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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13 **ABSTRACT**

14 Heterodonty in Crocodylia and associated taxa has not been defined quantitatively, as the teeth

15 rarely have been measured. This has resulted in a range of qualitative descriptors, with little

16 consensus on the condition of dental morphology in the clade. The purpose of this study is to

17 present a method for the quantification of both size- and shape-heterodonty in members of

18 Crocodyliformes. Data were collected from dry skeletal and fossil specimens of 34 crown

19 crocodylians and one crocodyliform. Digital photographs were taken of each tooth and the

20 skull, and the margins of both were converted into both landmarks and semilandmarks. We

21 expressed heterodonty through Foote's morphological disparity, and a Principal Components

22 Analysis visualized shape variance. This analysis reveals that all Crocodyliformes sampled are

23 heterodont to varying degrees. The majority of the shape variance was represented by a

24 'caniniform' to 'molariform' transition. Heterodonty varied significantly between positions; size

25 undulated whereas shape was significantly linear from mesial to distal. Size and shape

26 appeared to be primarily decoupled. Skull shape correlated significantly with tooth shape. High

27 size-heterodonty often correlated with very large caniniform teeth, reflecting a prioritization of

28 securing prey. Large, highly molariform, distal teeth may be a consequence of high-frequency

29 durophagy combined with prey size. The slender-snouted skull shape correlated with a

30 caniniform arcade with low heterodonty. This was reminiscent of other underwater-feeding

31 tetrapods, as they focus on small prey that requires minimal processing. Several extinct taxa

32 were very molariform, which was associated with low heterodonty. *Hamadasuchus rebouli* may

33 have dealt with vertebrate prey similar to large modern taxa, but prey processing may have

34 been different due to its terrestrial habitat. Disparity measures can be inflated or deflated if

35   numerous teeth are absent from the tooth row, and regression analysis may not best apply to

36   strongly slender-snouted taxa. Nevertheless, when these methods are used in tandem they can

37   give a complete picture of crocodylian heterodonty. Future researchers may apply our

38   proposed method to most crocodyliform specimens with an intact enough tooth row regardless

39   of age, species, or rearing conditions, as this will add rigor to many life history studies of the

40   clade.

43   **INTRODUCTION**

44   What constitutes heterodonty often seems like a moving target, with different qualitative

45   definitions in place depending on the clade being studied (Shimada, 2001). Kieser et al. (1993,

46   p.195) referred to the definition of heterodonty as "a bone of contention," and since then the

47   issue never has been fully resolved. Arguably, this lack of clarity is most pronounced within

48   members of Crocodylia. Researchers have often referred to crocodylians as homodont

49   (Langston, 1973; Osborn, 1998; Larsson & Sidor, 1999; Zahradnicek et al., 2014). Peyer (1968

50   p.17) defined the term as lacking the discrete dental categories seen in mammals (incisors,

51   canines, premolars, molars), even though he admitted, "a sharp distinction between homodont

52   and heterodont is not possible." Ferguson (1981) referred to *Alligator mississippiensis* as

53   "pseudoheterodont," because it showed a gradual, as opposed to punctuated, change in tooth

54   shape along the tooth row (see also Grigg and Gans, 1993; Hendrickx, Mateus, & Araújo,

55   2015a). Size variability along the tooth row has motivated the term "heterometric homodonty"

56   for *Crocodylus niloticus* (Fruchard, 2012). Others have applied anisodonty to the clade, which is

57   apparent size, but not shape, heterodonty (Vullo et al., 2016). Certain fossil crocodylians, often

58   interpreted as herbivores or omnivores, exhibit multi-cusped and/or grinding teeth, and are

59   specifically called "heterodont crocodylians" by researchers (e.g. Martin, 2007; Ősi, Clark, &

60   Weishampel, 2007; Novas et al., 2009). Lastly, some researchers have argued certain modern

61   crocodylians are heterodont, and argue dental categories do in fact exist (Aoki, 1989; Kieser et

62   al., 1993).

63   Semantics aside, one reason for the lack of resolution concerning crocodylian

64   heterodonty is that their teeth rarely have been measured. Few studies have performed

65   quantitative shape analyses of crocodylian teeth. Of these, linear-distance measures have been

66   used for fossil identification (Frey & Monninger, 2010), replacement rates (Bennett, 2012), and

67   biomechanical analyses (Monfroy, 2017). Aside from a study evaluating two fossil notosuchians

68   (Lecuona & Pol, 2008), and a preliminary geometric morphometric investigation of *Crocodylus*

69   *niloticus* (Farrugia, Polly, & Njau, 2016), no studies have quantitatively investigated heterodonty

70   either within or between species. Typically, crocodylian dentition is described qualitatively, with

71   the goal of characterization for phylogenetic analysis, or paleoecological inference (e.g.

72   Schwarz-Wings, Rees, & Lindgren, 2009; Young et al., 2012; Salas-Gismondi et al., 2015; Adams,

73   Noto, & Drumheller, 2017). Qualitative descriptors of crocodylian tooth morphology are

74   numerous, and include terms such as "blunt, bulbous, broadened, button-shaped, conical,

75   globular, fang, kidney-shaped, lanceolate, needle-like, procumbent, pseudocanine, robust,

76   short, slender, spike-like," and "thick" (e.g. Brazaitis, 1973; Groombridge, 1982; Aoki, 1989;

77   Brochu, 1999; Erickson, Lappin, & Vliet, 2003; Ősi, Clark, & Weishampel, 2007; Schwarz-Wings,

78   Rees, & Lindgren, 2009; Fruchard, 2012; Gignac & Erickson, 2014; Salas-Gismondi et al., 2015;

79   Berkovitz and Shellis, 2017). There is clearly a gap in our knowledge concerning the nature of

80   dental morphology in this clade, and closing this gap may be crucial for a more complete

81   understanding of performance, behavior, and trophic ecology within Crocodylia, as well as

82   more distantly related, crocodylian-line archosaurs.

83   The lack of quantitative studies on heterodonty in crocodylians and associated taxa is

84   not due to a lack of applicable methodology, as there has been a burst of morphometric

85   research in non-mammalian teeth in the past decade. Dinosaur teeth have probably received

86   the most attention, with multiple studies using linear-distance measures for the identification

87   of loose fossil crowns or to infer functional paleoecology (D'Amore, 2009; Larson & Currie,

88   2013; Buckley and Currie, 2014; Hendrickx and Mateus, 2014; Torices, Reichel, & Currie, 2014;

89   Hendrickx, Mateus, & Araújo, 2015b, Gerke and Wings, 2016; Larson, Brown, & Evans, 2016).

90   Extant reptiles have been investigated quantitatively as well, including colubrid snakes (Britt,

91   Clark, & Bennett, 2009) and varanid lizards (D'Amore, 2015). Prior to this, lamniform sharks

92   were studied heavily (Shimada, 2002b, 2004; Shimada and Seigel, 2005). These morphometric

93   analyses have shed light on the nature of heterodonty, dental allometry, and ecomorphology in

94   these vertebrates, and similar methods may be applied to Crocodyliformes in the hopes to

95   elaborate upon the state of heterodonty in this taxon.

96   The purpose of this study is to present a method for the quantification of both size- and

97   shape-heterodonty in members of Crocodyliformes. Data were collected from a multispecific

98   sample of both extant and extinct specimens housed in museum collections, and their tooth

99   morphology was assessed through two-dimensional geometric morphometrics. In addition to

100   this major goal, we also 1) outline and describe dental morphology within the specimens

101   sampled; 2) report any morphological consistencies found within the members of our sample;

102   and 3) present the advantages, limitations, and potential future uses of the method. Our

103   intention is to put forward a method for assessing heterodonty that may be applicable to most

104   crocodyliform specimens.

