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

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Heterodonty in Crocodylia and closely related 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 Crocodylia. Data were collected from dry skeletal and fossil specimens of 34 crown crocodylians and one crocodyliform, resulting in 21 species total. Digital photographs were taken of each tooth and the skull, and the margins of both were converted into landmarks and semilandmarks. We expressed heterodonty through Foote's morphological disparity, and a principal components analysis quantified shape variance. All specimens sampled were heterodont to varying degrees, with the majority of the shape variance represented by a 'caniniform' to 'molariform' transition. Heterodonty varied significantly between positions; size undulated whereas shape was significantly linear from mesial to distal. Size and shape appeared to be primarily decoupled. Skull shape correlated significantly with tooth shape. High size-heterodonty often correlated with very large caniniform teeth, reflecting a prioritization of securing prey. Large, highly molariform, distal teeth may be a consequence of high-frequency durophagy combined with prey size. The slender-snouted skull shape correlated with a caniniform arcade with low heterodonty. This was reminiscent of other underwater-feeding tetrapods, as they often focus on small prey that requires minimal processing. Several extinct taxa were very molariform, which was associated with low heterodonty. The terrestrial peirosaurid shared similarities with large modern crocodylian taxa, but may have processed prey differently. Disparity measures can be inflated or deflated if certain 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 crocodylian

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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2   extinct taxa.

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ABSTRACT

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

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

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

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

19   and one crocodyliform, resulting in 21 species total. Digital photographs were taken of each

20   tooth and the skull, and the margins of both were converted into landmarks and

21   semilandmarks. We expressed heterodonty through Foote's morphological disparity, and a

22   principal components analysis quantified shape variance. All specimens sampled were

23   heterodont to varying degrees, with the majority of the shape variance 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 often focus on small prey that requires minimal processing. Several extinct

32   taxa were very molariform, which was associated with low heterodonty. The terrestrial

33   peirosaurid shared similarities with large modern crocodylian taxa, but may have processed

34   prey differently. Disparity measures can be inflated or deflated if certain teeth are absent from

35   the tooth row, and regression analysis may not best apply to strongly slender-snouted taxa.

36   Nevertheless, when these methods are used in tandem they can give a complete picture of

37   crocodylian heterodonty. Future researchers may apply our proposed method to most

38   crocodylian specimens with an intact enough tooth row regardless of age, species, or rearing

39   conditions, as this will add rigor to many life history studies of the clade.

41   **INTRODUCTION**

42   What constitutes heterodonty in vertebrates is often difficult to delineate, with different

43   qualitative definitions in place depending on the clade being studied (Shimada, 2001). Kieser et

44   al. (1993, p.195) referred to the definition of heterodonty as "a bone of contention," and since

45   then the issue has not been fully resolved. Arguably, this lack of clarity is most pronounced

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

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

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

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

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

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

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

53   2015a). Size variability along the tooth row has motivated the term "heterometric homodonty"

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

55   an apparent change in tooth size but not shape (Vullo et al., 2016). Certain fossil crocodylians,

56   often interpreted as herbivores or omnivores, exhibit multi-cusped and/or grinding teeth, and

57   are specifically called "heterodont" crocodyliforms by researchers (e.g. Martin, 2007; Ősi, Clark,

58   & Weishampel, 2007; Novas et al., 2009; Ősi, 2014). Lastly, some researchers have argued

59   certain modern crocodylians are actually heterodont, and claim dental categories do in fact

60   exist (Aoki, 1989; Kieser et al., 1993).

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

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

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

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

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

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

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

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

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

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

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

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

73   "conical," "globular," "fang," "kidney-shaped," "lanceolate," "needle-like," "procumbent,"

74   "pseudocanine," "robust," "short," "slender," "spike-like," and "thick" (e.g. Brazaitis, 1973;

75   Groombridge, 1982; Aoki, 1989; Brochu, 1999; Erickson, Lappin, & Vliet, 2003; Ősi, Clark, &

76   Weishampel, 2007; Schwarz-Wings, Rees, & Lindgren, 2009; Fruchard, 2012; Gignac & Erickson,

77   2014; Salas-Gismondi et al., 2015; Berkovitz and Shellis, 2017). There is clearly a gap in our

78   knowledge concerning the nature of dental morphology in this clade, and closing this gap may

79   be crucial for a more complete understanding of performance, behavior, and trophic ecology

80   within Crocodylia, as well as more distantly related, crocodylian-line archosaurs.

81   The lack of quantitative studies on heterodonty in crocodylians and closely related taxa

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

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

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

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

86   2013; Buckley and Currie, 2014; Hendrickx and Mateus, 2014; Torices, Reichel, & Currie, 2014;

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

88   Similar measurements have been taken from a number of extinct marine reptiles (Foffa et al.,

89   2018). Extant reptiles have been investigated quantitatively as well, including colubrid snakes

90   (Britt, Clark, & Bennett, 2009; Juarez & D'Amore, 2018) and varanid lizards (D'Amore, 2015).

91   Prior to this, sharks were studied heavily (Shimada, 2002b, 2004; Shimada and Seigel, 2005;

92   Ciampaglio, Wray, & Corliss, 2005). These morphometric analyses have shed light on the nature

93   of heterodonty, dental allometry, and ecomorphology in these vertebrates, and similar

94   methods may be applied to Crocodylia to clarify the state of heterodonty in this taxon.

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

96   shape-heterodonty in members of Crocodylia. Data were collected from a multispecific sample

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

98   morphology was assessed through two-dimensional geometric morphometric methods. In

99 addition to this major goal, we also 1) outline and describe dental morphology within the

100 specimens sampled; 2) report any morphological consistencies found within the members of

101 our sample; and 3) present the advantages, limitations, and potential future uses of the

102 method. Our intention is to put forward a method for assessing heterodonty that may be

103 applicable to most crocodylian specimens, and may allow for direct comparisons between

104 crocodylians and a variety of other terrestrial and aquatic tetrapods.

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 Crocodylian teeth have very few discrete homologous anatomical loci, but, because they exhibit

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

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

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

114 premaxillae meet at the midline, or towards the mandibular symphysis; distal, away from the

115 medial premaxillae or the mandibular symphysis; lingual, towards the tongue; labial, towards

116 the "lips"; basal, towards the base of the tooth or alveolus; apical, away from the alveolus or

117 towards the apex. Crocodylians are known for a condition where a large tooth may be

118 surrounded by much smaller ones. This large tooth is typically referred to as a procumbent

119 tooth (Gignac & Erickson, 2014) or a pseudocanine (Brochu, 1999), but we simply refer to it as

120 'enlarged.'

