Quantitative heterodonty in Crocodylia: variability and decoupling in size and shape across modern and extinct taxa. (#29741)

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Quantitative heterodonty in Crocodylia: variability and decoupling in size and shape across modern and extinct taxa.

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Heterodonty in Crocodylia 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 state of dental morphology in the clade. The purpose of this study was to quantify both shape and size morphology along the tooth row in a multispecific sample of both extant and extinct members Crocodylia using geometric morphometrics. Data were collected from several crown crocodylian (and one peirosaurid) dry skeletal and fossil specimens. Digital photographs were taken of each tooth, and the margins of the tooth were converted into landmarks/semilandmarks. Heterodonty was expressed as Foote's morphological disparity, and a principal components analysis visualized shape variance. All living crocodylians 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, suggesting they are developmentally decoupled. Snout shape correlated to tooth shape but not size, with longirostrine taxa having more caniniform teeth and brevirostrine having more molariform. Caimanines and *Crocodylus porosus* had high size-heterodonty with large pseudocanines, reflecting a prioritization of securing struggling, compliant prey. *Alligator sinensis* and *Osteolaemus tetraspis* had large, highly molariform, distal teeth: a consequence of high-frequency durophagy combined with prey size. *Gavialis gengeticus*, *Mecistops cataphractus* and *Tomistoma schlegelii* had a caniniform arcade with low heterodonty, almost exclusively for capturing small underwater prey with minimal processing. *Alligator prenasalis*, *Brachychampsa sp.*, and "*Crocodylus*" *affinis* were primarily molariform. *Leidyosuchus* and *Borealosuchus* tooth sizes and shapes typical of modern *Alligator* and *Crocodylus* respectively, although the former may have been less durophagous. *Hamadasuchus rebouli* similarities to *C. porosus* indicate it may have dealt with vertebrate prey, but prey processing may have been different due to its terrestrial

habitat. Although Foote's disparity is a reliable method for assessing heterodonty, incomplete tooth rows may give inflated/deflated values. Our methods may be very useful for predicting the shape of missing teeth in fossil taxa, as well as inferring dietary behaviors and other life history characters.

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ABSTRACT

Heterodonty in Crocodylia 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 state of dental morphology in the clade. The purpose of this study was to quantify both shape and size morphology along the tooth row in a multispecific sample of both extant and extinct members Crocodylia using geometric morphometrics. Data were collected from several crown crocodylian (and one peirosaurid) dry skeletal and fossil specimens. Digital photographs were taken of each tooth, and the margins of the tooth were converted into landmarks/semilandmarks. Heterodonty was expressed as Foote's morphological disparity, and a principal components analysis visualized shape variance. All living crocodylians 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, suggesting they are developmentally decoupled. Snout shape correlated to tooth shape but not size, with longirostrine taxa having more caniniform teeth and brevirostrine having more molariform. Caimanines and *Crocodylus porosus* had high size-heterodonty with large pseudocanines, reflecting a prioritization of securing struggling, compliant prey. *Alligator sinensis* and *Osteolaemus tetraspis* had large, highly molariform, distal teeth: a consequence of high-frequency durophagy combined with prey size. *Gavialis gengeticus*, *Mecistops cataphractus* and *Tomistoma schlegelii* had a caniniform arcade with low heterodonty, almost exclusively for capturing small underwater prey with minimal processing. *Alligator prenasalis*, *Brachychampsa sp.*, and "*Crocodylus*" *affinis* were primarily molariform. *Leidyosuchus* and *Borealosuchus* tooth

sizes and shapes typical of modern *Alligator* and *Crocodylus* respectively, although the former may have been less durophagous. *Hamadasuchus rebouli* similarities to *C. porosus* indicate it may have dealt with vertebrate prey, but prey processing may have been different due to its terrestrial habitat. Although Foote's disparity is a reliable method for assessing heterodonty, incomplete tooth rows may give inflated/deflated values. Our methods may be very useful for predicting the shape of missing teeth in fossil taxa, as well as inferring dietary behaviors and other life history characters.

Keywords: Caniniform, Crown, Dentition, Diet, Geometric morphometrics, Molariform, Semilandmarks

INTRODUCTION

What constitutes heterodonty often seems like a moving target, with different qualitative definitions in place depending on the clade being studied (Shimada, 2001). In 1993, Kieser et al. referred to the exact definition of the term heterodont as "a bone of contention." Since that time, the issue never has been fully resolved. Nowhere is this lack of clarity more pronounced than within the non-mammalian vertebrate literature, especially the members of Crocodylia. Traditionally crocodylians were considered homodont, due to a lack of discrete dental categories or variability in cusp number as in mammals (Peyer, 1968; Langston, 1973; Osborn, 1998; Larsson & Sidor, 1999; Zahradnicek et al., 2014). Ferguson (1981) refers 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; Kieser et al., 1993; Hendrickx, Mateus, & Araújo, 2015b). Size changes have motivated the term

"heterometric homodonty" for *Crocodylus niloticus* (Fruchard, 2012). To add to the ambiguity, certain fossil crocodylians, especially those taxa that are interpreted as herbivores or omnivores, are called "heterodont" in order to distinguish their dentition from their modern relatives (e.g. Martin, 2007; Ősi, Clark, & Weishampel, 2007; Novas et al., 2009).

Semantics aside, one reason for the lack of resolution concerning crocodylian heterodonty is that their teeth have rarely been measured. There have been few studies looking at morphometrics of crocodylian teeth, and, of those studies, measurements have been Euclidean distances taken for determining replacement rates (Frey & Monninger, 2010; Bennett, 2012) or for biomechanical analyses (Monfroy, 2017). Aside from a single study measuring Euclidean distances in a fossil notosuchian (Lecuona & Pol, 2008), little research has quantitatively investigated heterodonty either within or between species. Typically, crocodylian dentition is described qualitatively, with the goal of fossil identification, 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, 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; Salas-Gismondi et al., 2015; Berkovitz and Shellis, 2017).

Research typically has focused on crocodylian tooth development and function as opposed to quantitative morphology, including numerous studies on material characteristics (Shimada, Sato, & Moriyama, 1992; Erickson, 1996; Enax et al., 2013), implantation and replacement (Edmund, 1962; Westergaard and Ferguson, 1986, 1987, 1990; LeBlanc et al., 2017), dental wear (Ősi & Barrett, 2011), jaw musculature and kinematics (Iordansky, 1964; Van Drongelen & Dullemeijer, 1982; Busbey, 1989; Cleuren & De Vree, 1992; Endo et al., 2002), bite force (Cleuren, Aerts, & Vree, 1995; Erickson, Lappin, & Vliet, 2003; Erickson et al., 2012, 2014), death rolling (Fish et al., 2007; SK Drumheller, unpublished data), and taphonomic traces on bone surfaces (Njau ~~and~~ Blumenschine, 2006, 2012; Drumheller ~~and~~ Brochu, 2014; 2016).

Non-mammalian dental morphometrics has seen a burst of research in the past decade. Dinosaur teeth have probably received the most attention, with multiple studies using Euclidean distances 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, 2015a, 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 investigated heavily (Shimada, 2002b, 2004; Shimada and Seigel, 2005). These morphometric analyses have shed light on the nature of heterodonty, dental allometry, and ecomorphology in non-mammalian vertebrates, and these methods may be applied to Crocodylia in the hopes to elaborate upon the state of heterodonty in this taxon.

The purpose of this study was to quantify both shape and size morphology along the tooth row in a multispecific sample of both extant and extinct members Crocodylia using geometric morphometrics. Our goals were to introduce a multifaceted method for assessing heterodonty in a given crocodylian specimen; 2) document any developmental consistencies found within the clade as a whole; 3) distinguish crocodylian dental morphotypes between individuals; and 4) outline the advantages, limitations, and potential future uses of the method when analyzing crocodylian heterodonty.

MATERIALS AND METHODS

Nomenclature

Crocodylian teeth have very few discrete homologous anatomical loci, but, because they exhibit thecodont dentition (Edmund, 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): 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/alveolus; apical, away from the alveolus/towards the apex. For simplicity the mesial-most teeth are referred to as 'mesials' and the distal-most as 'distals.'

Tooth position was indicated by either the presence of a tooth or an empty alveolus in the host bone. Cranial teeth included premaxillary and maxillary teeth, and dentary teeth only occurred on the dentary bone. Teeth were numbered in ascending order from mesial to distal positions. Not all crocodylian specimens had the same number of tooth positions. Maxillary

teeth ranged from M1 to M11-M24, and dentary teeth ranged from D1 to D14-D26. All specimens were assumed to have 5 premaxillary positions (P1–P5). Members of *Paleosuchus* and *Osteolaemus* have only 4 premaxillary teeth during early stages of ontogeny (Brochu and Storrs, 2012; Narvaez et al., 2015), whereas several other species atrophy an alveolus (usually P2) as they grow (Webb & Messel, 1978; Brown et al., 2015; personal observation). In order to standardize, the procumbent teeth were always assigned P4 and the other teeth and atrophied positions were numbered based off of it.

Specimens

Data were collected from 25 extant, and 14 extinct, crown crocodylian specimens. In addition, we added the peirosaurid crocodylomorph *Hamadasuchus rebouli*. ~~This resulting in a~~ total of 24 species. From these we measured 1,224 teeth in total. For extant crocodylian taxa, data was collected from dry skeletal specimens from the American Museum of Natural History (AMNH). At least 40% of the tooth positions had to be represented by measureable teeth on the left and/or right for the specimen to be considered. Specimens where the only teeth available biased towards the upper or lower size extremes were excluded. As ontogeny is beyond the scope of our present study, juveniles were avoided. Fossil taxa were sampled from the Royal Ontario Museum (ROM), the University of California Museum of Paleontology (UCMP), and the Smithsonian National Museum of Natural History (USNM). Completeness of tooth row was not considered in the inclusion of fossils. Although *Caiman crocodilus* is an extant species, a fossil specimen was included.

Data collection

Methods were similar to those proposed in D'Amore (2015). Teeth were photographed using either an Olympus Stylus or a Canon Rebel T3 EOS, alternating between a macro and an 18-55 mm lens depending on the size of the tooth, against a dark background with a scale (Figure 1A). Digital photographs were taken from the labial perspective, and a separate picture was taken for each tooth. Only fully erupted teeth with the neck visible were included. Tooth quality was variable in extant specimens. We included teeth with slightly worn apices, but excluded teeth that had large wear facets and chips as long as they interfered noticeably with the outline. 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 the 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 ceases to taper on the neck for both the mesial and distal side. The two traced margins were then each transformed into 30 equidistant coordinates, and the apical coordinates were combined into one. This resulted in 3 landmarks and 56 semilandmarks (Figure 1C), the latter of which were then slid to minimize the bending energy (Perez, Bernal, & Gonzalez, 2006; Gunz & Mitteroecker, 2013) using TpsRelw 1.53 (Rohlf, 2013). This program also performed generalized least squares Procrustes superimposition on the data, and calculated centroid size (CS). Bilateral symmetry of

the jaw was assumed, and the superimposed coordinates and CS were averaged between teeth from the same position on left and right sides.