105   **MATERIALS AND METHODS**

106   **Institutional abbreviations**

107   American Museum of Natural History, New York, NY (AMNH); Royal Ontario Museum, Toronto,

108   ON (ROM); University of California Museum of Paleontology, Berkeley, CA (UCMP)

109   **Nomenclature**

110   Crocodyliform teeth have very few discrete homologous anatomical loci, but, because they

111   exhibit thecodont dentition (sensu Edmund, 1962, 1969), we defined them as having a crown

112   with an apex, a neck, and a root within an alveolus. Nomenclature for tooth morphology used

113   here was proposed by Smith & Dodson (2003; Figure 1A-B): mesial, towards the central

114   premaxilla and mandibular symphysis; distal, away from the central premaxilla and mandibular

115   symphysis; lingual, towards the tongue; labial, towards the lips; basal, towards the base of the

116   tooth or alveolus; apical, away from the alveolus or towards the apex. An 'enlarged' tooth is the

117   largest tooth in a given section of the jaw independent of shape. This type of tooth is typically

118   referred to as a procumbent tooth (Gignac & Erickson, 2014) or a pseudocanine (Brochu, 1999).

119   Tooth position was indicated by either the presence of a tooth or an empty alveolus in

120   the host bone (Figure 1A). Teeth were lettered based on the host bone (premaxilla = P, maxilla

121   = M, dentary = D), and numbered in ascending order from mesial to distal positions (the mesial-

122   most dentary tooth was D1, followed by D2, D3, etc.). For consistency, all specimens were

123   assumed to have 5 premaxillary positions (P1–P5) (Berkovitz & Shellis, 2017). Members of

124   *Paleosuchus* and *Osteolaemus* have only 4 premaxillary teeth during early stages of ontogeny

125   (Brochu and Storrs, 2012; Narvaez et al., 2015), and an alveolus may atrophy in certain species

126   (usually P2) as they grow (Webb & Messel, 1978; Brown et al., 2015; DC D'Amore, personal

127   observation). If only four premaxillary positions were present, position P2 was assumed absent,

128   and skipped over during numbering. In one case, a specimen had 6 premaxillary teeth

129   (*Alligator mississippiensis*, ROM 4408). This tooth position was omitted for consistency. Our

130   *Alligator prenasalis* specimen (ROM 1375) had its distal-most cranial positions obscured by poor

131   preservation and matrix. We therefore based its maxillary tooth count on previous osteological

132   accounts (a total of 15 maxillary teeth based on Harvard Museum of Comparative Zoology

133   specimen #1015, Mook, 1932).

134   **Specimens**

135   Data were collected from 27 extant, and 8 extinct, crocodyliform specimens (Supplemental

136   Information Table S1). This resulted in a total of 21 species. Although *Caiman crocodilus* is an

137   extant species, a fossil specimen was also included. From these we measured 1,263 teeth in

138   total. Although we did not use any distinct criteria to distinguish juveniles from adults, larger

139   specimens were selected when possible. Specimens with the most complete tooth rows in the

140   collections were selected, in that they had the most of their tooth positions represented by

141   measurable teeth on at least one side of the mouth. Certain fossil specimens only had cranial

142   (*Alligator prenasalis* ROM 1375, *Borealosuchus sternbergii* UCMP 126099, "*Crocodylus*" *affinis*

143   UCMP 131090, *Hamadasuchus rebouli* ROM 52620, *Leidyosuchus canadensis* ROM 1903) or

144   dentary (*Borealosuchus sternbergii* UCMP 131769) material to sample.

145   **Tooth data collection**

146   Methods were similar to those proposed by D'Amore (2015). We photographed each tooth

147   using either an Olympus Stylus or a Canon Rebel T3 EOS camera with a non-zoom lens. Skulls

148   were positioned on a flat surface with a dark background such as a tabletop or camera stand,

149   and held stationary by an available prop such as a box or sandbag if necessary. A scale was

150   positioned at the same distance from the camera as the tooth. The camera was either mounted

151   on a camera stand, or was held stationary by a researcher (for larger specimens). Digital

152   photographs were taken from the labial perspective (Figure 1B). For each tooth, we positioned

153   the specimen so the camera lens was parallel to the host bone adjacent to the tooth. This

154   resulted in both carinae being visible in the shot (if present). We simultaneously positioned the

155   lens parallel to the apical-basal long axis, determined qualitatively as when the tooth looked its

156   tallest to the photographer regardless of any labio-lingual curvature. Each tooth was

157   photographed separately, and teeth from both sides were photographed if available. Only fully

158   erupted teeth with the neck visible were included (Figure 1B). Tooth quality was variable in

159   extant specimens. Teeth with slightly worn apices were included. As the outline of the tooth

160   margin was our basis of measurement, we omitted any teeth with large wear facets or chips

161   that largely interrupted this margin. Cracks down the long axis of the teeth were common, and

162   were omitted if the crack distorted the shape of the tooth or resulted in a space where light

163   could be seen from the other side.

164   We used a sliding semilandmark analysis (Bookstein, 1997; Sheets, Kim, & Mitchell 2004;

165   Zelditch et al., 2004; Mitteroecker et al., 2013) to derive shape measurements from each

166   tooth's outline. Photographs were entered in TpsDig 2.16, and the margin of the tooth was

167   traced using the curve drawing tool (Rohlf, 2010) (Figure 1B). Because the enamel margin was

168   not always clear, each tooth was traced from apex to the point where the tooth ceased to taper

169   on the neck for both the mesial and distal side. TpsDig then transformed each of the two traced

170   margins into 30 equidistant coordinates, and we combined the apical-most coordinates. This

171   resulted in 3 discrete landmarks (two at the base and one at the apex) and 56 semilandmarks

172   (Figure 1C). This number of coordinates has been used in previous studies of both dinosaur

173   (Smith, Vann, & Dodson, 2005) and monitor lizard (D'Amore, 2015) dentition, as well as claw

174   morphology (Tinius and Russel, 2016), in which it has been shown to accurately represent the

175   totality of two-dimensional shape (Tinius and Russel, 2016). We performed a generalized least

176   squares Procrustes (GLSP) superimposition on the data, calculated centroid size (CS), and slid

177   the semilandmarks to minimize the total bending energy (Perez, Bernal, & Gonzalez, 2006;

178   Gunz & Mitteroecker, 2013) using the program TpsRelw 1.53 (Rohlf, 2013).

179   **Skull data collection**

180   The shape of the skull, and particularly the rostrum, has long been considered both an

181   important phylogenetic and ecomorphological feature in crocodylians (Busbey, 1995; Daniel &

182   McHenry, 2001; Brochu, 2001; Sadleir & Makovicky, 2008; Salas-Gismondi et al., 2016;

183   Drumheller, Wilberg, & Sadlier, 2016; Wilberg, 2017). We attempted to determine if there was

184   a correlation between tooth morphology and head shape, as these traits may be linked. All

185   specimens' skulls were photographed from the dorsal perspective using the same cameras as

186   above (Figure 1E). Each skull was positioned so the palate was parallel with the tabletop, and

187   the camera was positioned with a camera stand and leveled. A scale was included. We derived

188   skull shape data using a modified version of our technique for tooth outlines. Using TpsDig

189   again, we traced the skull margin from the rostral-most point of contact between the

190   premaxillae to the caudal-most quadratojugal along the margin on each side. We chose this

191   margin because it outlined head-shape as close to as it would have appeared in life as possible,

192   but avoided internal structures such as the jaw articulations or occipital condyles. Each margin

193   was broken into 50 equidistant coordinates, and the rostral-most coordinates were combined.

194   This resulted in 3 landmarks (two at the quadratojugals and one at the premaxillary junction)

195   and 97 semilandmarks (Figure 1E). These also underwent a GLSP superimposition and the

196   semilandmarks were slid to minimize the total bending energy using TpsRelw 1.53. In

197   specimens with damaged or missing bones on one side, bilateral symmetry was assumed and

198   the coordinates on the intact side were mirrored.

199   A body-size metric was needed for several of the following analyses, but unfortunately

200   few were available for all specimens. Commonly used metrics such as snout-vent length and

201   mass were not recorded for most dry skeletons prior to cataloging, and many specimens

202   (especially fossils) lacked femora (see Farlow et al., 2005). Therefore, the length of the skull was

203   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, &

225   Fink, 2003; Sheets & Zelditch, 2013). Disparity (*MD*) was the sum of the differences of the

226   values of a given tooth (*i*) from the mean for all teeth from that specimen (*Di*, also known as the

227   grand mean) squared, with the number of tooth positions (*m*) factored in. We calculated

228   disparity for all tooth positions for each specimen. For size-heterodonty, *Di* was simply the

229   difference in CS of a tooth from the mean of the specimen (Zelditch et al., 2004). For shape-

230   heterodonty *Di* was the Procrustes distance between the tooth and the mean, and was

231   calculated using DisparityBox7 (Sheets, 2012). Heterodonty then was regressed with a reduced

232   major axis against head length to determine if there was a significant allometric change in the

233   clade.