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

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

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

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

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

126 *Paleosuchus* and *Osteolaemus* have only four premaxillary teeth during early stages of

127 ontogeny (Brochu and Storrs, 2012; Narvaez et al., 2015), and an alveolus may atrophy in

128 certain species (usually P2) as they grow (Webb & Messel, 1978; Brown et al., 2015; DC

129 D'Amore, personal observation). If only four premaxillary positions were present, position P2

130 was assumed absent, and skipped over during numbering. In one case, a specimen had six

131 premaxillary teeth (*Alligator mississippiensis*, ROM 4408). This tooth position (P6) was omitted

132 for consistency. Our *Alligator prenasalis* specimen (ROM 1375) had its distal-most cranial

133 positions obscured by poor preservation and matrix. We therefore based its maxillary tooth

134 count on previous osteological accounts (a total of 15 maxillary teeth based on Harvard

135 Museum of Comparative Zoology specimen #1015, Mook, 1932).

136 **Specimens**

137 Data were collected from 20 species of crown crocodylians, and one species of peirosaurid

138 crocodyliform (Supplemental Information Table S1). We included the later as it was readily

139 available with excellent tooth preservation, and allowed us to consider if characteristics

140   indicative of crocodylian heterodonty may be found in species outside the crown clade. The end

141   result was 27 extant and eight extinct specimens, from which we measured 1,263 teeth in total.

142   Although *Caiman crocodilus* is extant, a fossil specimen (UCMP 42844) was also included.

143   Although we did not use any distinct criteria to distinguish juveniles from adults, larger

144   specimens were selected when possible. We chose specimens with the most complete tooth

145   rows in the collections, in that they had the most tooth positions represented by measurable

146   teeth on at least one side of the mouth. Because of normal tooth replacement, post-mortem

147   damage, and/or poor preservation, the percentage of tooth positions represented by

148   measurable teeth was highly variable (Supplemental Information Table S2). Modern specimens

149   had tooth rows with 42-100% of their tooth positions represented, and fossil tooth rows ranged

150   30-78%. Certain fossil specimens only had cranial (*Alligator prenasalis* ROM 1375,

151   *Borealosuchus sternbergii* UCMP 126099, "*Crocodylus*" *affinis* UCMP 131090, *Hamadasuchus*

152   *rebouli* ROM 52620, *Leidyosuchus canadensis* ROM 1903) or dentary (*Borealosuchus sternbergii*

153   UCMP 131769) material to sample. This variability allowed us to consider in what way the

154   degree of incompleteness along the tooth row may affect the proposed method, as incomplete

155   tooth rows may be common in collections.

156   **Tooth data collection**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

174 could be seen from the other side.

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

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

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

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

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

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

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

182 resulted in three discrete landmarks (two at the base and one at the apex) and 56

183   semilandmarks (Figure 1B). This number of coordinates has been used in previous studies of

184   both dinosaur (Smith, Vann, & Dodson, 2005) and monitor lizard (D'Amore, 2015) dentition, as

185   well as claw morphology (Tinius and Russel, 2016; D'Amore et al., 2018), in which it has been

186   shown to accurately represent the totality of two-dimensional shape (Tinius and Russel, 2016).

187   We calculated centroid size (CS), and performed a generalized least squares Procrustes (GLSP)

188   superimposition while sliding the semilandmarks to minimize the total bending energy (Perez,

189   Bernal, & Gonzalez, 2006; Gunz & Mitteroecker, 2013), using the program TpsRelw 1.53 (Rohlf,

190   2013).

191   **Skull data collection**

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

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

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

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

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

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

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

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

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

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

202   premaxillae to the caudal-most quadratojugal along the margin on each side (Figure 1C). We

203   chose this margin because it outlined the shape of the head as close to as it would have

204   appeared in life as possible, but avoided internal structures such as the jaw articulations or

205   occipital condyles. Each margin was broken into 50 equidistant coordinates, and the rostral-

206   most coordinates were combined. This resulted in three landmarks (two at the quadratojugals

207   and one at the premaxillary junction) and 97 semilandmarks (Figure 1C). These also underwent

208   a GLSP superimposition and the semilandmarks were slid to minimize the total bending energy

209   using TpsRelw 1.53. In specimens with damaged or missing bones on one side, bilateral

210   symmetry was assumed and the coordinates on the intact side were mirrored. This was

211   achieved by placing another landmark along the mid-sagittal plane at the caudal-most point

212   available. This landmark and the one at the premaxillary junction resulted in a plane that the

213   landmarks were mirrored against.

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

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

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

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

218   used as a body size metric (see Fukuda et al. 2013 for potential influences on this

219   measurement). We derived skull length from the same landmarks outlining the skull above; it

220   was the linear distance from the rostral-most landmark to the posterior-most landmarks along

221   the mid-sagittal plane (Figure 1C). (Note: *Borealosuchus sternbergii* UCMP 131769 and

222   *Crocodylus niloticus* AMNH 142494 did not have intact skulls, and were therefore omitted from

223   all analyses involving skull data.)

224   **Statistical approaches**

225   All analyses were conducted in MorphoJ v. 106d (Klingenberg 2011), SPSS Version 19.0 [IBM

226   Corp, Armonk, NY], and PAST (Hammer, Harper, & Ryan, 2001). If both left and right teeth were

227   available at a given position, we averaged them. For size, CS values were simply averaged

228   together. For shape, each *x-y* coordinate of the GLSP superimposed landmarks and

229   semilandmarks was averaged with its counterpart for both teeth. To ensure that the left and

230   right sides were not significantly different, we ran a 10,000 permutations test on the Procrustes

231   distances between left and right teeth at positions that had both. This test failed to reject the

232   null hypothesis of bilateral symmetry ($p = 0.6785$). If only one tooth was available for a given

233   position, that tooth alone represented said position.

234   We tested the null hypothesis that there was no statistical difference between tooth

235   rows in our sample. We ran a 10,000 permutations test on the Procrustes distance between

236   cranial (premaxilla and maxilla) and dentary teeth for those that had both.

237   Skull shape and tooth orientation may be irregularly influenced by captive rearing

238   (Erickson et al., 2004; Drumheller, Wilberg, & Sadleir, 2016), and how this influences tooth

239   shape in crocodylians has yet to be determined. All the modern specimens sampled in this

240   study were categorized as wild caught or 'no data' (Supplemental Information Table S2). The

241   latter category indicated the host museum did not know the living conditions of the specimen

242   while alive, and could mean (but does not guarantee) that the specimen was captive raised. To

243   determine if rearing conditions influenced our shape data, we ran a 10,000 permutations test

244   on the Procrustes distances between wild caught and 'no data' specimens in MorphoJ. We

245   excluded *Gavialis gangeticus*, *Mecistops cataphractus*, and *Tomistoma schlegelii*, as they

246   represent an extreme cranial condition and only one individual of each species was available.

247   A singular measure of heterodonty was derived for each specimen in the form of Foote's

248   morphological disparity $[MD = (\sum_{i=1}^{m} D_i^2)/(m-1)]$ (Foote, 1993; Zelditch, Sheets, & Fink,

249   2003; Sheets & Zelditch, 2013). Disparity (*MD*) was the sum of the differences of the values of a

250   given tooth (*i*) from the mean for all teeth from that single specimen (*Di*, also known as the

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

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

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

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

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

256   major axis against skull length to determine if there was a significant allometric change in the

257   clade. To test if the more incomplete tooth rows were strongly affecting heterodonty, we ran

258   both regressions a second time, yet only included specimens that had no less than 70% of their

259   tooth rows represented by measurable teeth. If the regression statistics were similar to when

260   all specimens were included, this would suggest incompleteness had a minor effect on our

261   results.