Rostrum shape has long been considered both an important phylogenetic and ecomorphological feature in crocodylians (Busbey, 1995; Daniel & McHenry, 2000; Brochu, 2001; Sadleir & Makovicky, 2008; Salas-Gismondi et al., 2016). All specimens' skulls were photographed with a scale from the dorsal perspective. Snout shape data were derived following Drumheller et al., (2016) and Wilberg (2017), using a modified version of our technique for tooth outlines. We traced the skull margin from the rostral-most point of contact between the premaxillae to the caudal-most quadratojugal on each side in TpsDig, broke each margin into 50 equidistant coordinates, combined the anterior-most coordinate (resulting in 3 landmarks and 97 semilandmarks total), and slid them with TpsRelw again. Head length was derived from these landmarks, which began at the rostral-most landmark and ended in-between the posterior-most landmarks along the mid-sagittal plane. In specimens with damaged or missing bones on one side, bilateral symmetry was assumed and the intact side was mirrored. Head length was used as a measure of body size in lieu of snout-vent length, and all CS values were divided by it to normalize relative tooth size. *Allognathosuchus sp.* (UCMP 150180), *Argochampsa rebouli* (ROM 73872), and *Boverisuchus vorax* (UCMP 170767) did not have intact skulls associated with their dentition. Photographs of intact skulls of conspecifics were used instead to derive head shape and length (substituted specimens included: Yale Peabody Museum 17111, Field Museum of Natural History PR399, and Office Chérifien des Phosphates DEK-GE 1201)

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182

183 **Ordination and statistics**

184 All analyses were conducted in MorphoJ v. 106d (Klingenberg 2011) and SPSS Version
185 19.0 [IBM Corp, Armonk, NY]. A 10,000 permutations test was run on the Procrustes distance
186 between cranial and dentary teeth for extant specimens, and showed no significant differences
187 ($P = 0.2000$). Therefore, all subsequent analyses were conducted with both arcades combined
188 (unless position is being considered). Interspecific differences in mean tooth size and shape
189 were analyzed using an analyses of variance (ANOVA). Size was heteroscedastic according to
190 Levene's test ($P = 0.0002$), so we ran a Welch's ANOVA of normalized CS values for all members
191 of each species in SPSS. For shape, Procrustes ANOVA was run in MorphoJ.

192 A singular measure of heterodonty was derived for each specimen in the form of
193 Foote's morphological disparity $[MD = (\sum_{i=1}^{m} D_i^2)/(m-1)]$ (Foote, 1993; Zelditch, Sheets, &
194 Fink, 2003; Sheets & Zelditch, 2013). Disparity (*MD*) is the sum of the differences of the values
195 of a given tooth (*i*) from the mean for all teeth from that specimen (*Di*) squared, with the
196 number of tooth positions (*m*) factored in. We calculated disparity for both cranial and dentary
197 teeth together from each specimen. For size heterodonty, *Di* is simply the difference in CS of a
198 tooth from the mean of the individual (Zelditch et al., 2004). Only specimens with intact skulls
199 for normalization were included. For shape *Di* is the Procrustes distance between the tooth and
200 the mean, and was calculated using DisparityBox7 (Sheets, 2012).

Although Foote's MD is an inclusive measure of heterodonty, it is not descriptive of multivariate measures such as shape. Therefore, principal components analyses (PCA) were conducted to visualize the degree of shape variance within all cranial and dentary teeth separately. All PCs representing over 5% of the variance were considered, and shape variance was visualized in vector diagrams (Figure 1D). Both CS values and PC scores were graphed as box plots for all members of each species, to visualize the range of shape and size that contribute to MD. Similar to teeth, a PCA was run for skull shape. Skull shape PCs were compared to the average tooth PC for each extant individual in a bivariate plot, and regressed to determine if skull shape and tooth shape are correlated.

Shape and size were plotted against tooth position to visualize variability along the tooth row. For size, CS was plotted against tooth position. For shape, the aforementioned tooth PC scores were plotted against tooth position. Data were clustered into box plots to depict trends along the dental arcade for each family within our extant sample. Each box represented a position. Note that these positions were not normalized, so specimens with more tooth positions will be the only occupants of the distal-most categories. As positional data were often heteroscedastic, Welch's ANOVAs were conducted to determine if shape and/or size were significantly different by position for each arcade in each family. Shape data were also regressed to determine if serial homology is linear along the tooth row. To standardize these regressions, tooth position was normalized 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 placed the y-intercept

222 halfway along the arcade). Included PCs were then regressed against position-percentage, and
223 regression statistics were tabulated.

Results:

Shape variability in the sample

The majority of the shape variance was represented by the first principal component (PC1). It accounted for over 91.26% of the variance, and is the only PC considered further. When visualized, the axes indicated a 'caniniform' to 'molariform' transition with increased values. The negative-most condition was an elongate, narrow crown coupled with a gentle concavity on the distal margin. The positive-most values depicted an apical-basal shortening and mesial-distal broadening (Figure 2), giving the tooth a stout, rounded crown with a relatively narrow neck. Although PC1 was treated as a continuous variable in all subsequent analyses, we assigned names to ranges of PC scores for the purposes of description. These descriptors include; high-caniniform (<-0.25); mid-caniniform (-0.25 to -0.15); low-caniniform (-0.15 to -0.05); average (-0.05 to 0.05); low-molariform (0.05 to 0.15); mid-molariform (0.15-0.25); and high-molariform (> 0.25).

Skull morphology:

Mean tooth shape showed significant trends when regressed against head shape, but not size (Figure 3). Head shape yielded a PC1 encompassing 89.81% of shape variance, and represented the brevirostrine-to-mesorostrine-to-longirostrine transition (broad-, middle-, and slender-snouted conditions respectively) (Brochu, 2001; Wilberg, 2017). Significant regressions scaled with a slope of -0.67 for extant-only crocodylians. Generally speaking, longirostrine taxa had the most caniniform teeth and brevirostrine taxa had the most molariform teeth. Scatter increases among the broader-snouted specimens below the mean, and the relationship is less

well represented. When extinct taxa were included, the slope decreased to just under -1.0 but the goodness of fit dropped from 0.73 to 0.52. Most of our fossil taxa had broader teeth relative to head shape than the extant sample, which was most likely a consequence of sampling bias (see **DISCUSSION**).

Foote's disparity and morphotype ranges

When means were compared, ANOVA indicated significant differences in CS between species [$F(13,674) = 6.389$; $P < 0.0001$]. Heterodonty varied both between and among species (Figure 4). *Alligator* tended to have lower size heterodonty than the caimanines, because the latter had more teeth above the inter-quartile range. Crocodyloids had highly variable size heterodonty. Several members of *Crocodylus* were middle ranged, but both *Crocodylus porosus* specimens rose above the rest. A member *O. tetraspis* was the most size-heterodont, but the others were much lower. This species had the largest teeth relatively speaking. *Mecistops cataphractus* and *Tomistoma schlegelii* were the least heterodont crocodyloids, and had the narrowest size ranges with the lowest maximum tooth sizes. *Gavialis gengeticus* was the least size heterodont in our modern data set, with similar size ranges to the longirostrine crocodyloids.

As with size, shape was also significantly different between species [$F(1482,79572) = 19.61$; $P < 0.0001$]. The caimanines and most members of *Crocodylus* had similar shape heterodonty, and possessed crowns ranging from mid-caniniform to mid-molariform (Figure 4). *Crocodylus siamensis* was more shape heterodont than its congenerics. *Alligator* species had lower shape heterodonty than most caimanines, as their PC1 range was generally more

molariform. Unlike size, *O. tetraspis* had shape heterodonty similar to members of *Crocodylus*. *Alligator sinensis*, *C. siamensis*, and *O. tetraspis* were the only modern taxa with teeth in high-molariform range. Similar to size, the longirostrine taxa have the least shape heterodonty. *Gavialis gangeticus* teeth all ranged from average to the high-caniniform. *Tomistoma schlegelii* had teeth ranging from high-caniniform to low-molariform range, whereas *M. cataphractus* was more constrained between mid-caniniform and low-molariform.

Concerning fossil taxa, *C. crocodilus* was similar to modern caimanines concerning heterodonty, although the maximum tooth size was lower (Figure 4). *Alligator prenasalis*, *Brachychampsa sp.*, and *"C." affinis* had some of the lowest shape and size heterodonty in our sample. Tooth shape was limited from average to high-molariform, as they all lacked any disparately large teeth. *Leidyosuchus* heterodonty fell within the range of living alligatoroids, but the majority of the teeth were on the small end. *Borealosuchus sternbergii* had a range of tooth sizes typical of modern *Crocodylus*. Heterodonty was highly variable in this species. *Hamadasuchus rebouli* mirrored *C. porosus* in both size-ranges and size-heterodonty, but had higher shape heterodonty with more molariform teeth. *Allognathosuchus sp.* had the highest shape heterodonty by a large margin. *Argochampsa krebsi* and *B. vorax* both had low heterodonty, and were represented by only caniniform and molariform morphs respectively.

Heterodonty along the tooth row

In both extant Alligatoroidea and Crocodyloidea, size varied significantly between positions. Size undulated three times along the dental arcade resulting in significant differences between positions for both the cranium and mandible (Figure 5). Each undulation peaked with

287 a relatively large procumbent tooth (Gignac & Erickson, 2014). The largest procumbent teeth
288 included P4 for both clades, and M4 for alligatoroids and M5 for crocodyloids (sensu Brochu
289 and Storrs, 2012). Members of *Paleosuchus* has very large P3 and M3 teeth as well. A final
290 undulation resulted in a procumbent tooth at M9-11. In alligatoroids this final peak relatively
291 consistent throughout the group, but in crocodyloids these teeth varied greatly in size between
292 specimens concerning both position and degree. Interspersed between these were small teeth,
293 with the distal-most tooth often the smallest. The mandible was similar with procumbent D1
294 and D4, both followed by a series of small teeth. The third size-peak maximized between D11
295 and D14, reflecting similar levels of variability to its cranial counterpart. Gavialoids differed
296 markedly by having the two mesial-most teeth enlarged, and the remainder of the teeth show a
297 gradual decease in size distally.

298 Alligatoroids and crocodyloids both showed a general linear trend concerning tooth
299 shape, making positions significantly different (Figure 5). Mesial teeth ranged from mid-
300 caniniform to average, with distals approaching high-molariform. In cranial teeth there was an
301 apparent plateau from P1-M4, followed by a gradual increase in molariformy distally. Dentary
302 teeth represented a more linear caniniform-to-molariform transition. Crocodyloids were much
303 more varied than alligatoroids, with wider ranges and a series of low outliers (most of which are
304 *T. schlegii*). In *G. gangeticus*, most of the teeth are high-caniniform with a steep increase
305 towards average in the distal-most fifth of the arcade.

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When each modern individual's PC1 values were regressed against position, the resultant linear trends represented individual shape heterodonty very well (Table 1). All regressions were significant, and all except *G. gangeticus* had goodnesses of fit greater than 70%. Both cranial and dentary tooth rows typically had slopes between 0.25-0.55. More shape heterodont taxa typically had greater slopes, where *C. siamensis* had the highest slopes of the sample. All the longirostrine taxa had the lowest intercepts indicating high caniniformy, and members of *Alligator* had high *y*-intercepts indicating general molariformy.