234   We attempted to correlate skull shape to tooth shape between individuals by using a

235   two-block partial least squares (PLS) analysis in MorphoJ. Skull shape represented one block,

236   and average tooth shape represented the other. Average tooth shape was constructed by

237   averaging the corresponding GLSP superimposed landmarks and semilandmarks of every tooth

238   from an individual. The scores for the first PLS of each shape block were plotted against one

239   another and regressed with a reduced major axis. Visualization of variation along each PLS axis

240   was depicted through vector diagrams (Figure 1F).

241   To determine if size and shape were coupled in Crocodyliformes, shape coefficients

242   generated by MorphoJ were regressed against CS using a reduced major axes. Significance and

243   a high goodness of fit would be indicative of strong coupling between size and shape. A

244   Principal Components Analysis (PCA) was then conducted to visualize the degree of shape

245   variance within all cranial and dentary teeth. We only considered any PC representing over 5%

246   of the shape variance, which we then visualized using vector diagrams (Figure 1D).

247   We plotted shape and size against tooth position to visualize heterodonty along the

248   tooth row. For size CS was normalized by dividing it by head length, and then was plotted

249   against tooth position in a series of box plots. For shape, PC scores of PCs over 5% were plotted

250   against tooth position in a similar fashion. Each box represented a position. Note that we did

251   not do any adjustments to these positions, so specimens with more tooth positions will be the

252   only occupants of the distal-most categories. To determine if significant differences in these

253   size and shape metrics existed between these positions, we used separate analyses of variance

254   (ANOVA) for each superfamily. Both metrics had unequal variances according to Levene's test,

255   so we specifically ran Welch's ANOVAs in SPSS. Any positions represented by less than 7 teeth

256   were excluded from the ANOVAs.

257   Preliminary quantitative work has suggested a linear transition in tooth shape along the

258   arcade (Farrugia, Polly, & Njau, 2016). We test this by regressing shape data against tooth

259   position using ordinary least squares regressions for each individual. To standardize these

260   regressions, we normalized tooth position into a percentage. We numbered the positions along

261   the tooth row starting with 1 at the mesial-most position, divided each by the total number of

262   positions along the arcade, and then subtracted 0.5 (this subtraction placed the y-intercept

263   halfway along the arcade). PCs for each tooth were then regressed against this, and regression

264   statistics were collected. Several factors may be implied by a significantly linear crocodyliform

265   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

350   along the dentary tooth row, and vice versa. This resulted in an 'interlocking' pattern between

351   the size peaks of one arcade and the valleys of the other. The gavialoid specimen differed

352   markedly by having the two mesial-most teeth enlarged, and the remainder showed a gradual

353   decease in size distally (Figure 5C). *Hamadasuchus rebouli* had some of the largest teeth for its

354   head length with a dramatic variation in size.

355   Alligatoroids and crocodyloids both showed a similar trend concerning tooth shape.

356   Mesial teeth are typically the most caniniform in the mouth and distal teeth the most

357   molariform, resulting in positions being significantly different (Figure 5D-E). In cranial teeth P1-

358   M4 tend to exist primarily between PC scores and -0.25 and 0.00, followed by a gradual

359   increase in score values as positions become more distal. Dentary teeth represented a more

360   uniformly gradual caniniform-to-molariform transition. Both superfamilies were highly variable.

361   Alligatoroid had teeth generally more molariform, with upper outliers almost entirely

362   represented by *Alligator prenasalis*, *Alligator sinensis*, and *Brachychampsa* sp. (Figure 5D).

363   Crocodyloids were generally more caniniform, with mesial upper outliers represented by

364   "*Crocodylus*" *affinis* and lower outliers represented primarily by *Tomistoma* (Figure 5E). Both

365   *Borealosuchus* tooth rows had PC1 scores between -0.22 and 0.20, and *Hamadasuchus* ranged

366   between -0.19 and 0.23 (Figure 5F). Both taxa showed a similar progression from caniniformy

367   to molariformy as the alligatoroids and crocodyloids. *Gavialis* deviated from the others the

368   most, where most teeth had scores of < -0.20 with a steep increase towards the average in the

369   distal-most fifth of the arcade (Figure 5F).

370  Shape heterodonty was found to be strongly linear. When each modern individual's PC1

371 values were regressed against position, all regressions were significant (Supplemental

372 Information Table S3). The vast majority of tooth row regressions had r^2 values above 80%.

373 *Gavialis* had the lowest r^2 values (cranium=0.495, mandible=0.616), followed by the crania of

374 the fossil *Caiman crocodilus* (r^2=0.728) and *Tomistoma* (r^2=0.747). Both cranial and dentary

375 tooth rows typically had slopes between 0.25-0.55 (Figure 6). More shape heterodont taxa

376 typically had greater slopes, with *Crocodylus siamensis* specimens having some of the steepest

377 slopes (0.39-0.68). All the slender-snouted specimens had the *y*-intercepts between -0.25 and -

378 0.14, indicating strong caniniformy at the median position. The *Gavialis* specimen also had very

379 shallow slopes (<0.25). Living members of *Alligator* had *y*-intercepts between 0.029 and 0.085,

380 indicating molariformy at the median (Figure 6). *Alligator prenasalis, Brachychampsa* sp., and

381 *"Crocodilus" affinis* had the shallowest slopes (0.22-0.32) and the greatest *y*-intercepts (0.15-

382 0.24) in our sample, indicating molariform teeth consistent along the tooth row. *Hamadasuchus*

383 *rebouli*'s regression characteristics are similar to members of *Caiman* and *Osteolaemus*. The

384 slope of the fossil *Caiman crocodilus* differed from modern members of *Caiman* by being much

385 shallower (Figure 6).

386 **DISCUSSION**

387 **Defining heterodonty within Crocodyliformes**

388 The methods proposed here offer a multi-faceted approach to quantifying heterodonty in

389 Crocodyliformes. Foote's morphological disparity allows for a discrete measure of heterodonty

390 that may be used for comparison, or normalized with other variables (as was done here with a

391   body size metric). This is not limited to Crocodyliformes, and may be used to compare distantly

392   related taxa and/or a wide variety of dental morphotypes. This measure is ideal if one is

393   interested in *how much* heterodonty is apparent. Alternatively, if one is interested in what

394   characteristics make up tooth heterodonty, more traditional geometric morphometrics suffice

395   in describing shape variability. It is opportune that only PC1 accounted for over 90% of the

396   variance, allowing for us to use it as the sole measure of shape here. If more PCs accounted for

397   over 5% of the shape variance, it would be appropriate to depict those other PCs in the same

398   manner as PC1 for a comprehensive understanding of shape.

399   Regression analysis of shape is appropriate based on significance and high r^2 values, and

400   the coefficients associated with it are useful characters for comparison. Certain caveats should

401   be considered though. Regression may be more appropriate for the dentary than the cranium,

402   as the premaxillary teeth do not appear to differ from one another as much as the maxillary. In

403   most crocodylians this effect is mild, and r^2 values are still high. The effect is very pronounced in

404   *Gavialis* though, as both the premaxillary and the mesial maxillary teeth are similar in shape. It

405   is also interesting that this happens in the dentary as well. Future studies should consider this

406   when applying this method to Gavialoidea or dentally analogous taxa.