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

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

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

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

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

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

268   was depicted through vector diagrams.

269   To determine if size and shape were coupled, regression scores of full shape data were

270   generated by MorphoJ (as described in Drake and Klingenberg, 2008) and regressed against CS

271   using a reduced major axis. Significance and a high goodness of fit would be indicative of strong

272   coupling between size and shape. A principal component analysis (PCA) was then conducted to

273   visualize the degree of shape variance within all cranial and dentary teeth. PC scores were

274   represented in bivariate plots, and the shape variation of each PC axis was visualized using

275   vector diagrams.

276   As heterodonty is defined here as variability along the tooth row, we attempted to

277   evaluate the nature of this variability between tooth positions. We used an analysis of variance

278   (ANOVA) to determine if the teeth differed significantly in CS between positions for all

279   specimens sampled. This size metric had unequal variances according to Levene's test, so we

280   specifically ran a Welch's ANOVA. As shape is inherently a multivariate measure, we ran a

281   multivariate analysis of variance (MANOVA) comparing shape between positions. As some

282   specimens had fewer tooth positions than others, the number of teeth occupying the distal-

283   most positions ended up being low. These positions were excluded from the statistical tests,

284   resulting in the only positions considered having at least 7 teeth. To visually represent

285   variability by position, we plotted size and shape against tooth position in a series of box plots.

286   For size, CS was normalized by dividing it by skull length (so as to not obscure the degree of

287   variability in smaller specimens), and then was plotted against tooth position. For shape, PC

288   scores of biologically relevant PCs were plotted against tooth position in a similar fashion.

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

290   arcade from mesial to distal (Farrugia, Polly, & Njau, 2016). We test this by regressing shape

291   data against tooth position using ordinary least squares regressions for each individual. To

292   standardize these regressions, we normalized tooth position into a proportion. We numbered

293   the positions along the tooth row starting with 1 at the mesial-most position, divided each by

294   the total number of positions along the arcade, and then subtracted 0.5 (this subtraction placed

295   the *y*-intercept halfway along the arcade without affecting any ensuing statistics). PCs for each

296   tooth were then regressed against this, and regression statistics were collected. Several factors

297   may be implied by a significantly linear crocodylian tooth row. Slope may be linked to

298   heterodonty, as a steeper slope would imply more shape change along the PC1 scores at the *y*-

299   axis and consequently greater shape-heterodonty. The *y*-intercept represented the shape value

300   at the median position, as the intercept was located half-way along the tooth row. This allowed

301   for direct shape comparison between all taxa regardless of whether or not the tooth was

302   actually present at said position. To visualize these coefficients, we plotted both slope and *y*-

303   intercept for each regression in scatterplots for both the cranium and the dentary.

304   **Results:**

305   **Shape variability in the sample**

306   No statistically significant difference was found between cranial and dentary tooth rows

307   (p=0.2455) or wild caught versus 'no data' modern specimens (p=0.4229), failing to reject the

308   null hypothesis under both circumstances. When regression scores were plotted against CS,

309   the regression had a goodness of fit accounting for less than 10% of the variance (y=0.313x-

310   0.981; r^2=0.09; p<0.0001; 95% =0.296,0.328).

311   Most of the shape variance in Crocodylia was along a single PC axis. PC1 accounted for

312   over 92.11% of the variance (Supplemental information Table S3). The shape changes towards

313   negative PC1 scores include apical-basal elongation, narrowing at the base, and a gentle

314   concavity on the distal margin (Figure 2A). For simplicity, we will refer to this extreme as

315   'caniniform' (Erickson et al., 2012; 2014; Gignac & Erickson, 2014). Positive shape changes

316   depicted an apical-basal shortening and mesial-distal broadening, and we will refer to the

317   extreme as 'molariform' (Erickson et al., 2012; 2014; Gignac & Erickson, 2014). We describe

318   PC2 (3.22% of the variance) as the orientation of the tooth, or how much it 'leans' (Figure 2A).

319   Positive values indicate the apex leaning in the mesial direction, and negative values indicate a

320   lean in the distal direction. Note that this is not a measure of curvature, as neither margin

321   changes its concavity or convexity. We do not consider any other PCs, as the amount of

322   variance represented by them is very low (Supplemental Information Table S3).

323   Figure 2B illustrates the morphospace produced by PC1 and PC2 scores. At the

324   superfamily level, there was a large amount of overlap between alligatoroids and crocodyloids.

325   Most specimens had teeth ranging a large portion of the PC1 score spectrum, with little

326   separation between them. The only exceptions were some crocodyloid teeth below PC1 scores

327   of -0.2. Both *Borealosuchus sternbergii* tooth rows had PC1 scores between -0.22 and 0.20, and

328   *Hamadasuchus rebouli* ranged between -0.19 and 0.23. These were nested within the

329   alligatoroids and crocodyloids. *Gavialis gangeticus* deviated from the rest in that most teeth

330   had PC1 scores of <-0.20 (Figure 2B). PC2 scores did not differ between groupings of taxa, as

331   each group occupied most of the shape range.

332   **Skull vs. tooth morphology**

333   Skull and average tooth shape were significantly correlated. For the two-block PLS test, PLS1

334   encompassed 99.96% of total covariation and had a correlation coefficient of 0.7937. Shape

335   variability within the skull shape block showed the snout transitioning from narrow to broad

336   (Figure 3A). Taxa that occurred below a PLS1 score of -0.15 were the slender-snouted taxa as

337   defined by Brochu (2001), including *Gavialis gangeticus*, *Mecistops cataphractus*, and

338   *Tomistoma schlegelii*. The remainder of the species, defined as either generalized or blunt-

339   snouted (also by Brochu, 2001), occurred around the mean and positive half mixed together.

340   Shape variability within the tooth shape block was similar to the above PCA of tooth shape,

341   displaying a transition from caniniform to molariform with increasing values (Figure 3A). These

342   blocks regressed significantly against one another (Figure 3B), with slender-snouted taxa

343   separating out with the most caniniform teeth. Scatter increased around the means, indicating

344   the correlation was not as strong among the generalized-to-blunt snouted taxa. *Alligator*

345   *prenasalis*, *Brachychampsa* sp., and "*Crocodylus*" *affinis* were all relatively blunt-snouted, but

346   rose noticeably above the regression. This suggested they possessed much more molariform

347   teeth on average than their counterparts of similar skull shape.

348   **Foote's disparity and heterodonty**

349   Size-heterodonty was significantly correlated with skull length, with an r^2 of 0.760. The largest

350   individuals according to skull length (members of *Crocodylus niloticus* and *Crocodylus porosus*)

351   possessed the greatest unadjusted size-heterodonty (Figure 4A). Members of *Alligator* had

352   negative residual size heterodonty, with *Alligator prenasalis* as the lowest. On the other side of

353   the regression, residuals of caimanine specimens (*Caiman*, *Paleosuchus*) were all positive with

354   the exception of one individual. Several members of *Crocodylus* had values around or below

355   zero, but one *Crocodylus porosus* specimen had a high residual. One *Osteolaemus tetraspis*

356   individual had the highest size-heterodonty residual, with the other close to the regression.