Fossil taxa displayed a much more variable range of size and shape trends along their arcades (Table 2). All fossil specimens with intact teeth in the position showed a procumbent P4, but *"C." affinis* also had a similarly sized P3. Unlike other alligatoroids *L. canadensis* had both procumbent M4 and M5. Some of the largest teeth of *A. prenasalis, Brachychampsa,* and *"C." affinis*, were the molariform distals. These teeth typically approached the size of the largest mesial crowns. Regressions for shape were significant for all fossil taxa except the *"C." affinis* mandible (USNM 4048). The teeth of the fossil *Caiman crocodilus* had very similar sizes and shapes to those of modern *Caiman yacare* at the same positions. They only differed in that the coefficients of its cranial regression were dissimilar. All fossil specimens with intact teeth in the position showed a procumbent P4, but *"C." affinis* also has a similarly sized P3. ~~Unlike other alligatoroids *L. canadensis* has both procumbent M4 and M5. Some of the largest teeth of *A. prenasalis, Brachychampsa,* and *"C." affinis*, were the molariform distals. These teeth typically approached the size of the largest mesial crowns,~~ which themselves had very high PC1 values. This resulted in species having the shallowest slopes and the greatest *y*-intercepts. Although *Allognathosuchus* has similar distal teeth, a mesial crown steepened the regression. Both *B.*

sternbergii specimens' cranial teeth have similar slopes, but intercepts differed by ~0.15. *Hamadasuchus rebouli* had the largest teeth for its skull length with a dramatic undulation in size, and the greatest slope of any fossil cranial series. *Boverisuchus vorax* and *A. krebsi* both formed significant trends with very high slopes. It should be noted that these two species have less than a third of their teeth accounted for, and are all located in a narrow region of the dentary.

DISCUSSION

Developmental trends in crocodylian heterodonty

Multiple measures of heterodonty allow for us to describe morphological conditions across the crocodylian specimens sampled in a thorough manner, through a combination of disparity, morphotypes ranges, and serial homology along the tooth row. All living crocodylians are heterodont to varying degrees, and these data showed significant variability of morphotypes along the dental arcade for all specimens. Although dentition varies between species, certain consistencies were seen throughout the extant members of the clade:

1. Similar teeth occur on both the cranial and dentary dental arcades.
2. The vast majority of shape variance from the labial perspective ranges from high-caniniform to high molariform. Only minor distal curvature is apparent in more caniniform crowns.
3. There is serial homology in tooth shape from-mesial-to-distal along the tooth row, and molariformy increases in this direction. This is significantly linear for both dental arcades.

4. Size variability consists of an undulating pattern with three peaks, with large procumbent crowns interspersed within smaller crowns.

Shape- and size-heterodonty are clearly decoupled, as they change in dramatically different, and seemingly independent, fashions along the arcade. This 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 (see **INTRODUCTION**), surprisingly little has been done on what developmental influences affect tooth size and shape. Crocodylian teeth are replaced in waves, or Zahnreihe (Edmund, 1962; Westergaard ~~and~~ Ferguson, 1990; Osborn, 1998), but these waves appear to be unrelated to the morphological variables investigated here. Keiser et al., (1993) compartmentalized the dentition along the tooth row for *C. niloticus*, grouping teeth into 'incisor,' 'premolar,' and 'molar' regions with each reflecting a procumbent tooth. They did not offer a developmental mechanism that differentiates these categories though. Fruchard (2012) suggested that the only difference between procumbent 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.

Although we were able to define heterodonty successfully, the task of assigning a singular dental morphotype to any one species of crocodylian is much more 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 most 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; Gignac and Erickson, 2016; Gignac and O'Brien, 2016). Concerning teeth, a qualitative increase in overall molariformy was observed in *A. 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 *C. porosus* had a greater *y*-intercepts indicating greater molariformy. This trend was also seen in the *B. sternbergii* cranial specimens. In addition to allometry, phenotypic changes due to environmental factors may also influence teeth. Skull shape and tooth orientation are irregularly influenced by the captive rearing (Erickson et al., 2004; Drumheller et al., 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.

Adaptive explanations for interspecific variability in modern taxa

The method presented here implicates that significant differences in tooth morphology exist between modern members of Crocodylia. Bite force in crocodylians is primarily influenced by size (Erickson et al., 2012), 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 a specific tooth forms, shape and size will influence how a tooth interacts with a particular substrate. We therefore suggest that a biomechanical link should exist between the structural limits imposed by tooth form and the material properties of the substrates it interacts with.

As with all jawed vertebrates, crocodylian teeth must cope with different stresses based on their respective position along the arcade. Distal teeth will endure more force during a bite due to their close proximity to the hinge (Cleuren, Aerts, & Vree, 1995; Erickson, Lappin, & Vliet, 2003; Erickson et al., 2012; McHenry et al., 2006). This explains why these teeth are always 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, food processing typically occurs here (Busbey, 1989; Davenport et al., 1990; Cleurens and de Vree, 2000). Their short size also ensures they do not impede jaw closure. This necessity is very apparent in *G. gangeticus*, and explains the poor linear shape relationship along the tooth row. Having all the teeth be high- to mid-caniniform except for the distal-most region in attempt to reduce heterodonty as much

as possible (Grigg and Gans, 1993), while ensuring the distals do not impede jaw closure or break when processing food.

Particular attention should be paid to the distals in modern alligatoroids and crocodyloids, as their relative size varies noticeably between species (Figure 6a). Most members of these clades have a single procumbent tooth followed distally by several smaller teeth. These are typically mid-molariform, but even the high-molariform distals of *C. siamensis* were some of the smallest teeth in its arcade. *Alligator sinensis* differed from this, in that it had a row of 4-5 relatively large, high-molariform, crowns followed by only one crown reduced in size. Probably the most extreme condition, *O. tetraspis* had distals that were exceptionally large; the largest crowns at positions M10-12 and D11-13 all belonged to members of this species. Aoki (1989) qualitatively noted these unique conditions, and suggested they facilitated durophagy. All alligatoroids and crocodyloids sampled here have been recorded to consume at least some hard prey items though (e.g. Brazaitis, 1973; McIlhenny, 1976; Taylor, 1979; Groombridge, 1982; Ross ~~and~~ Magnusson, 1989; Santos et al., 1996; Selvaraj, 2012; Nifong & Silliman, 2013), so it is unclear what selection pressure resulted in these particular morphologies. It may be a result of body size. Bite force tests of *A. mississippiensis* showed the pressure produced at its procumbent distal (M11) to be adequate to crush its harder prey items (Erickson, Lappin, & Vliet, 2003; Gignac & Erickson, 2014). If this is the case in most of the large crocodylians, enlarging the distal-most crowns would be unnecessary. *Alligator sinensis* and *O. tetraspis,* on the other hand, may need more extreme dentition closer to the hinge; their smaller size would make it more difficult to process foods with similar mechanical properties. Another explanation for this is the frequency of consuming hard prey. Although both *A. sinensis* and *O. tetraspis*

435 have broad diets, studies have shown certain populations to consume disproportionately large
436 numbers of shelled mollusks and crustaceans (Cheng et al., 1957; Groombridge, 1982; Ross and
437 Magnusson, 1989; Luiselli, Akani, & Capizzi, 1999; Pauwels et al., 2007).

438 Caniniform mesials are ideal for the acquisition of prey, as pointed apices reduce
439 surface area to puncture compliant substrate (Frazetta, 1988). Being farther from the hinge,
440 these teeth move faster during a strike and are more likely to contact prey trying to escape
441 (Busbey, 1989). All taxa measured here also have two sets of large mesial teeth on both
442 arcades, often referred to as 'pseudocanines' (Brochu, 1999). These procumbent teeth are well
443 built for puncturing, likely make first contact with prey during jaw closure, and resilient against
444 struggling prey (Iordansky, 1964). High size heterodonty in caimanines was typically a
445 consequence of large pseudocanines and relatively small remaining crowns, (Figure 6b). Their
446 pseudocanines can become so large that dentary crowns may grow entirely through the cranial
447 rostrum in adults (Brazaitis, 1973). The molariform distals were rather small by comparison.
448 This suggests these taxa prioritize securing prey over processing it. This may be a specialization
449 for hunting mobile and/or compliant prey (Sampaio et al., 2013), as insects and fish can make
450 up a large portion of their diet (Santos et al., 1996). The exceptionally large pseudocanines of *C.*
451 *porosus* also show a prioritization for puncturing and securing soft-bodied prey in a larger
452 context, as this species is notorious for actively hunting large vertebrates such as sharks, cattle,
453 horses, and humans (e.g. Taylor, 1979; Kar & Bustard, 1981; Groombridge, 1982; Doody, 2009;
454 Hanson et al., 2015). Similar to caimanines, this species atrophies position P2 to make room for
455 enlarged D1 pseudocanines (Brown at al., 2015)

456 The longirostrine species have a reputation for eating small, aquatic prey with a focus
457 on fish (Peyer, 1968; Webb, Manolis, & Buckworth, 1982), and multiple lines of evidence
458 suggest the feeding apparatus is well designed for this function. The longirostrine shape
459 reduces resistance during both lateral motion and jaw adduction when feeding underwater,
460 and the increased snout length allows for a faster strike (Pooley, 1989; Thorbjarnarson, 1990;
461 McHenry et al., 2006; Pierce et al., 2008). Highly caniniform teeth can quickly puncture fast-
462 moving, compliant prey, and their elongate shape may also lower resistance. The longirostrine
463 cranio-dental morphotype may be prey-size prohibitive, as larger prey could damage it while
464 struggling. The elongate mandibular symphysis of longirostrines results in a mechanical
465 disadvantage against forces produced by shaking/twisting prey as well (Walmsley et al., 2013),
466 and there is a reduction in masticatory musculature relative to other crocodylians (Endo et al.,
467 2002). The gracile nature of the dentition means a lower bending strength, also making them
468 more susceptible to breakage by more powerful prey (Figure 6).

469 The longirostrine taxa also had the lowest heterodonty of modern crocodylians, which is
470 reminiscent the 'homodont' condition apparent in numerous aquatic predators such as
471 odontocetes whales (Rommel, 1990). This condition is believed to be ideal for catching and
472 holding, but not processing, small aquatic prey (MacLeod et al., 2007), as most prey items
473 consumed are under 10% of their body length (MacLeod et al., 2006). A convergent reduction
474 in heterodonty within both groups indicates a transition from a multi-functional dental arcade
475 to one almost exclusively for prey capture. This is clearly the condition in *G. gangeticus,* as it is
476 almost entirely caniniform along its tooth row and eats primarily fish (Groombridge, 1982). The
477 other longirostrine taxa, although also primarily caniniform, still displayed the linear shape

change typical of other crocodyloids. This may indicate a more versatile diet; these taxa have also been known to process larger/harder prey items, such as crustaceans, turtles, and immature primates (Brazaitis, 1973; Groombridge, 1982; Galdikas and Yeager, 1984; Selvaraj, 2012).