407   Although the task of assigning a singular dental morphotype to any one species of

408   crocodyliform is beyond the scope of the study, our data suggests that it would be potentially

409   difficult. Heterodonty seems to vary within species, making the assignment of a singular

410   heterodonty measure to an entire species dubious. As far as biological explanations for this,

411   tooth form is almost certainly influenced by allometry. Ontogenetic shifts in feeding niche have

412 been documented in modern crocodylian species (e.g. Groombridge, 1982; Webb, Manolis, &

413 Buckworth, 1982; Pooley & Gans, 1976; Pooley, 1989; Delany, 1990; Santos et al., 1996; Da

414 Silveira and Magnusson, 1999; Subalusky, A. L., Fitzgerald, L. A., & Smith, 2009 Wallace and

415 Leslie, 2008; Borteiro et al., 2009; Hanson et al., 2014), and allometric changes in the feeding

416 apparatus with size are often explained as a structural consequence of this (e.g. Dodson, 1975;

417 Webb and Messel, 1978; Hutton, 1987; Erickson, Lappin, & Vliet, 2003; Verdade, 2000; Wu et

418 al., 2006; Watanabe & Slice, 2014; Gignac and Erickson, 2016; Gignac & O'Brien, 2016).

419 Concerning teeth, a qualitative increase in overall molariformy was observed in *Alligator*

420 *mississippiensis*, and functioned to meet the mechanical demands of increased durophagy

421 (Erickson, Lappin, & Vliet, 2003; Gignac & Erickson, 2014). Although our sample size is too low

422 to confidently assess dental ontogeny within each species, we did see a similar general trend in

423 conspecifics of different sizes. In particular, the larger of our two *Crocodylus porosus* had a

424 greater *y*-intercepts indicating greater molariformy. In addition to allometry, phenotypic

425 changes due to environmental factors may also influence teeth. Skull shape and tooth

426 orientation are irregularly influenced by captive rearing (Erickson et al., 2004; Drumheller,

427 Wilberg, & Sadleir, 2016), and how this may also influence tooth shape has yet to be

428 determined. Many of our specimens had 'no data' concerning their rearing, so we do not know

429 if captivity influenced either tooth or skull morphology.

430 **Morphological trends within Crocodyliformes**

431 All crocodyliform specimens measured here were heterodont to varying degrees, and these

432 data showed significant variability of morphotypes along the dental arcade for all specimens

433   (Figure 7). Although dentition varied between species, certain consistencies were seen

434   throughout the clade:

435   1. Similar teeth occurred on both the cranial and dentary dental arcades.

436   2. As body size increased, size-heterodonty increased reliably with it. Shape-heterodonty

437   shows a much less reliable negative correlation with body size.

438   3. The vast majority of shape variance from the labial perspective occurred along a single

439   shape axis, representing the transition from caniniform to molariform. Only minor distal

440   curvature was apparent in very caniniform crowns.

441   4. There was serial homology in tooth shape from-mesial-to-distal along the tooth row,

442   and molariformy increased in this direction. The transition was significantly linear for

443   both dental arcades for all specimens.

444   5. Size variability consisted of an undulating pattern with three peaks that interlock with

445   the opposing row, with enlarged crowns interspersed within smaller crowns. This

446   corresponded with the festooning pattern seen in the tooth bearing bones, and was less

447   apparent in slender-snouted taxa.

448   Shape- and size-heterodonty were very loosely coupled in Crocodyliformes as they changed in

449   dramatically different, and primarily independent, fashions along the arcade. Some correlation

450   did occur; the regression's significance was probably the result of the fact that the distal-most

451   crowns were typically both the smallest crowns as well as the most molariform. Nevertheless,

452   the undulating pattern of tooth size did not align with linear shape heterodonty for the vast

453   majority of the tooth row, as indicated by the very low r^2.

454  The low degree of coupling begs the question; do developmental agents influence size

455 and shape separately? Although quite a bit of research has looked at how crocodylian teeth

456 grow and replace themselves (Edmund, 1962; Westergaard and Ferguson, 1986, 1987, 1990;

457 LeBlanc et al., 2017), surprisingly little has been done on what developmental influences affect

458 tooth size and shape. Modern crocodylians replace their teeth in waves, or Zahnreihe (Edmund,

459 1962; Westergaard and Ferguson, 1990; Osborn, 1998), but it is unclear how the nature of

460 these waves relate to the morphological variables investigated here. Keiser et al., (1993)

461 compartmentalized the dentition along the tooth row for *Crocodylus niloticus*, grouping teeth

462 into 'incisor,' 'premolar,' and 'molar' regions. These designations attempted to account for both

463 size and shape heterodonty; each was defined by an enlarged tooth, and each become

464 progressively more molariform. They did not offer a developmental mechanism that

465 differentiates these categories though. Fruchard (2012, p.7) suggested that the only difference

466 between enlarged teeth and their smaller counterparts was that the former was "programmed

467 to be bigger," suggesting some sort of additional developmental signaling to enlarge teeth.

468 More research is needed on how tooth shape and size are established developmentally in order

469 to truly understand what generates heterodonty.

470 **Adaptive explanations for morphological variability in modern taxa**

471 There is a wide range of tooth morphologies present in modern Crocodylia, and, as teeth are

472 anatomical units used for feeding and aggression, functional inferences may be drawn based on

473 our present understanding of behavior and performance. Bite force in crocodylians is primarily

474 influenced by size (Erickson et al., 2012, 2014), and our data set shows that similarly sized

475   crocodylians may have very different tooth dimensions. This rules out maximum bite force as

476   the sole limiting factor dictating tooth form. Although we are reluctant to associate specific

477   prey items with specific tooth forms, size and shape will influence how a tooth interacts with

478   food items possessing certain physical properties. We therefore suggest that a biomechanical

479   link should exist between the structural limits imposed by tooth form and the material

480   properties of the substrates with which it interacts.

481   As with all jawed vertebrates, crocodylian teeth will succumb to different speeds and

482   stresses based on their respective position along the arcade. Caniniform mesial teeth are ideal

483   for the initial acquisition of prey. Pointed apices reduce surface area to puncture compliant

484   foods that deform under pressure, such as muscle, fat, and fibrous connective tissue (Frazetta,

485   1988). Being farther from the hinge, these teeth move faster during a strike and are more likely

486   to contact prey trying to escape (Busbey, 1989). They will also will endure less force based on

487   their position, and can afford to be relatively elongate and gracile. On the other end, distal

488   teeth need to withstand greater forces due to their close proximity to the hinge (Cleuren, Aerts,

489   & Vree, 1995; Erickson, Lappin, & Vliet, 2003; McHenry et al., 2006; Erickson et al., 2012). This

490   explains why these teeth are typically on the molariform half of the shape spectrum; the larger

491   base-to-height ratio gives them greater relative bending strengths (Van Valkenburgh and Ruff,

492   1987; Gignac & Erickson, 2014; Monfroy, 2017). Because force is highest in this region, it is ideal

493   for processing food items after they are acquired (Busbey, 1989; Davenport et al., 1990;

494   Cleurens and de Vree, 2000). The reduced height of these teeth also ensures they do not

495   impede jaw closure. This necessity is very apparent in our representative member of *Gavialis*,

496   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

541   diet (Santos et al., 1996). The *Crocodylus porosus* specimens had the largest M5 crowns in our

542   sample, which may also show a prioritization for puncturing and securing soft-bodied prey in a

543   larger context (Figure 7B). This species is notorious for actively hunting large vertebrates such

544   as sharks, cattle, horses, and humans (e.g. Taylor, 1979; Kar & Bustard, 1981; Groombridge,

545   1982; Doody, 2009; Hanson et al., 2015), and these teeth are ideal for puncturing and securing

546   such prey. Similar to caimanines, this species atrophies position P2 to make room for its

547   enlarged D1 crowns (Brown at al., 2015)

548   The slender-snouted species possessed generally more caniniform teeth, which may be

549   a consequence of feeding habitat and prey preference. These taxa have a reputation for eating

550   small, aquatic prey with a focus on fish (Peyer, 1968; Webb, Manolis, & Buckworth, 1982), and

551   multiple lines of evidence suggest the feeding apparatus is well suited for this function. The

552   slender shape reduces resistance during both lateral motion and jaw adduction when feeding

553   underwater, and the increased snout length allows for a faster strike (Taylor, 1987; Pooley,

554   1989; Thorbjarnarson, 1990; McHenry et al., 2006; Pierce et al., 2008). Highly caniniform teeth

555   can quickly puncture fast-moving, compliant prey, and their elongate shape may also lower

556   their mechanical resistance (Figure 7C). The longirostrine condition, defined as a snout that is

557   both slender and elongate (Brochu, 2001), resulted in increased tooth positions; *Tomistoma*

558   had more teeth than any other crocodyloid, and *Gavialis* has the most teeth out of all

559   crocodylians sampled. This cranio-dental morphotype may be prey-size prohibitive though, as

560   larger prey could damage the slender rostrum while struggling. Their elongate mandibular

561   symphysis results in a mechanical disadvantage against the forces produced by shaking and

562   twisting prey (Walmsley et al., 2013). The gracile nature of the dentition means a lower bending

563 strength, making them more susceptible to breakage from larger and/or harder prey as well. On

564 rare occasions, large individuals have been known to take land-based, vertebrate prey

565 (Thorbjarnarson, 1990; Selvaraj, 2012). This is most likely because the overwhelming size of

566 these crocodylians allows their feeding apparatus to withstand the forces exerted by said prey.