357   *Hamadasuchus rebouli* had positive residuals, similar to the larger *Crocodylus porosus* and the

358   caimanine specimens. The slender-snouted taxa (*Gavialis gangeticus*, *Mecistops cataphractus*,

359   *Tomistoma schlegelii*) had some of the more negative residuals. For the regression excluding

360   individuals with less than 70% of either tooth row represented, the regression statistics

361   (y=2.208x-8.583; r^2=0.770; p<0.0001) were strikingly similar to those of the complete dataset

362   (y=2.196x-8.549; r2=0.760; p<0.0001).

363   Shape-heterodonty was highly variable. Shape regressed significantly, but had a rather

364   poor correlation (r^2=0.157), with skull length (Figure 4B). Similar to size-heterodonty, the

365   slender-snouted taxa had some of the lowest shape-heterodonty, although *Tomistoma*

366   *schlegelii* was greater than several other taxa. In addition, members of *Brachychampsa* sp. and

367   *Alligator prenasalis* also had some of the lowest shape-heterodonty in our sample. *Crocodylus*

368   *siamensis* specimens were more shape-heterodont than their congenerics, with one individual

369   being the most shape-heterodont in our sample. Several caimanine individuals, and both

370   *Osteolaemus tetraspis* specimens, also had relatively high shape heterodonty. For the

371   regression excluding individuals with less than 70% of either tooth row represented, regression

372   statistics (y=-0.648x-0.235; r^2=0.238; p<0.0397) were also similar to those of the complete

373   dataset (y=-0.715x-0.172; r2=0.157; p<0.0223).

374   **Heterodonty along the tooth row**

375   Tooth position count varied between species (see Supplemental Information Table S2). Most

376   alligatoroids had between 19-20 positions on the cranial tooth row. Many had a similar number

377   on the dentary, except that members of *Paleosuchus* had 22 positions. *Leidyosuchus canadensis*

378   had the most (23) cranial positions of the alligatoroids. *Hamadasuchus reboulii* (20 cranial) and

379   *Borealosuchus sternbergii* (23 cranial and 20 dentary) specimens fit within ranges of

380   alligatoroids. Members of *Crocodylus* and *Mecistops cataphractus* had between 18-19 cranial

381   and 15 dentary positions. *Osteolaemus* specimens had the least tooth positions for any

382   crocodyloid (17 cranial and 14 dentary), and *Tomistoma schlegelii* had the most (21 cranial and

383   19 dentary). The *Gavialis gangeticus* specimen had more positions than any other species

384   sampled (28 cranial and 26 dentary). These tooth counts are similar to previous published

385   accounts (Brown et al., 2015; Berkovitz & Shellis, 2017).

386   In all taxa combined, ANOVA indicated size differed significantly between tooth

387   positions [$F_{(34, 261.45)}$=4.57; p<0.0001]. In Alligatoroidea and Crocodyloidea, size undulated

388   three times along the dental arcade resulting in significant differences between positions for

389   both the cranium and mandible (Figure 5A-B). Each undulation peaked with an enlarged tooth.

390   These were typically represented by P4 for both clades, and M4 for alligatoroid and M5 for

391   crocodyloid specimens (sensu Brochu and Storrs, 2012). In addition, members of *Paleosuchus*

392   had very large P3 and M3. "*Crocodylus*" *affinis* also had a large P3. Unlike other alligatoroid

393   specimens, *Leidyosuchus canadensis* had both M4 and M5 enlarged, and the *Brachychampsa*

394   sp. had an enlarged M5 like crocodyloids (sensu Norell, Clark, & Hutchison, 1994). A final

395   undulation resulted in an enlarged tooth at M9-11 (Figure 5A-B). Interspersed between these

396   were smaller teeth, with the distal-most tooth often the smallest. The dentary was similar to

397   the cranium, with three undulations in size. Enlarged teeth were found at positions D1 and D4,

398   with a third size-peak between D11 and D14. Note that the position of the enlarged teeth along

399   the cranial tooth row tended to align with smaller teeth along the dentary tooth row, and vice

400   versa. This resulted in an 'adjoining' pattern between the size peaks of one arcade and the

401   valleys of the other. The gavialoid specimen differed markedly by having the two mesial-most

402   teeth enlarged, and the remainder showed a gradual decease in size distally (Figure 5C).

403   *Hamadasuchus rebouli* had some of the largest teeth for its skull length with a dramatic

404   variation in size.

405   Shape also differed significantly between positions according to MANOVA

406   [$F(4046,23939.54)=1.27$; $p<0.0001$; Wilk's $\Lambda=0.002$; partial $\eta^2=0.171$], although in a visibly

407   different fashion than size. We only graphed PC1 scores against tooth position, as the other PCs

408   represented under 5% of the variance each and were not considered biologically relevant to

409   tooth position (for a justification, see Supplemental Information). Alligatoroids and crocodyloids

410   both had mesial teeth that were typically the most caniniform in the mouth, and distal teeth

411   the most molariform (Figure 5D-E). In cranial teeth P1-M4 tend to exist primarily between PC1

412   scores of -0.25 and 0.00, followed by a gradual increase in score values as positions become

413   more distal. Dentary teeth represented a more uniformly gradual caniniform-to-molariform

414   transition. Both superfamilies were highly variable. Alligatoroidea had teeth generally more

415   molariform, with upper outliers almost entirely represented by *Alligator prenasalis*, *Alligator*

416   *sinensis*, and *Brachychampsa* sp. (Figure 5D). Crocodyloidea was generally more caniniform,

417   with mesial upper outliers represented by *"Crocodylus" affinis* and lower outliers represented

418   primarily by *Tomistoma schlegelii* (Figure 5E). Both *Borealosuchus sternbergii* tooth rows had

419   PC1 scores between -0.22 and 0.20, and *Hamadasuchus* ranged between -0.19 and 0.23 (Figure

420   5F). Both taxa showed a similar progression from caniniformy to molariformy as the

421   alligatoroids and crocodyloids. *Gavialis gangeticus* deviated from the others the most, where

422   most teeth had scores of < -0.20 with a steep increase towards the average in the distal-most

423   fifth of the arcade (Figure 5F).

424   Tooth shape was strongly influenced by tooth position (Figure 6). When each modern

425   individual's PC1 values were regressed against position, all linear regressions were significant

426   (Supplemental Information Table S2). The vast majority of tooth row regressions had r^2 values

427   above 80%. *Gavialis gangeticus* had the lowest r^2 values (cranium=0.495, mandible=0.616),

428   followed by the crania of the fossil *Caiman crocodilus* (r^2=0.728) and *Tomistoma schlegelii*

429   (r^2=0.747). Both cranial and dentary tooth rows typically had slopes between 0.25-0.55 (Figure

430   6). More shape heterodont taxa typically had greater slopes, with *Crocodylus siamensis*

431   specimens having some of the steepest slopes (0.39-0.68). All the slender-snouted specimens

432   had the *y*-intercepts between -0.25 and -0.14, indicating strong caniniformy at the median

433   position. Living members of *Alligator* had *y*-intercepts between 0.029 and 0.085, indicating

434   molariformy at the median (Figure 6). *Alligator prenasalis, Brachychampsa* sp., and *"Crocodilus"*

435   *affinis* had the shallowest slopes (0.22-0.32) and the greatest *y*-intercepts (0.15-0.24) in our

436   sample, indicating molariform teeth are consistent along the tooth row. *Hamadasuchus*

437   *rebouli*'s regression characteristics are similar to members of *Caiman* and *Osteolaemus*

438   *tetraspis*. The slope of the fossil *Caiman crocodilus* differed from modern members of *Caiman*

439   by being much shallower (Figure 6).