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

Fossil taxa and the appropriateness of analogues

Certain fossil taxa were reminiscent of modern counterparts. *Caiman crocodilus* and *C. yacare* are highly similar. This was expected as these species are closely related and were once considered subspecies, and both eat insects, crustaceans, and fish (Brazaitis, 1973; Groombridge, 1982; Da Silveira and Magnusson, 1999). Any differences in size and shape ranges appear to simply be a consequence of the former's incomplete arcades; no distal

maxillary or any dentary crowns were available. Both *Borealosuchus* and *Leidyosuchus* possess dentition somewhat typical of large modern crocodylians (Figure 6). *Alligator mississippiensis* makes for an excellent dental analogue for one particular *Leidyosuchus* specimen (ROM 01903) as heterodonty and shape regressions overlap consistently. The fact that *Leidyosuchus* lacks any evidence of enlarged distal teeth may be indicative of a difference in the degree these taxa process hard materials, although no taphonomic evidence for this currently exists associated with *Leidyosuchus*. The four specimens of *B. sternbergii* all varied, most likely due to an allometric increase in molariformy (see above), but certain consistencies are apparent. Based on linear shape change, all specimens in this genus were projected to have mid-caniniform and –molariform teeth, with smaller specimens projected to additionally have the high-caniniform mesials and larger specimens having high-molariform distals. The best analogue for this species may be a member of *Crocodylus* where larger individuals have distals approaching high-molariform range such as *C. niloticus*.

The fact that *H. rebouli* surpasses our larger *C. porosus* in size heterodonty, and has a similar upper maximum in relative tooth size, indicates that it may have dealt with similar prey from a mechanical standpoint (Figure 6e). Peirosaurids are believed to be primarily terrestrial crocodyliforms (Tavares et al., 2017), and this dentition argues *H. rebouli* may have focused on mobile, terrestrial vertebrates (Larsson & Sues, 2007). Its large pseudocanines would puncture vertebrates tissue with similar effectiveness to those of *C. porosus*. Noticeable differences are the very large distal procumbent crowns of *H. rebouli*, which suggest potential differences in prey processing. These teeth may have been used for either sheering soft tissue or breaking

bone similar to modern mammalian carnassials, as rolling on land is not an effective means of dismemberment (Fish et al., 2007).

It has been stated that modern taxa do not have, or have secondarily lost, the degree of molariformy commonly found in extinct representatives. Known as “globidonty” (Norell, Clark, & Hutchison, 1994; Brochu, 1999; 2001; Ősi & Barrett, 2011), this term describes enlarged, high-molariform crowns potentially used for durophagy (Figure 6f). *Allognathosuchus* and *Brachychampsa* are ‘textbook’ examples of globidont taxa (Case, 1925; Carpenter ~~and~~ Lindsey, 1980). Although we agree with Brochu (2001, 2004) that *O. tetraspis* is not as extreme, its enlarged distals do overlap with these taxa in both size and shape. *Alligator prenasalis* and *“C.” affinis* distals are similar to *A. sinensis*, also creating a ridge of robust teeth (Mook, 1932). The mechanical capabilities of these particular crowns in ‘modern globidonts’ should be similar to the extinct taxa, 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. The modern globidonts also have caniniform mesials and pseudocanines, suggesting a division of labor along the tooth row. Contrarily, almost all teeth of *A. prenasalis, Brachychampsa,* and *“C.” affinis* on the molariform half of the shape-spectrum. 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 semi-aquatic, ambush predators. *Allognathosuchus’* pseudocanine suggests a potential division of labor along the tooth row more like modern globidont taxa, but a more complete tooth row is necessary to confirm.

The nature of heterodonty in fossil taxa with less than 40% of their tooth row represented is especially difficult to determine. *Allognathosuchus* was represented here by a pseudocanine and globidont distals, but previous studies have shown a great degree of tooth and alveolar size variation that our specimen is missing (Case, 1925; Brochu, 2004). The teeth of *A. krebsi* only occur between D6-D12. This region is so narrow that the slope is a poor indicator of the shape range. Although it is a gavialoid, its teeth are most similar to *M. cataphractus* in shape, and may be its most appropriate analogue. Salas-Gismondi et al., (2016) argued that the lack of 'telescoped' eyes in *A. krebsi* is indicative of its marine habit (see also Hua & Jouve, 2004). *Mecistops cataphractus* superficially shares this condition, and has been known to frequent brackish and costal environments (Brazaitis, 1973; Ross ~~and~~ Magnusson, 1989).

CONCLUSION

Foote's MD is a reliable method for assessing heterodonty if the tooth row is near complete, but much of the variability in MD seen here is the result of incompleteness. Foote's MD relies on, among other things, the Grand mean and the sample size. Size heterodonty was greatly underrepresented in one specimen of *O. tetraspis* (AMNH 101417) as its pseudocanines were missing. These teeth would have deviated greatly from the Grand mean if present, and their inclusion would most certainly have raised the value. Our *Allognathosuchus* specimen had four teeth, with three being globidont and one an average-shaped pseudocanine. ~~The result was a shape Grand mean that the pseudocanine deviated from greatly.~~ That, compounded with the low sample size, resulted in an inflated shape MD. A similar principle may be applied to both *A. krebsi* and *B. vorax*; because only a small area of the tooth row was represented all the

562 individual tooth shape values were close to the Grand mean, so the MD values were deflated.
563 Slope of shape heterodonty is also influenced by the completeness of the tooth row. Several
564 specimens have similar PC1 values for the same positions, but their slopes differed. This is
565 typically due to one or both missing the mesial- or distal-most teeth. This was apparent in *C.*
566 *crocodilus*; even though it shared almost identical tooth morphology with *C. yacare*, its cranial
567 regression coefficients deviated because the distal 30% of its teeth were missing.

568 did not consider all three dimensions here. Living crocodylian teeth are often
569 discussed as conical (Edmund, 1969) or conidont (Hendrickx, Mateus, & Araújo, 2015b). Studies
570 of bending strengths show variation between mesial-distal and labial-lingual axes as well as
571 variation between species (Monfrey, 2017), indicating that functional information may be
572 drawn from the dimesion not considered here. This is especially important concerning fossil
573 taxa, as pronounced lateral compression is commonplace. *Boverisuchus vorax* distals plotted
574 similarity to globidont crowns using our method, but they are clearly ziphodont (Brochu, 2001,
575 2003). Future studies should consider this third dimension at least qualitatively, in order to
576 avoid conflating disparate tooth morphotypes such as these.

577 These limitations aside, the methods proposed here could be very useful in dealing with
578 incomplete fossils. It is common for fossil crocodylian specimens to be lacking many/most of
579 their teeth. The linear nature of tooth shape can predict the shape of these missing teeth.
580 Although slopes may vary between species, a record of the ranges of slopes evident in a certain
581 taxonomic group may be applied to a fossil with few teeth. The preserved tooth/teeth can be
582 plugged into the linear equation, and the shapes of missing teeth may be predicted with a high

583 degree of certainty. This would result in a more complete representation of the extinct animal's
584 anatomy, useful from the standpoint of both anatomical science and paleontological
585 reconstruction.

586 Quantifying the teeth of crocodylians will add rigor to future life history studies of the
587 clade. As a quantifiable trait, both tooth shape in a single position and heterodonty as a whole
588 may be incorporated into character matrices of phylogenetic analyses. As we have shown
589 heterodonty be very real in Crocodylia, descriptors of dentition can describe a numerical
590 range of morphology as opposed to cherry-picking an average tooth or single position.
591 Monospecific comparisons of multiple specimens can quantify the allometric changes in tooth
592 morphology often alluded to in the literature. The teeth of fossil taxa can be compared
593 statistically to modern taxa to determine the best analogue, and rigorous hypotheses about
paleobehavior and paleoecology may be drawn. Crocodylians, both living and extinct, may be
595 grouped in dental categories, allowing for species and specimens to be compared to one
596 another. Frequency, size, and hardness of food items may be compared to these categories to
597 determine if a link exists between dental morphotypes and dietary patterns. Crocodylians are
598 used in both performance and actualistic taphonomy studies frequently, and the output of
599 these studies could be correlated with tooth dimensions; tooth shape may be compared to
600 bite-force, death-rolling, and bone-modification.

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608

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965 **TABLE LEGENDS**

966 **Table 1:** Size, disparity, and regression information for modern crocodylian specimens. Head
967 lengths are in millimeters. Morphological disparity (MD) is for all teeth for each specimen. "N"
968 represents number for teeth available versus number of positions total. Regression
969 information is for Principal Component 1 plotted against tooth position.

970 **Table 2:** Size, disparity, and regression information for fossil crocodylian specimens. Head
971 lengths are in millimeters. Morphological disparity (MD) is for all teeth for each specimen. "N"
972 represents number for teeth available versus number of positions total. Regression
973 information is for Principal Component 1 plotted against tooth position.

974

975 **FIGURE LEGENDS**

976 **Figure 1: Methodology for data collection.** A) skulls were selected based on number and
977 condition of teeth present (data was not collected from this photo). B) Each tooth was
978 photographed individually, and the margins were traced (Rohlf, 2016). C) Each outline was
979 converted to 30 equidistant semilandmarks which were then slid. D) Tooth shape variance was
980 represented by vector diagrams, with the mean depicted as points and deviation by vector
981 lines.

982 **Figure 2: Principal component one.** Vector diagrams indicate the maximum range of variance
983 (vectors) from the mean (points) for both cranial and dentary teeth.

984 **Figure 3: Average tooth size** (above) **and shape** (below) **plotted against skull shape**. Gray error
985 bars indicate standard deviation as a consequence of heterodonty. Solid markers depict extant
986 specimens, and hollow markers depict extinct. The solid regression line indicates only extant
987 specimens, while the dashed line indicates all specimens. Maximum shape range is
988 represented through vector diagrams.

989 **Figure 4: Foote's morphological disparity** (A, B) **and ranges** (C, D) **for both size and shape**. Size
990 is represented by centroid size and shape is represented by Principal Component 1. For each
991 species, all teeth in the sample are represented. For MD, multiple individuals from a single
992 species are listed in a single column, and those with lower values are superimposed in front of
993 those with higher values. Ranges are a composite of all members of a species.

994 **Figure 5: Heterodonty by tooth position.** Centroid Size (CS) and Principal Component one (PC1)
995 for extant Alligatoroidea (top), Crocodyloidea (middle), and Gavialoidae (bottom) plotted

against position along the arcade. Welch's ANOVA output comparing positions is listed for each graph with multiple specimens.

Figure 6: Direct comparisons between selected extant and extinct taxa. The "size" axis represents normalized centroid size, and the "shape" axis represents principal component one. A) modern taxa with high molariformy, B) Caimaninae with high size-heterodonty, C) longirostrine taxa, D) mid-heterodont fossil taxa, E) crocodyloids and peirosaurids with high-heterodonty, F) fossil globidont taxa. Note: *Allognathosuchus*, *Argochampsa krebsi*, and *B. sternbergii* were not size normalized by their own skull length, as indicated by empty symbols.

Table 1(on next page)

Size, disparity, and regression information for modern crocodylian specimens.

Head lengths are in millimeters. Morphological disparity (MD) is for all teeth for each specimen. “N” represents number for teeth available versus number of positions total. Regression information is for Principal Component 1 plotted against tooth position.