567   The slender-snouted taxa had some of the lowest size- and shape-heterodonty of

568 modern crocodylians, which is reminiscent of several other clades of aquatic predators. They

569 share certain traits with the anisodont plesiosauromorphs (Sassoon et al., 2015; Kear et al.,

570 2017). Although these crocodylians are not anisodont in the strict sense (they all have some

571 shape heterodonty), both taxa have elongate mesial crowns transitioning to smaller distal ones.

572 These taxa also reflect similarities with the 'homodont' condition apparent in odontocete

573 whales (Rommel, 1990), where all the teeth in the arcade possess a similar, peg-like shape. This

574 condition is believed to be ideal for catching and holding, but not processing, small aquatic prey

575 (MacLeod et al., 2007), as most prey items consumed are under 10% of their body length

576 (MacLeod et al., 2006). A convergent reduction in size- and shape-heterodonty within these

577 independently aquatic groups may indicate a transition from a multi-functional dental arcade to

578 one almost exclusively for prey capture. This is clearly the condition in members of *Gavialis,* as

579 it is almost entirely caniniform along its tooth row and eats primarily fish (Groombridge, 1982,

580 Figure 7C). Members of *Mecistops* and *Tomistoma*, although also primarily caniniform, still

581 displayed the linear shape change typical of other crocodyloids. These species may consume

582 prey that require relatively more processing with their distal crowns, and there are numerous

583 reports of them eating prey such as crustaceans, turtles, and immature primates (Brazaitis,

584 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).

628   Several authors have stated that modern taxa do not have, or have secondarily lost, an

629   extreme degree of molariformy commonly found in extinct representatives. 'Globidonty'

630   describes the enlarged, highly molariform crowns in fossil taxa potentially used for durophagy

631   (Norell, Clark, & Hutchison, 1994; Brochu, 1999; 2001; Ősi & Barrett, 2011). Species of

632   *Brachychampsa* are textbook examples of a globidont taxon (Case, 1925; Carpenter and

633   Lindsey, 1980, Figure 7F), and our specimen is the only one in the sample with distal teeth so

634   molariform their PC1 scores exceed 0.349. Although we agree with Brochu (2001, 2004) that

635   *Osteolaemus tetraspis* is not as extreme, the PC1 scores of its enlarged distal teeth are closer to

636   our *Brachychampsa* than another other taxon sampled (0.322-0.341). *Alligator prenasalis* and

637   *"Crocodylus" affinis* distal crowns are similar to *Alligator sinensis* in shape, and also create a

638   ridge of robust teeth (Mook, 1932). The mechanical capabilities of these particular crowns in

639   modern taxa should be similar to the extinct, which suggests similar processing abilities in the

640   distal regions of the skull. The similarities break down when the rest of the jaw is considered

641   though. In addition to these highly molariform teeth, modern taxa also possess caniniform

642   mesial teeth suggesting a division of labor along the tooth row. Contrarily, almost all teeth of

643   members of *Alligator prenasalis, Brachychampsa* sp.*,* and *"Crocodylus" affinis* are on the

644   molariform half of the shape-spectrum (Figure 7F), making both their size- and shape-

645   heterodonty rather low. These extinct taxa probably did not need to do as much puncturing of

646   compliant substrate, which supports the argument that they may have foraged for mollusks and

647   slow moving turtles (Carpenter and Lindsey, 1980; similar to Salas-Gismondi et al., 2015) rather

648   than being ambush predators.

649   **Limitations and future work**

650   Foote's morphological disparity is a reliable method for assessing heterodonty if the tooth row

651   is near complete, but some of the variability in heterodonty seen here is the result of

652   incompleteness. This measure of disparity relies on, among other things, the grand mean and

653   the sample size. Size heterodonty may be underrepresented if, for example, an enlarged tooth

654   is missing. This tooth would deviate greatly from the grand mean if present, so its exclusion

655   would deflate size heterodonty. As shape is linear in Crocodyliformes, missing the mesial- or

656   distal-most teeth would deflate size heterodonty. This was apparent in the fossil *Caiman*

657   *crocodilus*; even though it shared almost identical tooth morphology with modern congenerics

658   when positions were compared, its shape heterodonty was much lower because the distal 30%

659   of its teeth were missing. This also affected the shape regression, as the fossil specimen's

660   cranium slope was much shallower than the modern members of *Caiman*.

661   We did not consider all three dimensions here. Living crocodylian teeth are often

662   discussed as conical (Edmund, 1969) or conidont (Hendrickx, Mateus, & Araújo, 2015b). Studies

663   of bending strengths show variation between mesial-distal and labial-lingual axes (Monfrey,

664   2017), indicating that functional information may be drawn from the dimension not measured

665   here. This is especially important concerning fossil taxa, as pronounced lateral compression is

666   commonplace. *Hamadasuchus* distal teeth have been referred to as ziphodont (Larsson & Sidor,

667   1999), but, as this is defined by lateral flattening, our method did not register this character.

668   Future studies should consider this third dimension at least qualitatively, in order to avoid

669   conflating disparate tooth morphotypes such as these.

670   Principal component scores as shape measurements are very much dependent on the

671   nature of the sample. Although they are very revealing concerning shape variability, they are

672   not transferable between different data sets. A potential method for creating transferable

673   shape metrics is using our PC1 axis as a guide to derive linear distance measures that would

674   account for the serial shape homology seen in Crocodyliformes. Since PC1 essentially

675   represents molariformy vs. caniniformy from the labial perspective, it could possibly be

676   simplified into a comparison of linear distance measures such as maximum mesial-distal widths

677   and apical-basal heights. These metrics would be not only easy to collect, but also transferable

678   between data sets.

679   These limitations aside, future researchers may apply our proposed method to any

680   crocodyliform specimen with an intact enough tooth row. We limit our evaluation of

681   interspecific differences, and make no attempt to analyze other factors such as ontogenetic

682   changes or the effect of captive rearing (Erickson, Lappin, & Vliet, 2003; Erickson et al., 2004;

683   Gignac & Erickson, 2014; Drumheller, Wilberg, & Sadleir, 2016). All of these variables may be

684   investigated in the future using our method, as there is nothing to suggest that crocodyliform

685   individuals of most species, ages, and/or rearing conditions would not be able to be quantified

686   in a similar manner. This method could be very useful in dealing with incomplete fossils. It is

687   common for fossil crocodylian specimens to be lacking many, or even most, of their teeth. The

688   linear nature of tooth shape can predict the shape of these missing teeth. A record of the

689   ranges of slopes may be accumulated for fossil specimens with intact teeth. These slopes may

690   then be used as a reference, and be applied to a fossil with the missing teeth. The preserved

691   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**

713   Multiple measures of morphology have allowed us to describe heterodonty in a

714   thorough manner across a number of both extinct and extant crocodyliform specimens.

715   Through a combination of Foote's morphological disparity and regression analysis along the

716   tooth row, our data indicated that crocodylians are indeed heterodont non-mammals with a

717   number of dental morphotypes available spanning from extreme cases of caniniform to

718   molariform. This variability may be functional in nature, and relate to the size, frequency, and

719   compliance of certain prey in their typically generalist diets. The methods used here should be

720   applied in the future to most crocodylian specimens to investigate dental morphology in the

721   context of a number of natural history related questions.