440   **DISCUSSION**

441   **Defining heterodonty within Crocodylia**

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

443   Crocodylia. As was first proposed in D'Amore (2015), outlining the margin of the tooth is a

444   comprehensive method for measuring two-dimensional tooth shape. This type of semilandmark

445   analysis is ideal for any cylindrical, conical, caniniform, or ziphodont dentition, and would

446   include many archosaurs, squamates, sauropterygians, ichthyosaurs, teleosts, sharks, etc. As

447   tooth morphology is often compared between taxonomically disparate groups (examples in

448   Ciampaglio et al. 2005; Foffa et al., 2018), future studies should use semilandmark analyses to

449   compare crocodylians to these groups to answer numerous phylogenetic and ecomorphological

450   questions.

451   Foote's morphological disparity allows for a continuous and quantitative measure of

452   heterodonty that may be used for comparison between taxa, or compared with other variables

453   (as was done here with skull length). This measure is ideal if one is interested in *how much*

454   heterodonty is apparent. Alternatively, if one is interested in what shape characteristics make

455   up tooth heterodonty, ordination approaches suffice in describing shape variability. Although

456   plotting PC scores as Cartesian coordinates in a morphospace is traditionally done to visualize

457   shape variability (as in Figure 2B), overlap due to shape-heterodonty makes specimens, species,

458   and even superfamilies almost indistinguishable from one another. This exemplifies why

459   methods such as box plots and linear regressions may be preferable over the more 'standard'

460   morphospace depiction when heterodonty is concerned. It is convenient that only PC1

461   accounted for over 90% of the variance, allowing for us to use it as the sole measure of shape

462   here. If more PCs accounted for over 5% of the shape variance, it would be appropriate to

463   depict those other PCs in the same manner as PC1 for a comprehensive understanding of

464   shape.

465   Regression analysis of shape against position generally yielded strong correlations

466   (Supplemental Information Table S2), and the resulting coefficients were useful for comparison

467   between individuals. Certain caveats should be considered though. Regression may be more

468   appropriate for the dentary than the cranium, because in the cranial arcade the mesial-most

469   teeth do not appear to differ from one another as much as the remainder. In most crocodylians

470   this effect is mild, and r^2 values are still high. The effect is very pronounced in *Gavialis*

471   *gangeticus* though, as both the premaxillary and most maxillary teeth are similar in shape. It is

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

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

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

475   crocodylian is beyond the scope of the study, our data suggest that it would be potentially

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

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

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

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

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

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

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

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

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

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

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

487   *mississippiensis*, as it functioned to meet the mechanical demands of increased durophagy

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

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

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

491   greater *y*-intercepts indicating greater molariformy.

492   Although there was no significant effect of captive rearing on our specimens, we believe

493   this principle should still be investigated further. Some cases of captive rearing have resulted in

494   very different, and easily distinguishable, cranial morphologies, but there is also quite a bit of

495   overlap concerning others (Drumheller, Wilberg & Sadleir, 2016). This may, or may not, happen

496   with teeth. A larger data set, looking at multiple ontogentic stages, is necessary to determine if

497   rearing condition has any measurable effects on teeth. The method proposed here would allow

498   for the rigorous comparison between these two rearing conditions, and determine if any

499   changes do occur as well as other factors may correlate to said changes.

500   **Morphological trends within Crocodylia**

501   All crocodylian specimens measured here were heterodont to varying degrees, and these data

502   showed significant variability of morphotypes along the dental arcade for all specimens (Figure

503   7). Although dentition varied between species, certain consistencies were seen throughout the

504   clade:

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

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

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

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

509   shape axis, representing the transition from caniniform to molariform.

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

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

512   both dental arcades in all specimens.

513   5. Size variability consisted of a non-linear, undulating pattern with three peaks that adjoin

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

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

516   apparent in slender-snouted taxa.

517   Size- and shape-heterodonty were very loosely coupled in Crocodylia as they changed in

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

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

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

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

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

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

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

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

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

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

528   1962; Westergaard and Ferguson, 1990; Osborn, 1998), but it is unclear how the nature of

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

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

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

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

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

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

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

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

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

538   to truly understand what generates heterodonty.

539   The fact that *Hamadasuchus rebouli* showed similar trends in heterodonty to crown

540   crocodylians was particularly revealing. This indicated the methods proposed here may be

541   transferable to at least some crocodyliforms outside of Crocodylia. It should also be noted that

542   this consistency exists in spite of the numerous craniodental characteristics that differ between

543   *Hamadasuchus rebouli* and the crocodylians, including a deep-snout and ziphodont teeth

544   (Larsson & Sues, 2007). The characteristic heterodonty may be covergently derived or

545   homologous with what is seen in this peirosaurid, and further research should investigate how

546   frequent it is seen in Crocodyliformes as a whole.

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

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

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

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

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

552   crocodylians may have very different tooth dimensions. This rules out adductor-generated

553   maximum bite force as the sole limiting factor dictating tooth form. Although we are reluctant

554   to associate specific prey items with specific tooth forms, size and shape will influence how a

555   tooth interacts with food items possessing certain physical properties. We therefore suggest

556   that a biomechanical link should exist between the structural limits imposed by tooth form and

557   the material properties of the substrates with which it interacts.

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

559   pressures based on their respective position along the arcade. Caniniform mesial teeth are ideal

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

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

562   1988). Being farther from the hinge, these teeth move faster during a strike and are more likely

563   to contact prey trying to escape (Busbey, 1989). They will also endure less pressure during a

564   bite based on their position (Erickson et al., 2012), and can afford to be relatively elongate and

565   gracile. On the other end, distal teeth need to withstand greater tooth pressures due to their

566   close proximity to the hinge (Cleuren, Aerts, & Vree, 1995; Erickson, Lappin, & Vliet, 2003;

567   McHenry et al., 2006; Erickson et al., 2012). This explains why these teeth are typically on the

568   molariform half of the shape spectrum; the larger base-to-height ratio gives them greater

569   relative bending strengths to withstand said pressures (Van Valkenburgh and Ruff, 1987; Gignac

570   & Erickson, 2014; Monfroy, 2017). Because force is highest in this region, it is ideal for

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

572   and de Vree, 2000). The reduced height of these teeth also ensures they do not impede jaw

573   closure. This necessity is very apparent in our representative member of *Gavialis gangeticus*,

574   and provides a functional explanation for the poor linear shape relationship along the tooth

575   row in this individual. Having all the teeth be highly caniniform except for the distal-most region

576   may be interpreted as an attempt to reduce heterodonty as much as possible (Grigg and Gans,

577   1993), while ensuring the distal crowns do not impede jaw closure or break when processing

578   food.