Genus	Species	Number	Head Length	MD (size)	MD (shape)	Host bone
Alligator	*mississippiensis*	AMNH 71621	407.81	0.00052	0.0205	cranium mandible
Alligator	*sinensis*	AMNH 23900	161.87	0.00040	0.0241	cranium mandible
		AMNH 23907	139.89	0.00034	0.0170	cranium mandible
Caiman	*yacare*	AMNH 97297	206.96	0.00084	0.0300	cranium mandible
		AMNH 97300	347.30	0.00102	0.0217	cranium mandible
Crocodylus	*acutus*	AMNH 7856	486.60	0.00051	0.0208	cranium mandible
		AMNH 7857	436.66	0.00073	0.0251	cranium mandible
Crocodylus	*niloticus*	AMNH 23471	639.27	0.00064	0.0143	cranium mandible
		AMNH 142494	N/A	N/A	0.0277	cranium mandible
Crocodylus	*palustris*	AMNH 75707	400.85	0.00063	0.0203	cranium mandible
		AMNH 96134	236.82	0.00031	0.0250	cranium mandible
Crocodylus	*porosus*	AMNH 66639	426.22	0.00071	0.0182	cranium mandible
		AMNH 94957	575.23	0.00115	0.0179	cranium mandible
Crocodylus	*siamensis*	AMNH 49231	381.95	0.00049	0.0339	cranium mandible
		AMNH 72640	251.86	0.00042	0.0289	cranium

						mandible
Gavialis	*gangeticus*	AMNH 131377	428.63	0.00023	0.0110	cranium mandible
Mecistops	*cataphractus*	AMNH 107634	330.37	0.00035	0.0137	cranium mandible
Osteolaemus	*tetraspis*	AMNH 101417	247.98	0.00026	0.0236	cranium mandible
		AMNH 117801	203.14	0.00121	0.0239	cranium mandible
		AMNH 117802	149.97	0.00049	0.0264	cranium mandible
Paleosuchus	*palpebrosus*	AMNH 93812	164.41	0.00071	0.0210	cranium mandible
		AMNH 97328	212.42	0.00112	0.0241	cranium mandible
Paleosuchus	*trigonatus*	AMNH 58136	228.20	0.00091	0.0291	cranium mandible
		AMNH 137174	188.83	0.00055	0.0161	cranium mandible
Tomistoma	*schlegelii*	AMNH 113078	449.56	0.00033	0.0180	cranium mandible

1

2

N	m	b	r^2	*p*	0.95 confidence	
17:20	0.3718	0.0342	0.8488	<0.0001	0.2855	0.4582
18:20	0.4203	0.0390	0.8820	<0.0001	0.3388	0.5018
15:19	0.4228	0.0608	0.8398	<0.0001	0.3122	0.5334
14:19	0.3898	0.0604	0.8965	<0.0001	0.3065	0.4731
15:19	0.4037	0.0415	0.8718	<0.0001	0.3109	0.4964
15:19	0.3147	0.0779	0.8095	<0.0001	0.2232	0.4062
13:20	0.5163	-0.0207	0.8703	<0.0001	0.3841	0.6486
15:20	0.4553	-0.0080	0.9522	<0.0001	0.3942	0.5165
14:20	0.4812	-0.0605	0.8360	<0.0001	0.3472	0.6153
16:20	0.4257	-0.0180	0.8304	<0.0001	0.3154	0.5359
15:18	0.4179	-0.0520	0.8805	<0.0001	0.3257	0.5102
11:15	0.4049	-0.0424	0.9060	<0.0001	0.3066	0.5033
10:18	0.4042	-0.0580	0.7943	0.0005	0.2365	0.5720
13:15	0.4218	-0.0301	0.8908	<0.0001	0.3238	0.5199
16:19	0.3287	-0.0064	0.8035	<0.0001	0.2355	0.4219
15:15	0.3485	-0.0419	0.8417	<0.0001	0.2579	0.4391
11:19	0.3530	0.0639	0.8241	0.0001	0.2300	0.4760
11:15	0.4699	-0.0221	0.8724	<0.0001	0.3344	0.6054
9:19	0.3473	-0.0252	0.9072	0.0001	0.2480	0.4465
12:15	0.4753	0.0113	0.9176	<0.0001	0.3750	0.5756
14:19	0.4691	-0.0254	0.8365	<0.0001	0.3386	0.5995
9:15	0.3642	-0.0143	0.8966	0.0001	0.2537	0.4748
11:19	0.4053	-0.0970	0.8253	0.0001	0.2646	0.5459
10:15	0.3515	-0.1030	0.8275	0.0003	0.2207	0.4824
15:19	0.4037	-0.0142	0.8783	<0.0001	0.3137	0.4938
9:15	0.2896	-0.0392	0.7868	0.0014	0.1549	0.4244
8:19	0.6219	-0.0505	0.8926	0.0004	0.4064	0.8373
12:15	0.5154	-0.0615	0.8591	<0.0001	0.3683	0.6625
16:19	0.6298	-0.0499	0.8213	<0.0001	0.4614	0.7981

12:15	0.3921	-0.0374	0.8814	<0.0001	0.2907	0.4934
22:28	0.0963	-0.2404	0.4500	0.0006	0.0466	0.1459
24:26	0.1942	-0.2153	0.5749	<0.0001	0.1204	0.2681
15:18	0.3457	-0.1549	0.8265	<0.0001	0.2508	0.4406
15:15	0.2757	-0.1393	0.9136	<0.0001	0.2249	0.3265
12:17	0.4274	-0.0094	0.7938	0.0001	0.2739	0.5809
9:14	0.5613	-0.0506	0.8028	0.0011	0.3127	0.8100
12:17	0.4923	-0.0301	0.8541	<0.0001	0.3489	0.6356
11:14	0.4432	0.0027	0.8192	0.0001	0.2862	0.6002
12:17	0.4296	0.0134	0.6648	0.0001	0.2547	0.6045
14:14	0.4656	0.0163	0.8694	<0.0001	0.3520	0.5791
19:20	0.4627	-0.0214	0.8683	<0.0001	0.3705	0.5549
21:22	0.3804	0.0034	0.8727	<0.0001	0.3106	0.4501
18:20	0.4648	-0.0341	0.8598	<0.0001	0.3654	0.5643
13:22	0.4898	0.0015	0.8896	<0.0001	0.3753	0.6043
16:20	0.5404	-0.0660	0.9131	<0.0001	0.4448	0.6359
21:22	0.4078	0.0248	0.7765	<0.0001	0.3028	0.5129
14:20	0.5228	-0.0732	0.8433	<0.0001	0.3811	0.6646
15:22	0.3673	-0.0074	0.7522	<0.0001	0.2410	0.4937
13:21	0.3346	-0.1641	0.7179	0.0003	0.1954	0.4738
18:19	0.2887	-0.1628	0.8109	<0.0001	0.2148	0.3626

3

Table 2(on next page)

Size, disparity, and regression information for fossil crocodylian specimens.

Head lengths are in millimeters. Morphological disparity (MD) is for all teeth for each specimen. “N” represents number for teeth available versus number of positions total. Regression information is for Principal Component 1 plotted against tooth position.

Genus	Species	Number	Head Length	MD (size)	MD (shape)	Host bone
Alligator	*prenasalis*	ROM 01375	317.20	0.00030	0.0143	cranium
Allognathosuchus	*sp.*	UCMP 150180	N/A	N/A	0.0511	mandible
Argochampsa	*krebsi*	ROM 73872	N/A	N/A	0.0136	mandible
Borealosuchus	*sternbergii*	NMNH 6533	336.21	0.00003	0.0123	cranium
		UCMP 126099	209.05	0.00070	0.0201	cranium
		UCMP 130435	N/A	N/A	0.0210	mandible
		UCMP 131769	N/A	N/A	0.0158	mandible
Boveriosuchus	*vorax*	UCMP 170767	N/A	N/A	0.0114	mandible
Brachychampsa	*sp.*	ROM 68491	624.15	0.00032	0.0108	cranium mandible
Caiman	*crocodilus*	UCMP 42844	301.93	0.00084	0.0186	cranium mandible
"Crocodylus"	*affinis*	UCMP 131090	534.10	0.00037	0.0161	cranium
		NMNH 4048	N/A	N/A	0.0118	mandible
Hamadasuchus	*rebouli*	ROM 52620	416.92	0.00108	0.0272	cranium
Leidyosuchus	*canadensis*	ROM 01903	463.35	0.00069	0.0202	cranium
Leidyosuchus	*sp.*	ROM 1425	N/A	N/A	0.0136	mandible

1

2

N	m	b	r^2	*p*	0.95 confidence	
7:16	0.2430	0.1597	0.9638	0.0001	0.1888	0.2971
4:19	0.4690	0.0785	0.9938	0.0031	0.3561	0.5818
5:17	0.5499	-0.1334	0.9562	0.0039	0.3336	0.7661
8:23	0.4539	0.0546	0.9179	0.0002	0.3183	0.5894
7:23	0.5223	-0.0850	0.9026	0.0010	0.3250	0.7196
5:20	0.5318	-0.0320	0.9798	0.0012	0.3914	0.6721
11:20	0.3622	-0.0103	0.7930	0.0002	0.2227	0.5017
6:18	0.5937	0.0753	0.9062	0.0034	0.3286	0.8589
12:18	0.1981	0.1923	0.9162	0.0000	0.1559	0.2403
6:20	0.1559	0.2097	0.8106	0.0144	0.0513	0.2606
7:20	0.3036	-0.0521	0.7237	0.0152	0.0879	0.5193
14:20	0.4063	-0.0140	0.8369	0.0000	0.2935	0.5191
11:15	0.2000	0.1133	0.9363	0.0000	0.1607	0.2394
6:19	0.2025	0.1932	0.5669	0.0840	-0.0432	0.4483
14:20	0.5420	-0.0274	0.9550	0.0000	0.4680	0.6160
20:23	0.3967	0.0303	0.9522	0.0000	0.3527	0.4408
8:19	0.3365	0.0486	0.9570	0.0000	0.2653	0.4078

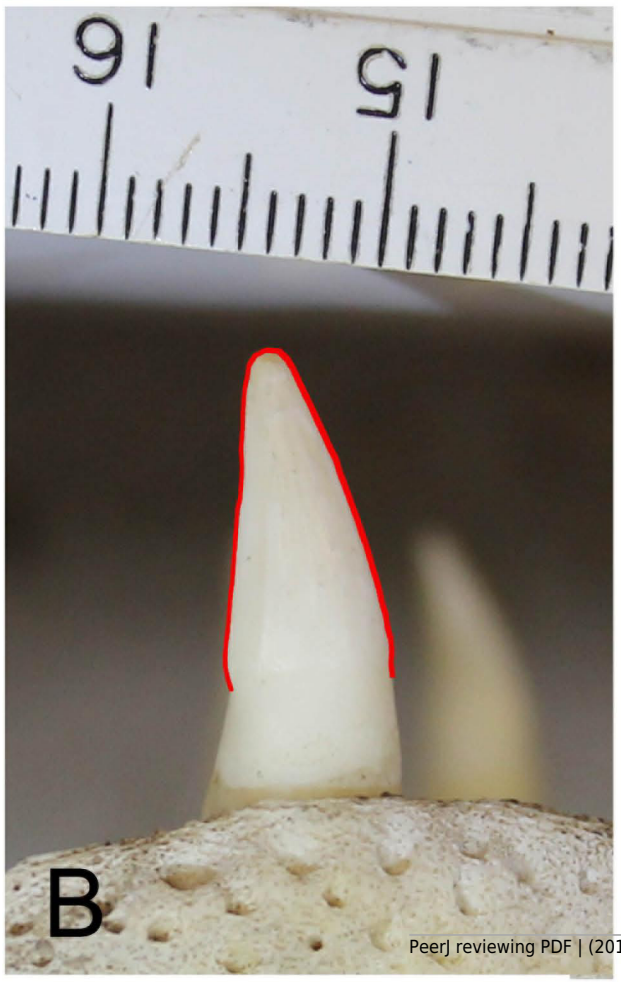
3

Figure 1(on next page)

Methodology for data collection.