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1085 **FIGURE LEGENDS**

1086 **Figure 1: Data collection methods.** A) We numbered teeth based on position and host bone

1087 (only the left teeth are labeled). Teeth P4, M5, and M10 are defined as the enlarged teeth. B)

1088 We photographed each tooth individually, and traced the margins. C) The software converted

1089 each outline into 30 equidistant coordinates. Three coordinates were transformed into

1090 landmarks (magneta) and the rest into semilandmarks (green). D) We represented tooth shape

1091 variance through vector diagrams, with points representing the mean and vectors representing

1092 shape deviation. E) For skulls, we produced an outline from the dorsal perspective, with 50

1093 coordinates on each margin that were transformed into landmarks (magenta) and

1094 semilandmarks (green). F) We represented shape variance with vector diagrams similar to

1095 above. (Specimen depicted: *Crocodylus palustris* AMNH 96134.) [Half page width]

1096 **Figure 2: Variability within the first Principal Component for teeth.** Vector diagrams indicate

1097 the maximum range of variance (vectors) from the mean (points) for both cranial and dentary

1098 teeth. Landmarks are in magenta and semilandmarks are in green. [Half page width]

1099 **Figure 3: Partial Least Squared (PLS) two-block analysis of shape**. A) Vector diagrams indicate

1100 shape variance of PLS1 for skull shape (Block 1) and average tooth shape (Block 2). B) PLS1

1101 scores for both Blocks were regressed, with colors representing major taxonomic groups. Solid

1102 markers depict extant specimens, and hollow markers depict extinct. [Full page width]

1103 **Figure 4: Heterodonty represented by Foote's morphological disparity.** Ln scaling of

1104 Morphological Disparity (MD) for size (A) and shape (B) are plotted against the ln of skull length.

1105   Colors represent major taxonomic groups, solid markers depict extant specimens, and hollow

1106   markers depict extinct.   [Half page width]

1107   **Figure 5: Heterodonty by tooth position.** Centroid Size (CS) and Principal Component one (PC1)

1108   for extant Alligatoroidea, Crocodyloidea, and remaining taxa, plotted against position along the

1109   arcade. Welch's ANOVA output comparing positions is listed for each graph with multiple

1110   specimens. Colors represent major taxonomic groups. See Figure 2 for a visual representation

1111   of shape change depicted by PC1 scores. [Full page width]

1112   **Figure 6: Regression information for shape heterodonty.** Slope (*m*) and y-intercept (*b*) data for

1113   regressions of the first Principal Component plotted against tooth position for individuals. Error

1114   bars indicate 95% confidence intervals. Colors represent major taxonomic groups, with solid

1115   markers depicting extant specimens and hollow markers depicting extinct. Regression statistics

1116   are available in Table S3. [Full page width]

1117   **Figure 7: Direct comparisons between selected extant and extinct taxa**. The size axis

1118   represents normalized centroid size (ranging from 0.00-0.20), and the shape axis represents

1119   scores from the first principal component (ranging from -0.04-0.04). Taxa are grouped by A)

1120   specimens with high molariform distal teeth, B) modern taxa that display high size heterodonty,

1121   C) slender-snouted taxa, D) *Hamadasuchus rebouli*, E) *Borealosuchus sternbergii* and

1122   *Leidyosuchus canadensis*, and F) fossil globidont taxa. (Note: *B. sternbergii* teeth were not size

1123   normalized by its own skull length, as indicated by hollow bars.) Scale = 5 cm. [Full page width]

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 (magenta) 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.)
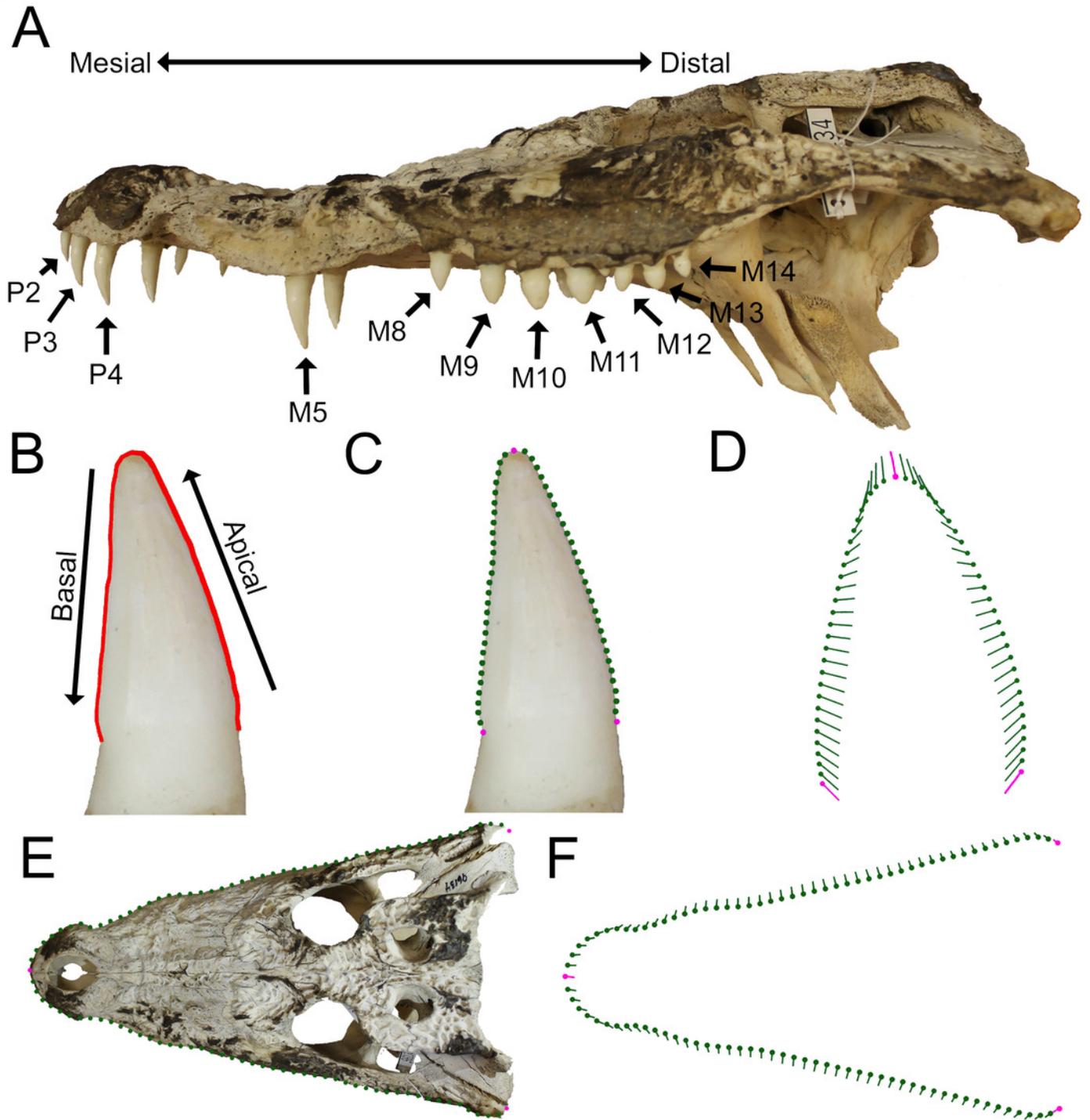
Figure 2

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.