579   Particular attention should be paid to the relative size of the distal-most crowns, as they

580   vary considerably within our sample. Most modern alligatoroids and crocodyloids have a single

581   enlarged tooth followed distally by several smaller teeth on the caudal half of their jaw. These

582   teeth typically had positive PC1 scores, especially within *Alligator mississippiensis* and

583   *Crocodylus siamensis*, and were also some of the smallest teeth in their arcades (Figure 7A).

584   Members of *Alligator sinensis* differed from this though, in that they had a row of 4-5 relatively

585   large, high-molariform crowns (followed by only one crown reduced in size). Probably the most

586   extreme condition, *Osteolaemus tetraspis* specimens had distal crowns that were exceptionally

587   large; the largest relative crowns at positions M10-12 and D11-13 for modern taxa all belonged

588   to members of this species. These two species also have the lowest number of teeth for

589   modern alligatoroids and crocodyloids respectively, a reduction potentially based on the need

590   to fit these enlarged teeth. Aoki (1989) qualitatively noted these unique conditions, and

591   suggested they facilitated durophagy. All alligatoroids and crocodyloids sampled here have

592   been recorded to consume at least some hard prey items though (e.g. Brazaitis, 1973;

593   McIlhenny, 1976; Taylor, 1979; Groombridge, 1982; Ross and Magnusson, 1989; Santos et al.,

594   1996; Selvaraj, 2012; Nifong & Silliman, 2013), so it is unclear what selection pressure resulted

595   in these particular morphologies. It may be a result of body size. Bite force tests of *Alligator*

596   *mississippiensis* showed the pressure produced at its enlarged M11 to be adequate to crush its

597   harder prey items (Erickson, Lappin, & Vliet, 2003; Gignac & Erickson, 2014). If this is the case in

598   most of the large crocodylians, enlarging the distal-most crowns would be unnecessary.

599   *Alligator sinensis* and *Osteolaemus tetraspis,* on the other hand, may need more extreme

600   dentition closer to the hinge; their smaller size would make it more difficult to process foods

601   with similar mechanical properties. Another explanation for this may be the frequency of

602   consuming hard prey. Although both these species have broad diets, studies have shown

603   certain (but not all) populations of these species to consume disproportionately large numbers

604   of shelled mollusks and crustaceans (Cheng-Kuan, 1957; Groombridge, 1982; Ross and

605   Magnusson, 1989; Luiselli, Akani, & Capizzi, 1999; Pauwels et al., 2007).

606   All taxa measured here also have two sets of enlarged mesial teeth on both arcades.

607   These teeth are well built for puncturing, likely making first contact with prey during jaw

608   closure, and are resilient against struggling prey (Iordansky, 1964). An apparent trade-off to

609   enlarging these teeth is the need to reduce the size of teeth on the opposing tooth row. This

610   character played a large role in size-heterodonty, with different crocodylians undulating their

611   tooth sizes to different degrees. High relative size-heterodonty in specimens found within

612   Caimaninae was typically a consequence of the dramatic size difference between the enlarged

613   teeth and the small remaining crowns, (Figure 7B). Their dentary crowns in particular became

614   so large they often grew entirely through the cranial rostrum in adults (as mentioned in

615   Brazaitis, 1973), which suggests securing prey takes priority. The remaining crowns were rather

616   small by comparison, including the distal crowns: the teeth with the greatest mechanical

617   advantage when processing hard prey. This overall condition may be specialized for hunting

618   more mobile and/or compliant prey, as these types of prey may be punctured quickly and

619   securely with the enlarged, pointed crowns (Sampaio et al., 2013). The *Crocodylus porosus*

620   specimens had the largest M5 crowns in our sample, which may also show a prioritization for

621   puncturing and securing soft-bodied prey in a larger context (Figure 7B). This species is

622   notorious for actively hunting large vertebrates such as sharks, cattle, horses, and humans (e.g.

623   Taylor, 1979; Kar & Bustard, 1981; Groombridge, 1982; Doody, 2009; Hanson et al., 2015), and

624   these teeth are ideal for puncturing and securing such prey. Similar to the caimanine

625   specimens, this species atrophies position P2 to make room for its enlarged D1 crowns (Brown

626   at al., 2015)

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

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

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

630   Erickson et al., 2012), and multiple lines of evidence suggest the feeding apparatus is well

631   suited for this function. The slender shape reduces resistance during both lateral motion and

632   jaw adduction when feeding underwater, and the increased snout length allows for a faster

633   strike (Taylor, 1987; Pooley, 1989; Thorbjarnarson, 1990; McHenry et al., 2006; Pierce et al.,

634   2008). Highly caniniform teeth can quickly puncture fast-moving, compliant prey, and their

635   elongate shape may also lower their mechanical resistance (Figure 7C). The longirostrine

636   condition, defined as a snout that is both slender and elongate (Brochu, 2001), resulted in

637   increased tooth positions; *Tomistoma schlegelii* had more teeth than any other crocodyloid,

638   and *Gavialis gangeticus* has the most teeth out of all crocodylians sampled. This cranio-dental

639   morphotype may be prey-size prohibitive though, as larger prey could damage the slender

640   rostrum while struggling. Their elongate mandibular symphysis results in a mechanical

641   disadvantage against the forces produced by shaking and twisting prey (Walmsley et al., 2013).

642   The gracile nature of the dentition means a lower bending strength, making them more

643   susceptible to breakage from larger and/or harder prey as well. On rare occasions, large

644   individuals have been known to take land-based, vertebrate prey (Thorbjarnarson, 1990;

645   Selvaraj, 2012). This is most likely because the overwhelming size of these crocodylians allows

646   their feeding apparatus to withstand the forces exerted by said prey.

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

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

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

650   2017). Although these crocodylians are not anisodont in the strict sense (they all have some

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

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

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

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

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

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

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

658   one almost exclusively for prey capture. This morphological condition is best exemplified by

659   *Gavialis gangeticus,* as it is almost entirely caniniform along its tooth row and eats primarily fish

660   (Groombridge, 1982, Figure 7C). Members of *Mecistops cataphractus* and *Tomistoma schlegelii*,

661   although also primarily caniniform, still displayed the linear shape change typical of other

662   crocodyloids. These species may consume prey that require relatively more processing with

663   their distal crowns, and there are numerous reports of them eating prey such as crustaceans,

664   turtles, and immature primates (Brazaitis, 1973; Groombridge, 1982; Galdikas and Yeager,

665   1984; Selvaraj, 2012).

666   Tooth shape may indicate differences in feeding behavior and processing ability, even

667   though overlap exists in prey selection. *Alligator mississippiensis* and *Crocodilus niloticus* both

668   consume a wide variety of prey, including both large and small mammals, crustaceans, fish,

669   water fowl, snakes, turtles, and conspecifics (McIlenny, 1976; Pooley & Gans, 1976;

670   Groombridge, 1982; Delany and Abercrombie, 1986; Hutton, 1987; Shoop & Ruckdeschel, 1990;

671   Rootes & Chabreck, 1993; Elsey, Trosclair III, & Linscombe, 2004; Wallace and Leslie, 2008;

672   Gabrey, 2010). A comparison of controlled feedings of each of these species showed *Alligator*

673   *mississippiensis* to fracture and consume noticeably more bovine skeletal elements than

674   *Crocodylus niloticus* (Njau & Blumenschine, 2006; Drumheller & Brochu, 2014; 2016). Our

675   *Alligator mississippiensis* specimens was generally more molariform than *Crocodylus niloticus.*

676   These teeth would have greater bending strengths to resist breakage when processing hard

677   material such as bone.