A) skulls were selected based on number and condition of teeth present (data was not collected from this photo). B) Each tooth was photographed individually, and the margins were traced (Rohlf, 2016). C) Each outline was converted to 30 equidistant semilandmarks which were then slid. D) Tooth shape variance was represented by vector diagrams, with the mean depicted as points and deviation by vector lines.


A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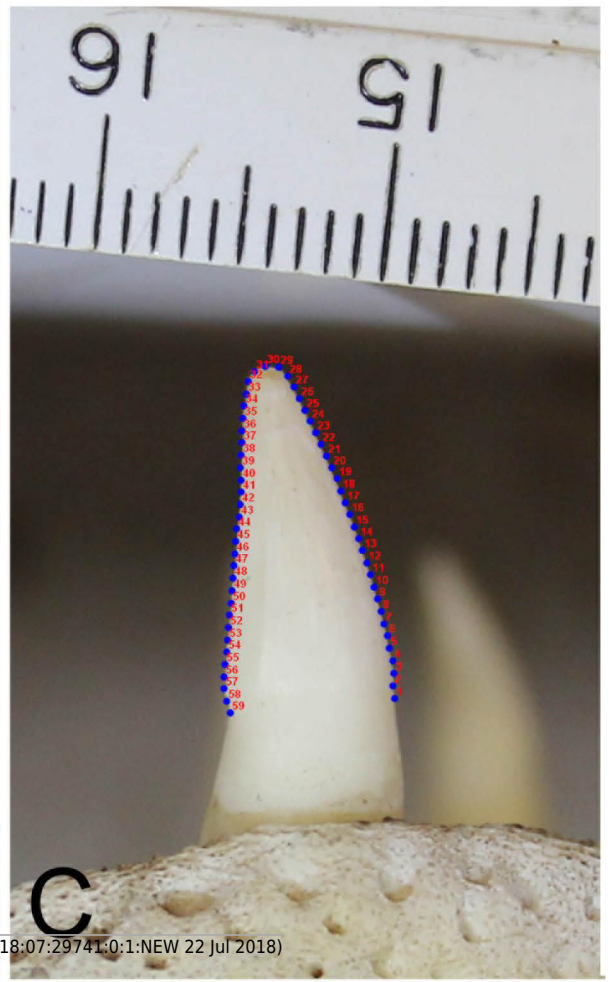

C

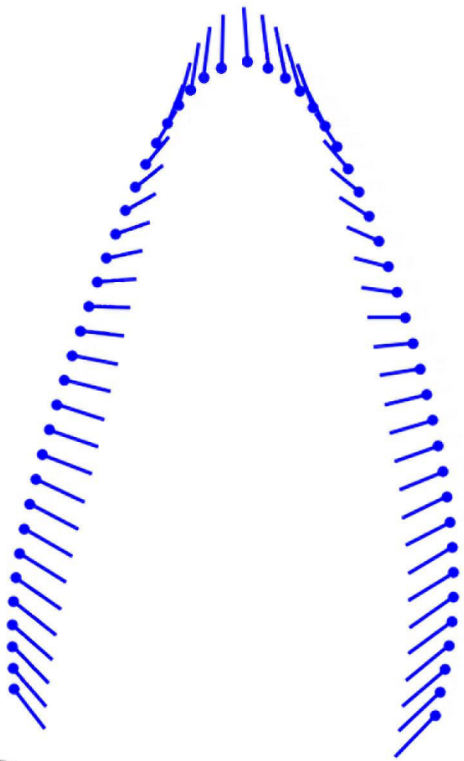

D

Figure 2(on next page)

Principal component one.

Vector diagrams indicate the maximum range of variance (vectors) from the mean (points) for both cranial and dentary teeth.

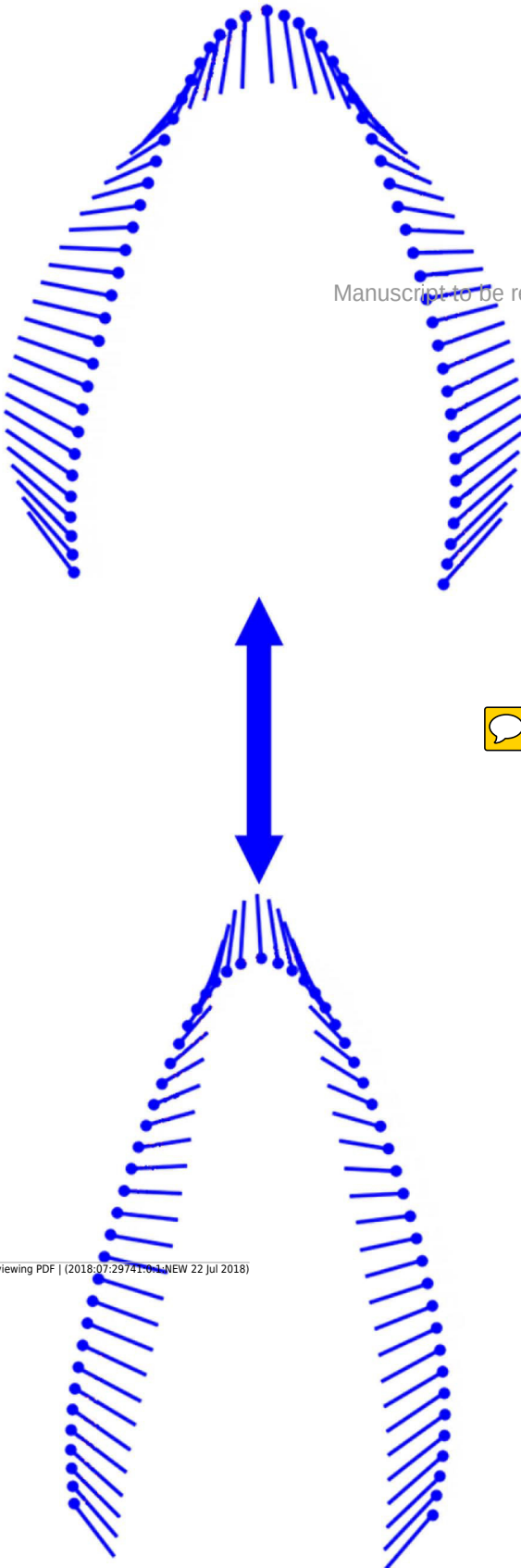
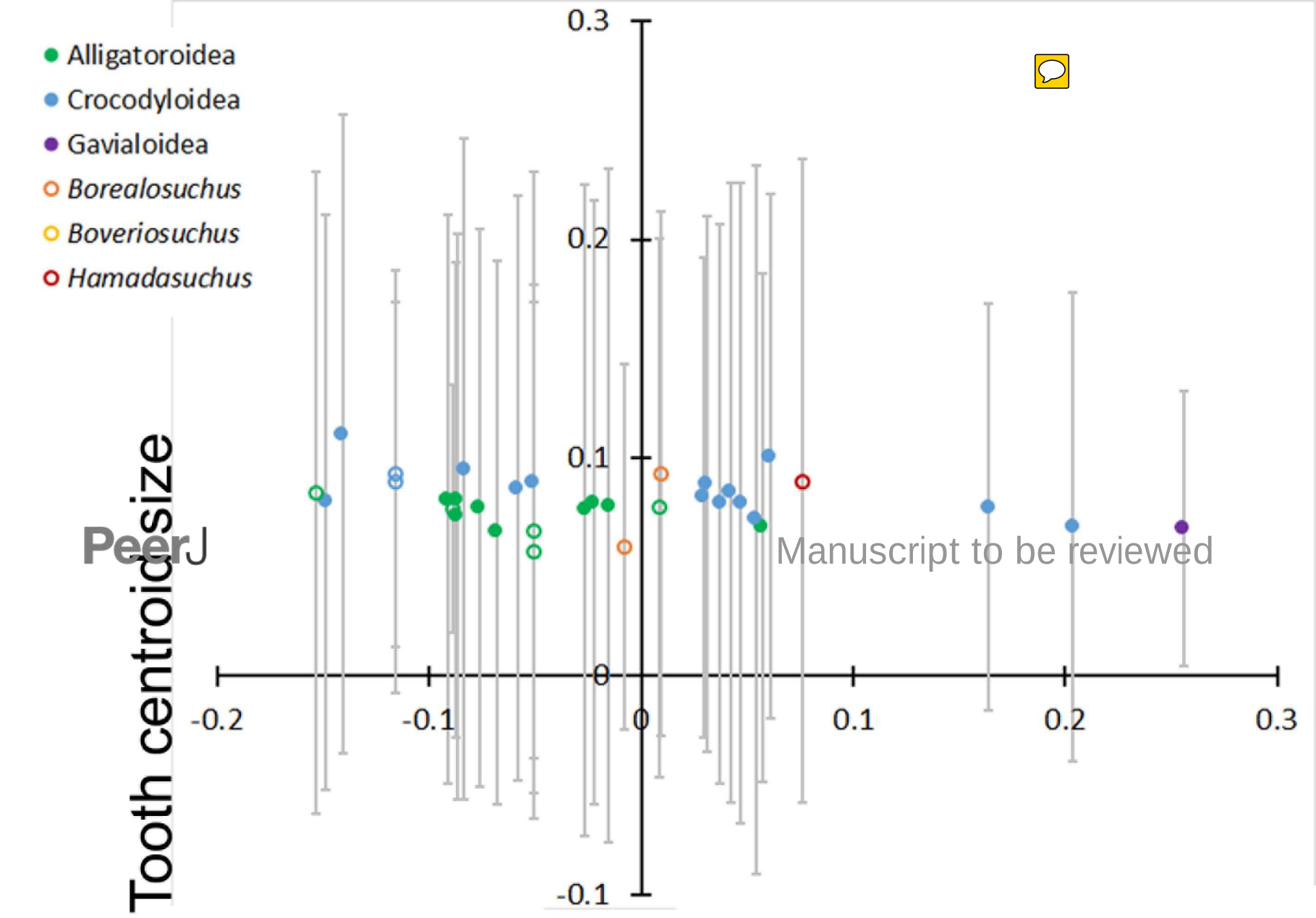


Figure 3(on next page)

Average tooth size (above) and shape (below) plotted against skull shape.

Gray error bars indicate standard deviation as a consequence of heterodonty. Solid markers depict extant specimens, and hollow markers depict extinct. The solid regression line indicates only extant specimens, while the dashed line indicates all specimens. Maximum shape range is represented through vector diagrams.



