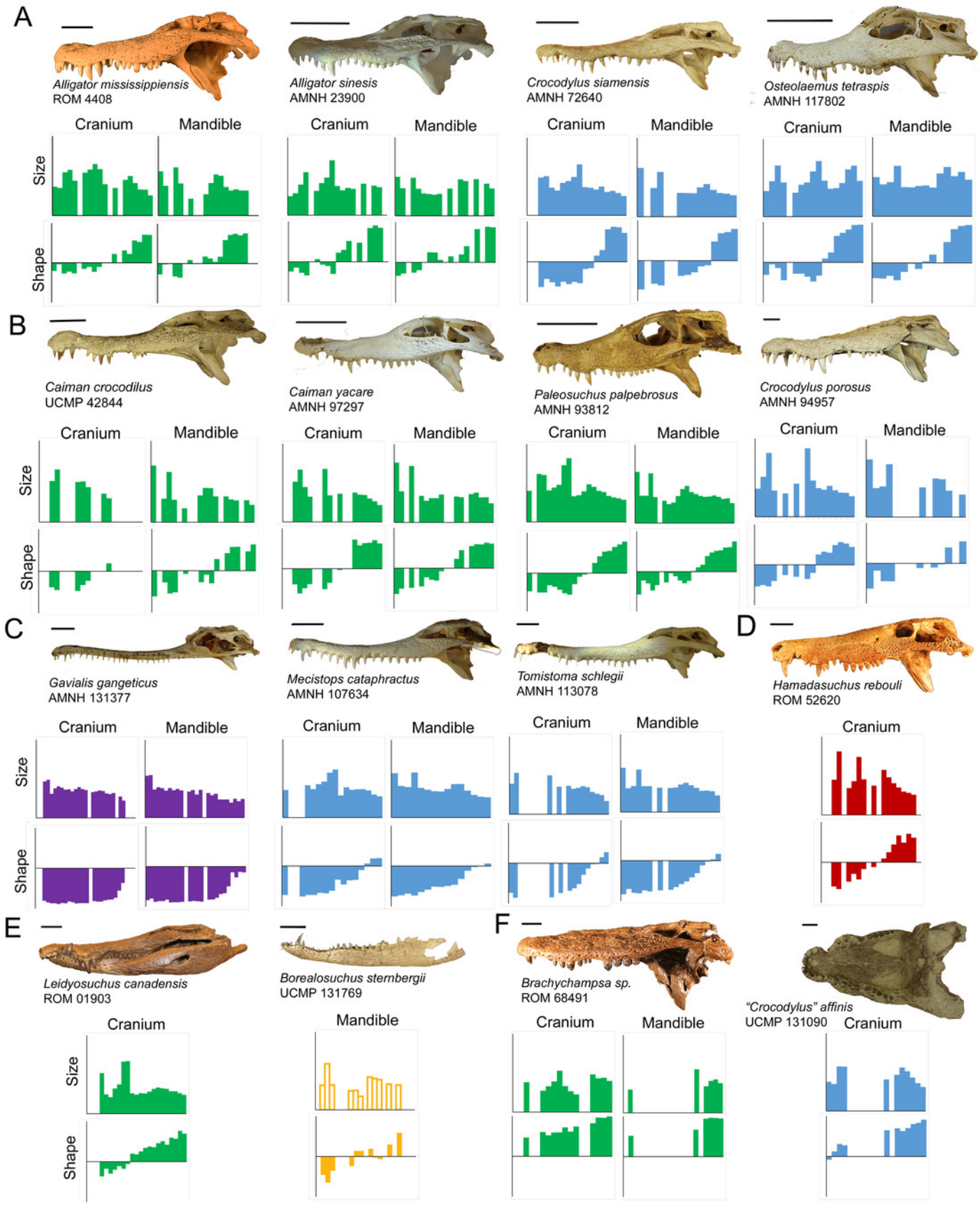
A
Alligator mississippiensis
ROM 4408
Alligator sinesis
AMNH 23900
Crocodylus siamensis
AMNH 72640
Osteolaemus tetraspis
AMNH 117802
Cranium
Mandible
Size
Shape
B
Caiman crocodilus
UCMP 42844
Caiman yacare
AMNH 97297
Paleosuchus palpebrosus
AMNH 93812
Crocodylus porosus
AMNH 94957
C
Gavialis gangeticus
AMNH 131377
Mecistops cataphractus
AMNH 107634
Tomistoma schlegii
AMNH 113078
D
Hamadasuchus rebouli
ROM 52620
E
Leidyosuchus canadensis
ROM 01903
Borealosuchus sternbergii
UCMP 131769
F
Brachychampsa sp.
ROM 68491
"Crocodylus" affinis
UCMP 131090