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

679   Certain fossil taxa were reminiscent of modern counterparts. We expected the fossil *Caiman*

680   *crocodilus* to be similar to its congenerics, due to the fact that these specimens are closely

681   related and all consume insects, crustaceans, and fish (Brazaitis, 1973; Groombridge, 1982; Da

682   Silveira and Magnusson, 1999). Any differences in size and shape ranges appear to simply be a

683   consequence of the former's incomplete arcades; no distal maxillary or dentary crowns were

684   available (see **Limitations** below). *Alligator mississippiensis* specimens have similar shape

685   regression statistics to our *Leidyosuchus canadensis* specimen, but, unlike members of *Alligator*,

686   this specimen lacked enlarged distal teeth (Figure 7D). This caused size heterodonty to differ

687   noticeably, and may be indicative of a difference in the degree these taxa process hard

688   materials (although no taphonomic evidence for this currently exists associated with

689   *Leidyosuchus canadensis*). The two specimens of *Borealosuchus sternbergii* differed from one

690   another in median shape as indicated by *y*-intercepts, which may due to an allometric increase

691   in molariformy. The best analogue for this species may be a member of *Crocodylus* with similar

692   slopes such as *Crocodylus palustris*, but more data are necessary to confirm this (Figure 7D).

693   *Hamadasuchus rebouli* had similar relative size-heterodonty and relative maximum

694   tooth size to the larger *Crocodylus porosus* specimen, which indicates it may have dealt with

695   similar prey from a mechanical standpoint (Figure 7E). The greatly enlarged mesial teeth would

696   puncture vertebrate tissue with similar effectiveness (Figure 7B). *Hamadasuchus rebouli*

697   differed in that it had very large distal crowns, which, unlike *Osteolaemus tetraspis*, are laterally

698   flattened (Larsson & Sidor, 1999). This suggests potential differences in prey processing.

699   Peirosaurids are believed to be primarily terrestrial crocodyliforms (Tavares et al., 2017), and

700   they most likely did not occupy the semi-aquatic, sit-and-wait predator niche dominated by

701   modern crocodylians (Larsson & Sues, 2007). It may have used these for either sheering soft

702   tissue or breaking bone similar to modern mammalian carnassials, as rolling on land is not an

703   effective means of dismemberment (Fish et al., 2007).

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

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

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

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

708   *Brachychampsa* are textbook examples of a globidont taxa (Case, 1925; Carpenter and Lindsey,

709   1980, Figure 7F), and our specimen is the only one in the sample with distal teeth so molariform

710   their PC1 scores exceed 0.349. Although we agree with Brochu (2001, 2004) that *Osteolaemus*

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

712   *Brachychampsa* sp. than any other taxon sampled (0.322-0.341). *Alligator prenasalis* and

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

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

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

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

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

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

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

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

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

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

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

724   than being ambush predators.

725   **Limitations and future work**

726   A complete tooth row with all positions represented would be the most thorough way to assess

727   heterodonty in any specimen. Nevertheless, complete tooth rows may not be available under

728   many circumstances. Although we cannot propose a threshold for what number of teeth is

729   'enough' to accurately assess heterodonty, there are factors that influence some of these

730   methods more than others. Foote's morphological disparity relies on, among other things, the

731   grand mean and the sample size. Size-heterodonty may be underrepresented if, for example, an

732   enlarged tooth is missing. This tooth would deviate greatly from the grand mean if present, so

733   its exclusion would deflate size heterodonty. Due to their greater frequency, small teeth would

734   typically be closer to the grand mean. Therefore, if a single small tooth was missing

735   heterodonty would slightly inflate. It should also be noted that if the majority of small teeth

736   were missing their absence would end up decreasing heterodonty, as the grand mean would

737   approach the value of the remaining large teeth. Shape-heterodonty will not be as influenced

738   by enlarged teeth missing, but more so by a lack of the mesial- or distal-most teeth. Missing

739   many of the caniniform or molariform teeth will deflate shape-heterodonty, as the overall

740   variance would be reduced. This would also influence regression statistics, as a lack of either

741   extreme would raise or lower the slope and/or *y*-intercept.

742   Even though our data set included several specimens with tooth rows with less than

743   70% completeness, we feel our data is reliable enough for the morphological and functional

744   conclusions we draw. The similarity between the heterodonty regressions representing all

745   specimens, versus those with more complete specimens only, suggests that incompleteness did

746   not influence our heterodonty values very much. This is most likely because the factors that

747   would strongly influence size- and shape-heterodonty mentioned above were relatively rare in

748   our data set. Few specimens sampled lacked enlarged teeth. The teeth that were missing were

749   typically spread throughout the tooth row, and not localized to the mesial or distal extremes.

750   There were several specimens whose heterodonty results were probably strongly influenced.

751   The very low size-heterodonty in *Alligator prenasalis* may be a consequence of the loss of

752   enlarged teeth, but the relatively small P4 crown suggests this value should be on the low-end

753   regardless. The fossil *Caiman crocodilus* was also affected by missing teeth. It shared almost

754   identical tooth morphology with modern congenerics at similar positions. Because the distal

755   30% of its teeth were missing, Foote's disparity of shape was reduced. This also affected the

756   shape regression, as the lack of high PC1 scores on the distal end reduced the slope. Although

757   both *Crocodylus siamensis* specimens have very high shape-heterodonty due to having both

758   very caniniform and molariform crowns along their arcade, one specimen (AMNH 49231)

759   yielded a very high shape disparity value. This was most likely partially influenced by missing

760   teeth.

761   The two-block PLS test did not factor in heterodonty. Although this was not the goal of

762   this particular analysis, it should be noted that the averaged tooth used for one block

763   essentially eliminates variability of tooth shape along the arcade. Specimens with both low and

764   high shape-heterodonty could produce very similar averages. This highlights the pitfalls of

765   simply averaging all the teeth in the arcade together for the purposes of understanding dental

766   morphology, and why it is avoided in our assessments of heterodonty here.

767   We did not consider all three dimensions. Living crocodylian teeth are often described

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

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

770   2017), indicating that functional information may be drawn from the dimension not measured

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

772   commonplace. *Hamadasuchus rebouli* distal teeth have been referred to as ziphodont (Larsson

773   & Sidor, 1999), but, as this is defined by lateral flattening, our method did not register this

774   character. Future studies should consider this third dimension at least qualitatively, in order to

775   avoid conflating disparate tooth morphotypes such as these.

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

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

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

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

780   account for the serial shape homology seen in Crocodylia. Since PC1 essentially represents

781   molariformy vs. caniniformy from the labial perspective, it could possibly be simplified into a

782   comparison of linear distance measures such as maximum mesial-distal widths and apical-basal

783   heights. These metrics would be not only easy to collect, but also transferable between data

784   sets.