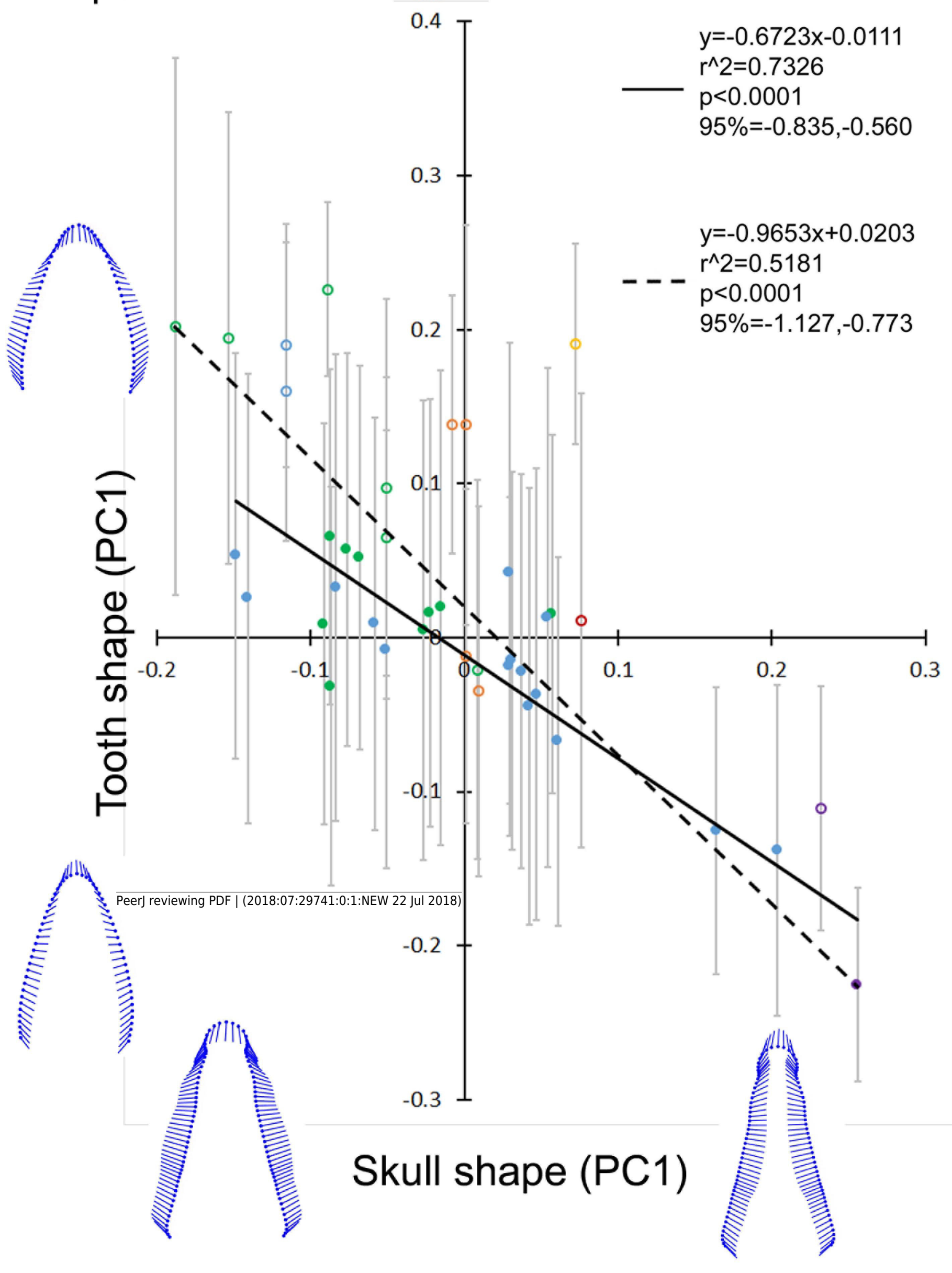


Figure 4(on next page)

Foote’s morphological disparity (A, B) and ranges (C, D) for both size and shape.

Size is represented by centroid size and shape is represented by Principal Component 1. For each species, all teeth in the sample are represented. For MD, multiple individuals from a single species are listed in a single column, and those with lower values are superimposed in front of those with higher values. Ranges are a composite of all members of a species.

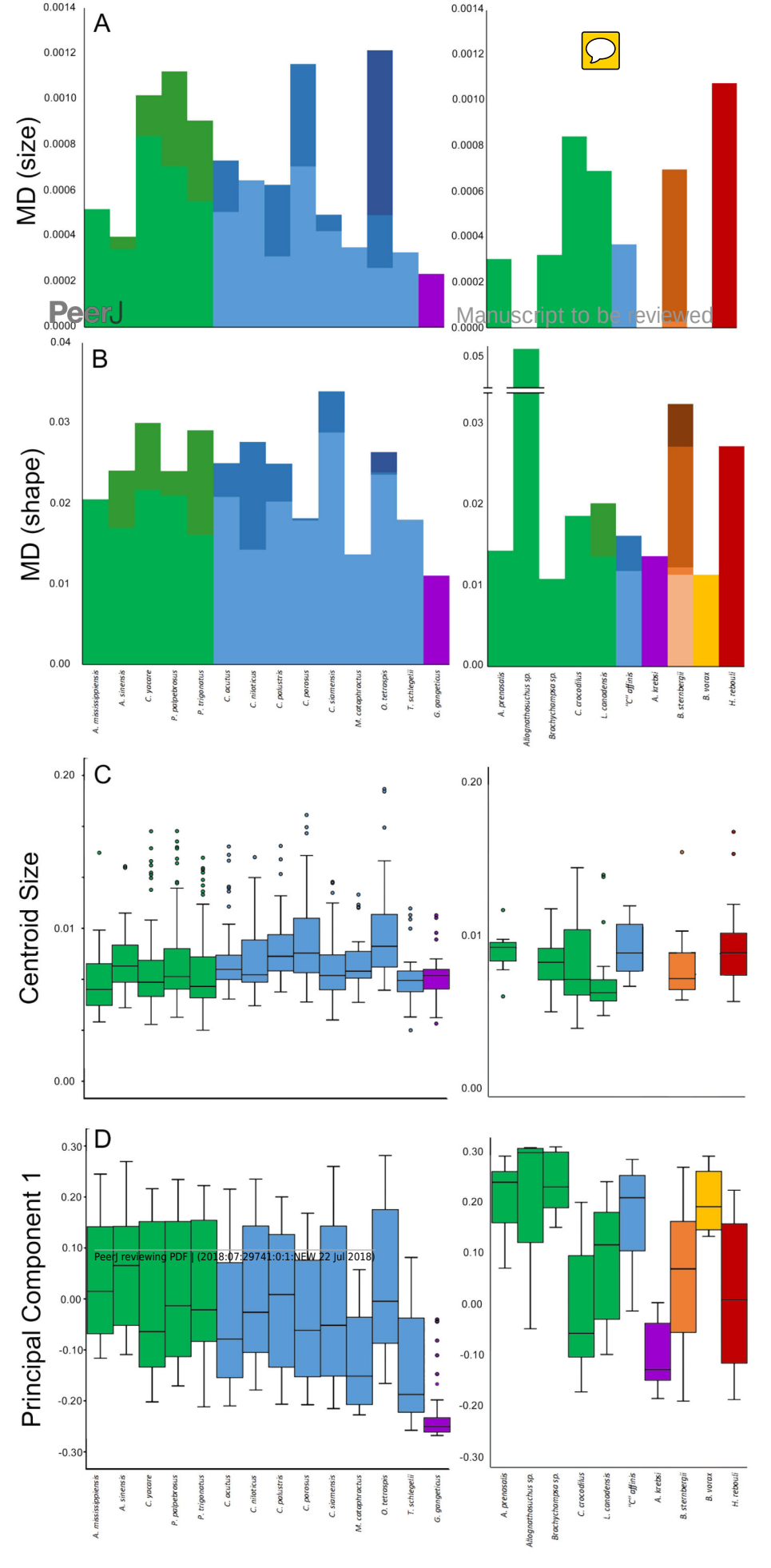

A
MD (size)
0.0014
0.0012
0.0010
0.0008
0.0006
0.0004
0.0002
0.0000
B
MD (shape)
0.04
0.03
0.02
0.01
0.00
0.05
A. mississippiensis
A. sinensis
C. yacare
P. palpebrosus
P. trigonatus
C. acutus
C. niloticus
C. palustris
C. porosus
C. siamensis
M. catapiractus
O. tetraspis
T. schlegelii
G. gangeticus
A. prenasalis
Allognathosuchus sp.
Brachychampsa sp.
C. crocodilus
L. canadensis
"C" affinis
A. krebsi
B. sternbergii
B. vorax
H. rebouli
C
Centroid Size
0.20
0.01
0.00
D
Principal Component 1
0.30
0.20
0.10
0.00
-0.10
-0.20
-0.30
PeerJ
Manuscript to be reviewed
PeerJ reviewing PDF | (2018:07:29741:0:1:NEW 22 Jul 2018)

Figure 5 (on next page)

Heterodonty by tooth position.

Centroid Size (CS) and Principal Component one (PC1) for extant Alligatoroidea (top), Crocodyloidea (middle), and Gavialoidae (bottom) plotted against position along the arcade. Welch's ANOVA output comparing positions is listed for each graph with multiple specimens.