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.
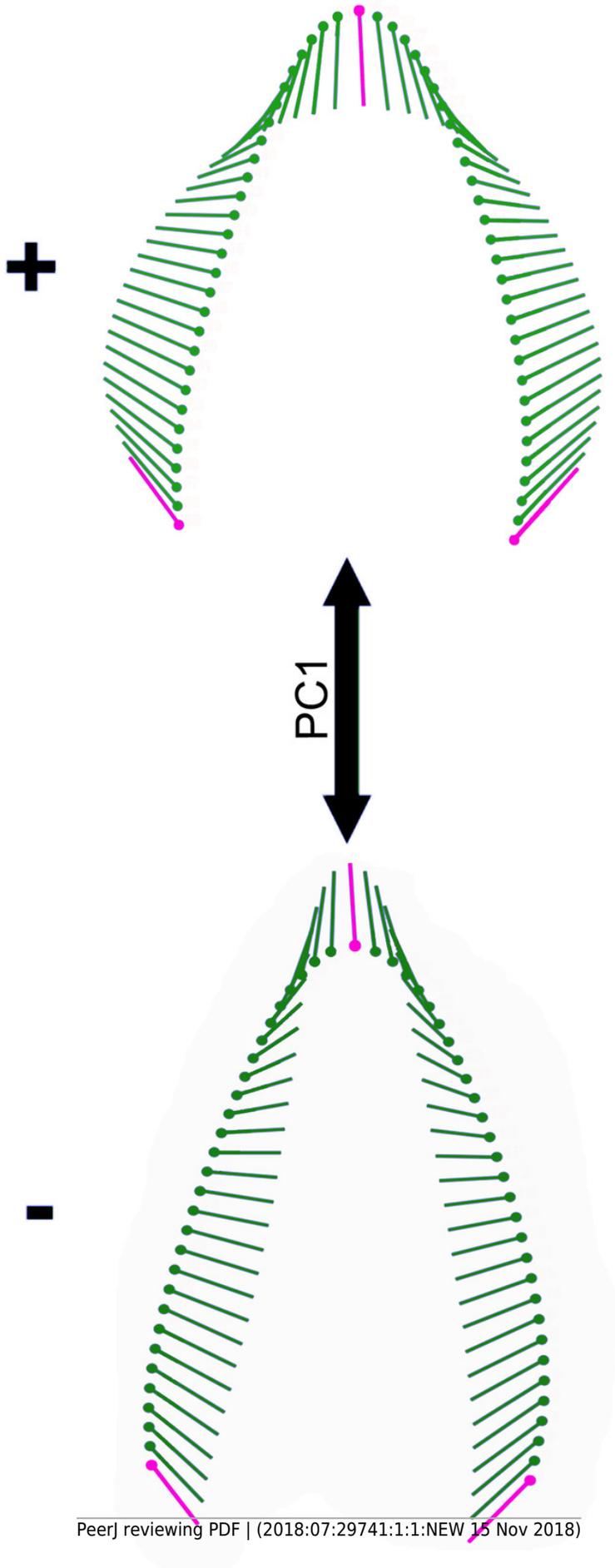
Figure 4

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*

y=2.196x-8.549
R^2=0.760
P<0.0001
95%=1.917,2.500

B

y=-0.715x+0.172
R^2=0.1566
P=0.0223
95%=-0.907,-0.460

ln[MD(size)]

ln[MD(shape)]

ln(Head Length)
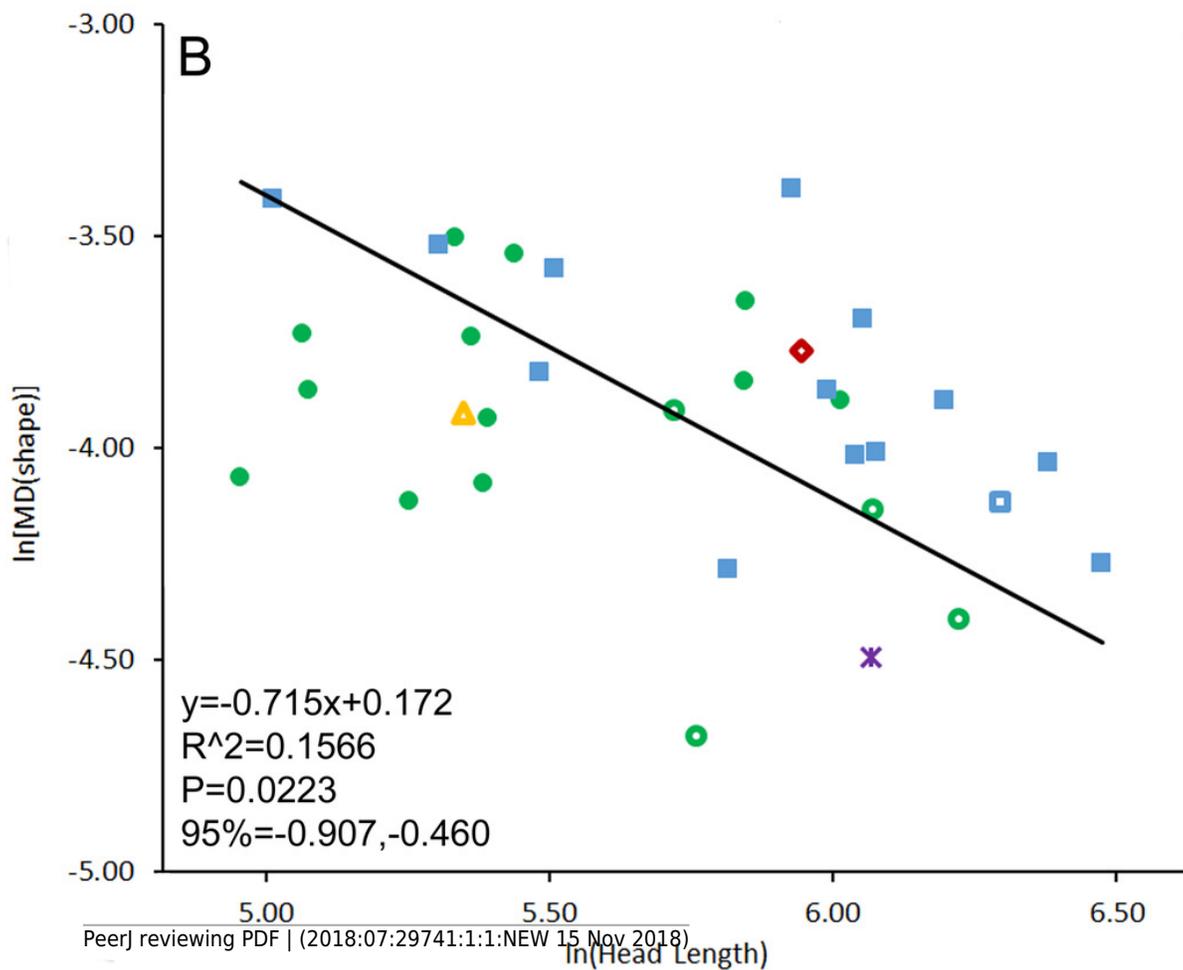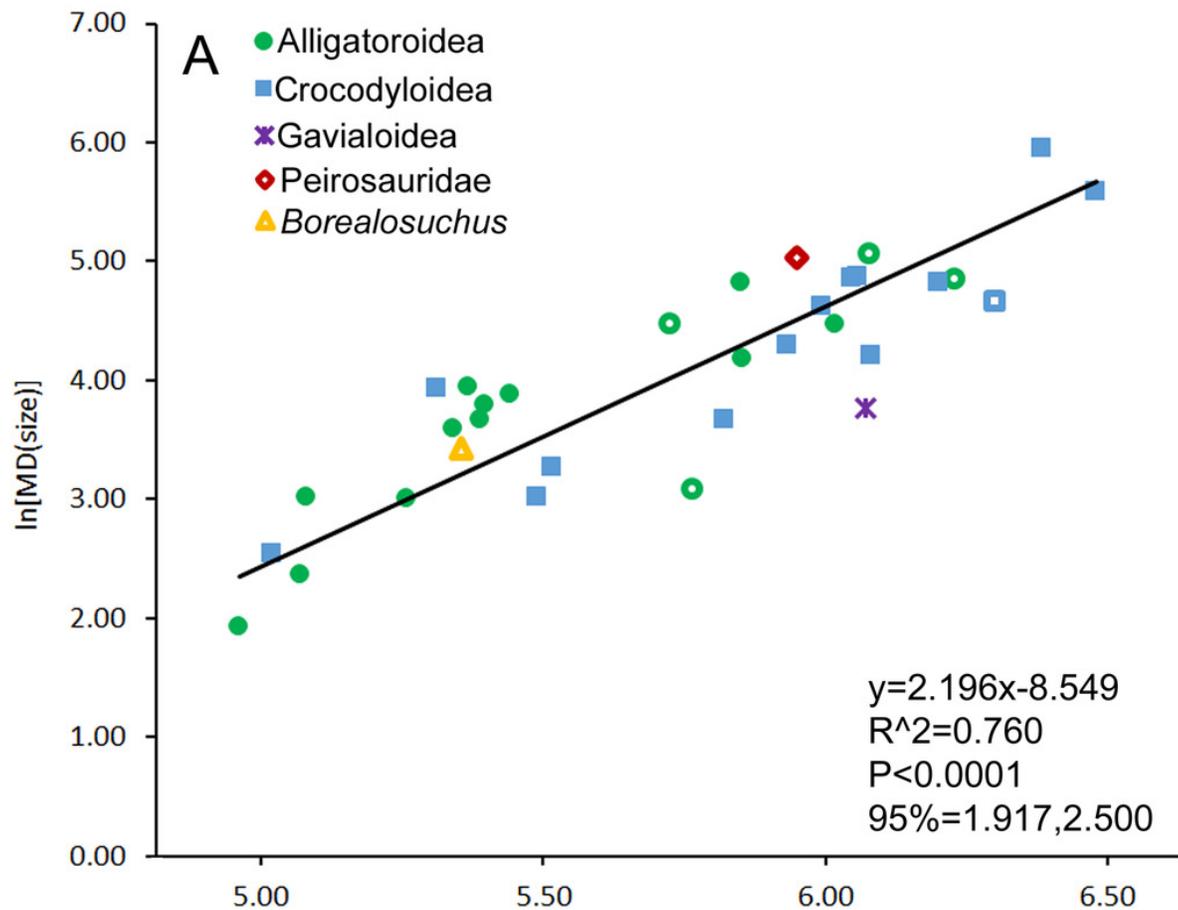
Figure 5