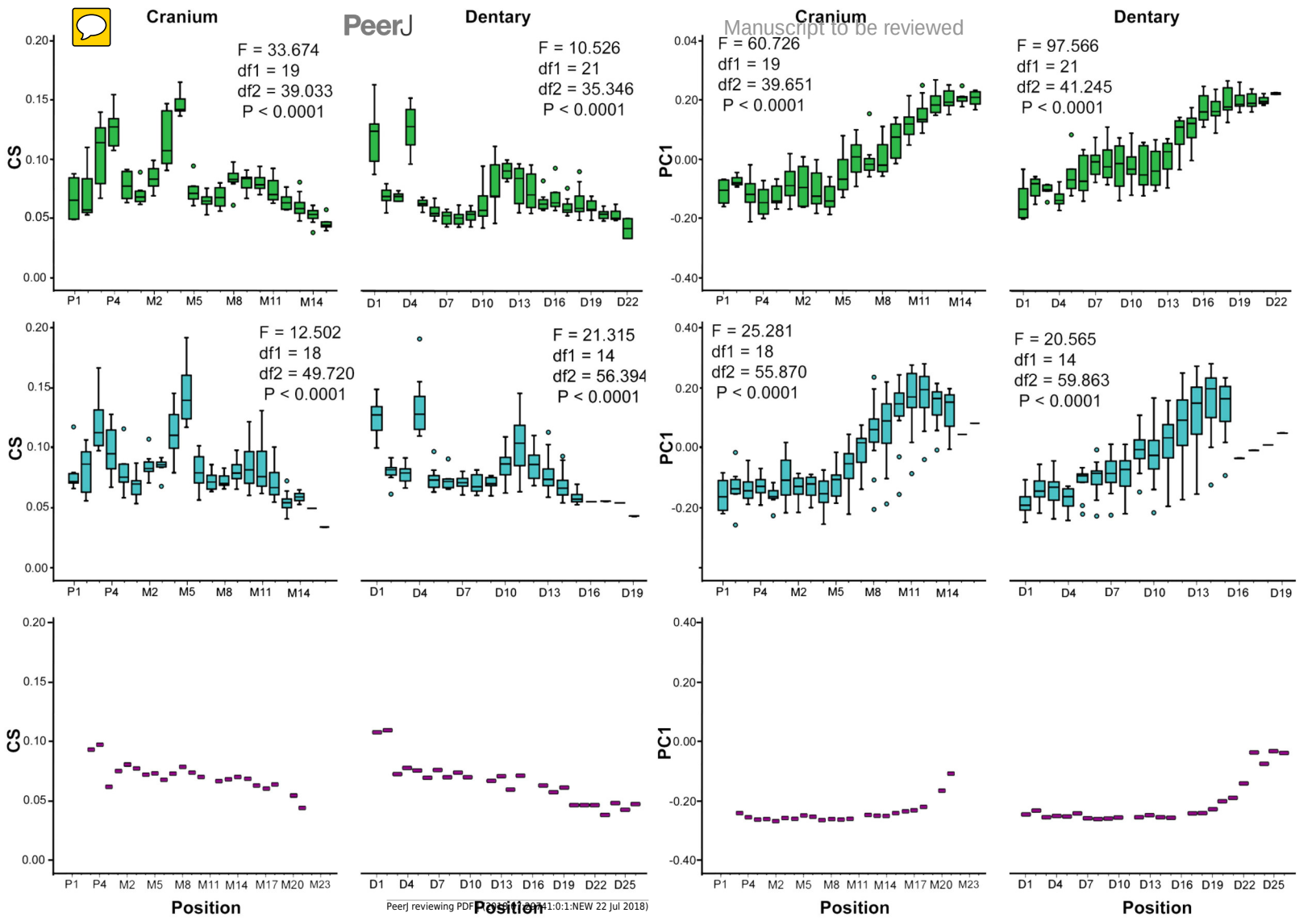


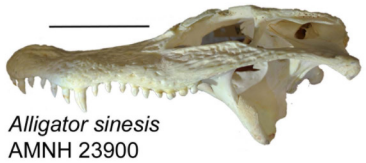
Figure 6(on next page)

Direct comparisons between selected extant and extinct taxa.

The “size” axis represents normalized centroid size, and the “shape” axis represents principal component one. A) modern taxa with high molariformy, B) Caimaninae with high size-heterodonty, C) longirostrine taxa, D) mid-heterodont fossil taxa, E) crocodyloids and peirosaurids with high-heterodonty, F) fossil globidont taxa. Note: *Allognathosuchus*, *Argochampsa krebsi*, and *B. sternbergii* were not size normalized by their own skull length, as indicated by empty symbols.

A

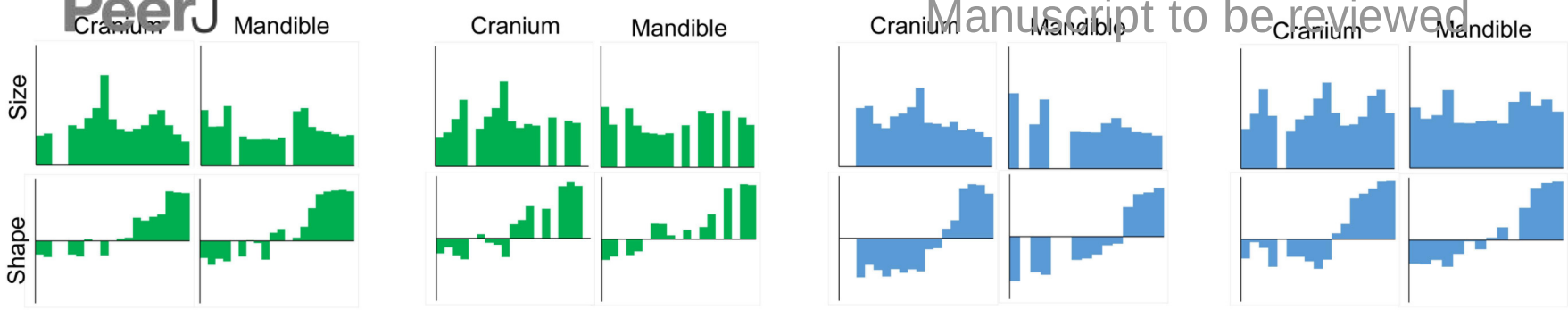
Alligator mississippiensis
AMNH 71621



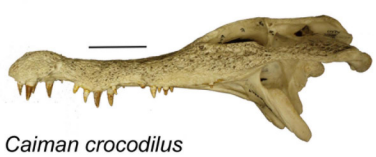
Alligator sinesis
AMNH 23900

Crocodylus siamensis
AMNH 72640

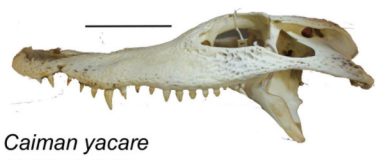
Osteolaemus tetraspis
AMNH 117802



B



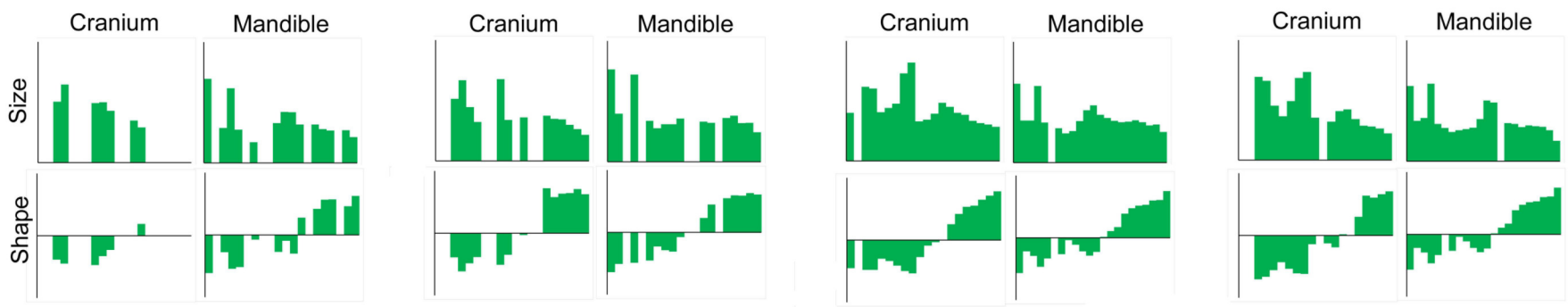
Caiman crocodilus
UCMP 42844



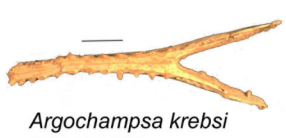
Caiman yacare
AMNH 97297

Paleosuchus palpebrosus
AMNH 93812

Paleosuchus trigonatus
AMNH 58136



C

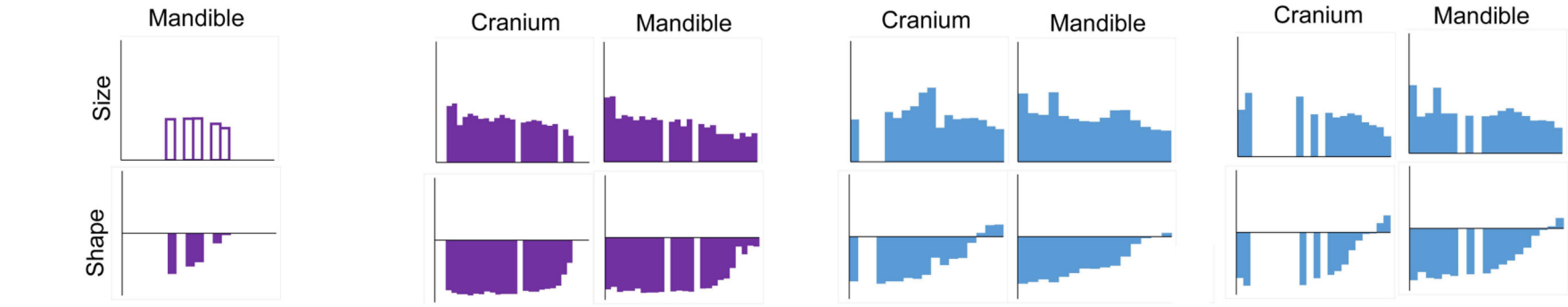


Argochampsa krebsi
ROM 73872

Gavialis gangeticus
AMNH 131377

Mecistops cataphractus
AMNH 107634

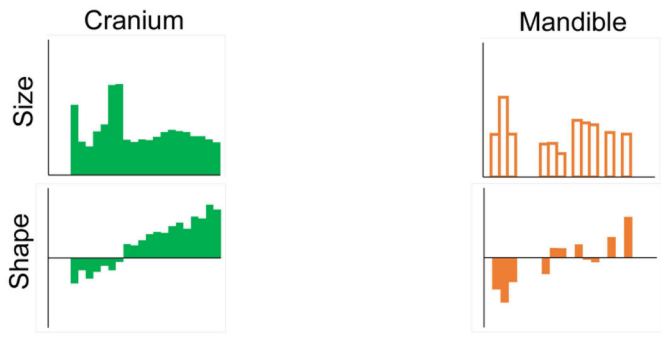
Tomistoma schlegii
AMNH 113078



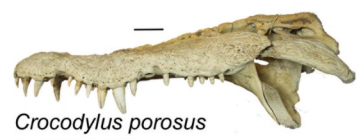
D

Leidyosuchus canadensis
ROM 01903

Borealosuchus sternbergii
UCMP 131769

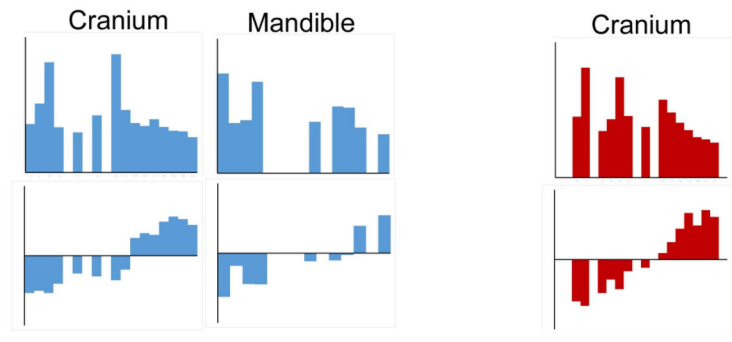


E

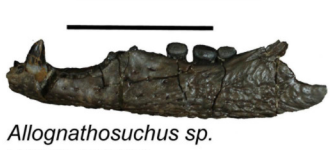


Crocodylus porosus
AMNH 94957

Hamadasuchus rebouli
ROM 52620



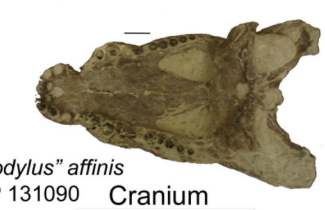
F



Allognathosuchus sp.
UCMP 150180

Brachychampsa sp.
ROM 68491

Alligator prenasalis
ROM 01375



"Crocodylus" affinis
UCMP 131090