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.
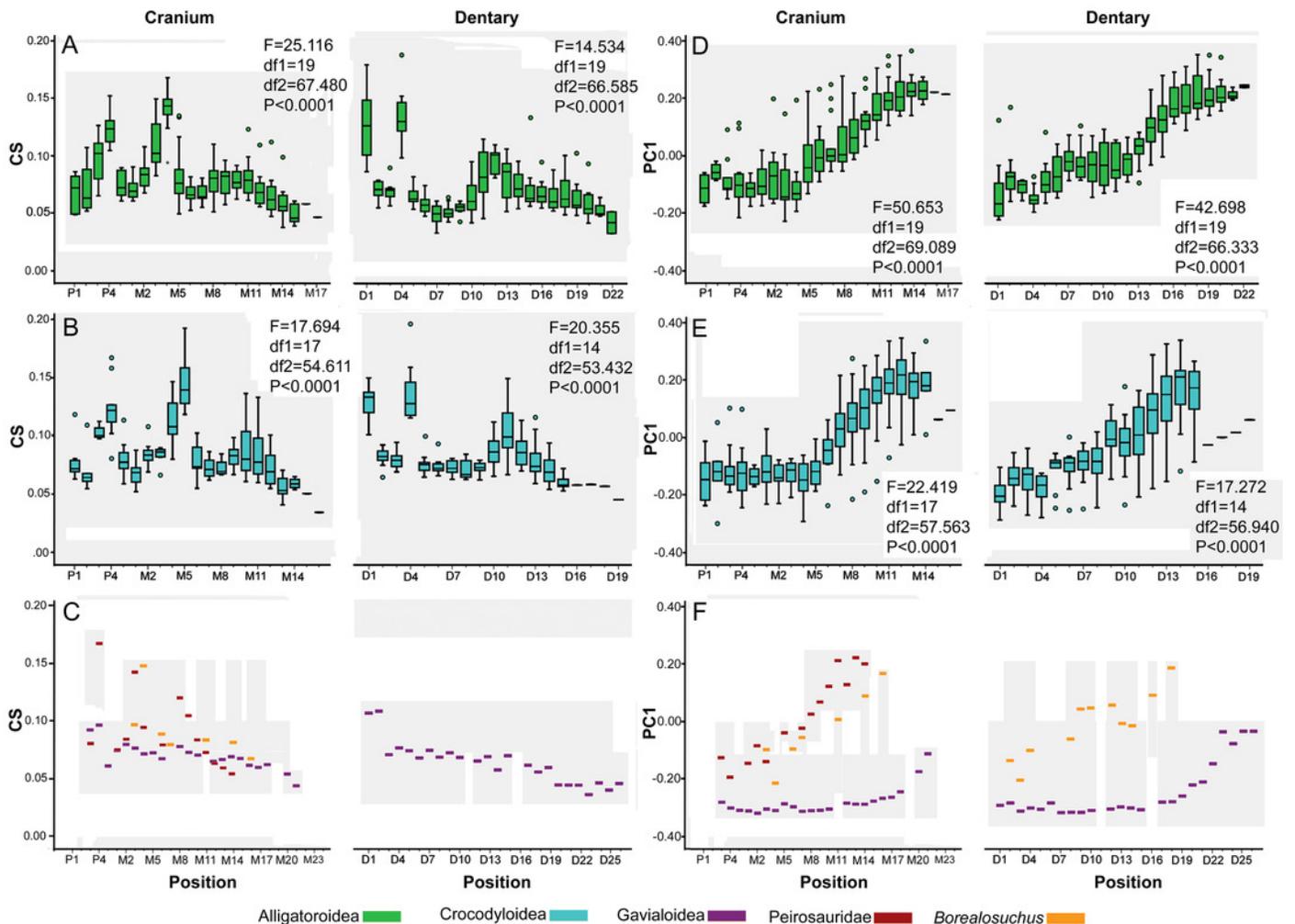
Figure 6

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.
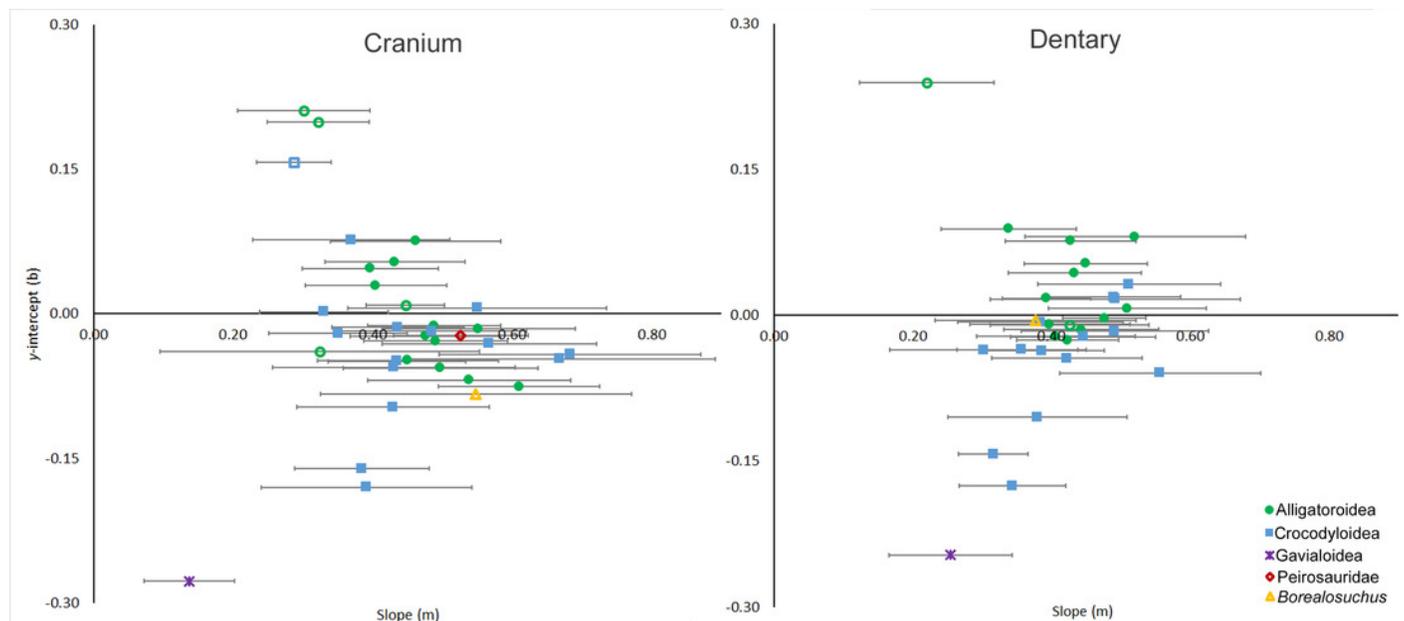
Figure 7

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.