785   These limitations aside, future researchers may apply aspects of this method to a host of

786   non-mammalian taxa. As stated above the semilandmark analysis is very versatile, especially for

787   single-cusped teeth. Foote's disparity can be applied to any measurable taxon with a complete

788   enough tooth row, and is transferable between even disparate groups. Mesial-to-distal linear

789   regressions may be directly applied to any crocodylian, and perhaps certain crocodyliform,

790   specimens with an intact enough tooth row. This could also be applied to PC scores in other

791   non-mammalian taxa, to determine what degree (if any) shape change is linear.

792   We limit our evaluation of interspecific differences, and make no attempt to analyze

793   other factors such as ontogenetic changes (Erickson, Lappin, & Vliet, 2003; Erickson et al., 2004;

794   Gignac & Erickson, 2014; Drumheller, Wilberg, & Sadleir, 2016). These variables may be

795   investigated in the future using our method, as there is nothing to suggest that crocodylian

796   individuals of most species and/or ages could not be be quantified in a similar manner. This

797   method could be very useful in dealing with incomplete fossils. It is common for fossil

798   crocodylian specimens to be lacking many, or even most, of their teeth. The linear nature of

799   tooth shape can predict the shape of these missing teeth. A record of the ranges of slopes may

800   be accumulated for fossil specimens with intact teeth. These slopes may then be used as a

801   reference, and be applied to a fossil with the missing teeth. The preserved teeth can be plugged

802   into the linear equation, and the shapes of missing teeth may be predicted with a high degree

803   of certainty. This would result in a more complete representation of the extinct animal's

804   anatomy, useful from the standpoint of both anatomical science and paleontological

805   reconstruction.

806   Quantifying the teeth of Crocodylia will add rigor to future life history studies of the

807   clade. First and foremost, values may be applied to the plethora of qualitative terms used by

808   researchers (see **Introduction**). This would allow for stricter definitions of the terms when used

809   in the future. As a quantifiable trait, both tooth shape in a single position and heterodonty as a

810   whole may be incorporated into character matrices for phylogenetic analyses. Quantitative

811   descriptors of dentition can describe a numerical range of morphology as opposed to cherry-

812   picking an average tooth or single position. The teeth of fossil taxa can be compared statistically

813   to modern taxa to determine the best analogue, and rigorous hypotheses about paleobehavior

814   and paleoecology may be drawn. Crocodylia, both living and extinct, may be grouped into

815   dental categories, allowing for species and specimens to be compared to one another (similar

816   to snouts in Brochu, 2001). Frequency, size, and hardness of food items may be compared to

817   these categories to determine if a link exists between dental morphotypes and dietary patterns

818   (similar to Aoki, 1989). Crocodylians are used in both performance and actualistic taphonomy

819   studies frequently (Njau & Blumenschine, 2006; Erickson et al., 2012, 2014; Drumheller &

820   Brochu, 2014; 2016), and the output of these studies could be correlated with tooth

821   dimensions. Tooth shape may also be compared to bite-force, death-rolling, bone-modification,

822   and prey preferences and mechanical properties.

823   **CONCLUSION**

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

825   thorough manner across a number of both extinct and extant crocodylian specimens. Through a

826   combination of Foote's morphological disparity and regression analysis along the tooth row,

827   our data indicates that crocodylians are indeed heterodont with a number of dental

828   morphotypes available spanning from extreme cases of caniniform to molariform. This

829   variability may be functional in nature, and relate to the size, frequency, and compliance of

830   certain prey in their typically generalist diets. The methods used here should be applied in the

831   future to most crocodylian specimens, as well as other non-mammalian tetrapods, to

832   investigate dental morphology in the context of a number of natural history related questions.

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1210 **FIGURE LEGENDS**

1211 **Figure 1: Data collection methods.** A) We numbered teeth based on position and host bone

1212 (only the left teeth are labeled). Teeth P4, M5, and M10 are defined as the enlarged teeth in

1213 this specimen. B) We photographed each tooth individually, and traced the margins. The

1214 software converted each outline into 30 equidistant coordinates. Three coordinates were

1215 transformed into landmarks (magenta) and the rest into semilandmarks (green). C) For skulls,

1216 we produced an outline from the dorsal perspective, with 50 coordinates on each margin that

1217 were transformed into landmarks (magenta) and semilandmarks (green). (Specimen depicted:

1218 *Crocodylus palustris* AMNH 96134.) [Half page width]

1219 **Figure 2: Variability within the first principal component for teeth.** A) Vector diagrams indicate

1220 the maximum range of variance (vectors) from the mean (points) for both cranial and dentary

1221 teeth. Landmarks are in magenta and semilandmarks are in green. B) Scores from the first and

1222 second principal components are plotted in a morphospace, with major taxonomic groupings

1223 labeled. [Full page width]

1224 **Figure 3: Partial Least Squared (PLS) two-block analysis of shape**. A) Vector diagrams indicate

1225 shape variance of PLS1 for skull shape (Block 1) and average tooth shape (Block 2). B) PLS1

1226 scores for both blocks were regressed, with colors and shapes representing species. Regression

1227 information is listed. [Full page width]

1228 **Figure 4: Heterodonty represented by Foote's morphological disparity.** Ln scaling of

1229 Morphological Disparity (MD) for size (A) and shape (B) are plotted against the ln of skull length.

1230 Colors and shapes represent species, and regression information is listed. [Half page width]

1231 **Figure 5: Heterodonty by tooth position.** Centroid Size (CS) and principal component one (PC1)

1232 for extant Alligatoroidea (A,D), Crocodyloidea (B,E) , and remaining taxa (C,F), plotted against

1233 position along the arcade. Colors represent major taxonomic groups. See Figure 2 for a visual

1234 representation of shape change depicted by PC1 scores. [Full page width]

1235 **Figure 6: Regression information for shape heterodonty.** Slope (m) and y-intercept (b) data for

1236 regressions of the first principal component plotted against tooth position for individuals. Error

1237 bars indicate 95% confidence intervals, and colors and shapes represent species. Regression

1238 statistics are available in Table S2. [Full page width]

1239 **Figure 7: Direct comparisons between selected extant and extinct taxa.** The size axis

1240 represents normalized centroid size (ranging from 0.00 to 0.20), and the shape axis represents

1241 scores from the first principal component (ranging from -0.04 to 0.04). Taxa are grouped by A)

1242 modern specimens with high molariform distal teeth, B) modern specimens that display high

1243 size heterodonty, C) slender-snouted specimens, D) *Hamadasuchus rebouli*, E) *Borealosuchus*

1244 *sternbergii* and *Leidyosuchus canadensis*, and F) fossil globidont specimens. (Note:

1245 *Borealosuchus sternbergii* teeth were not size normalized by its own skull length, as indicated

1246 by hollow bars.) Scale = five 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 in this specimen. B) We photographed each tooth individually, and traced the margins. The software converted each outline into 30 equidistant coordinates. Three coordinates were transformed into landmarks (magenta) and the rest into semilandmarks (green). C) 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). (Specimen depicted: *Crocodylus palustris* AMNH 96134.) [Half page width]
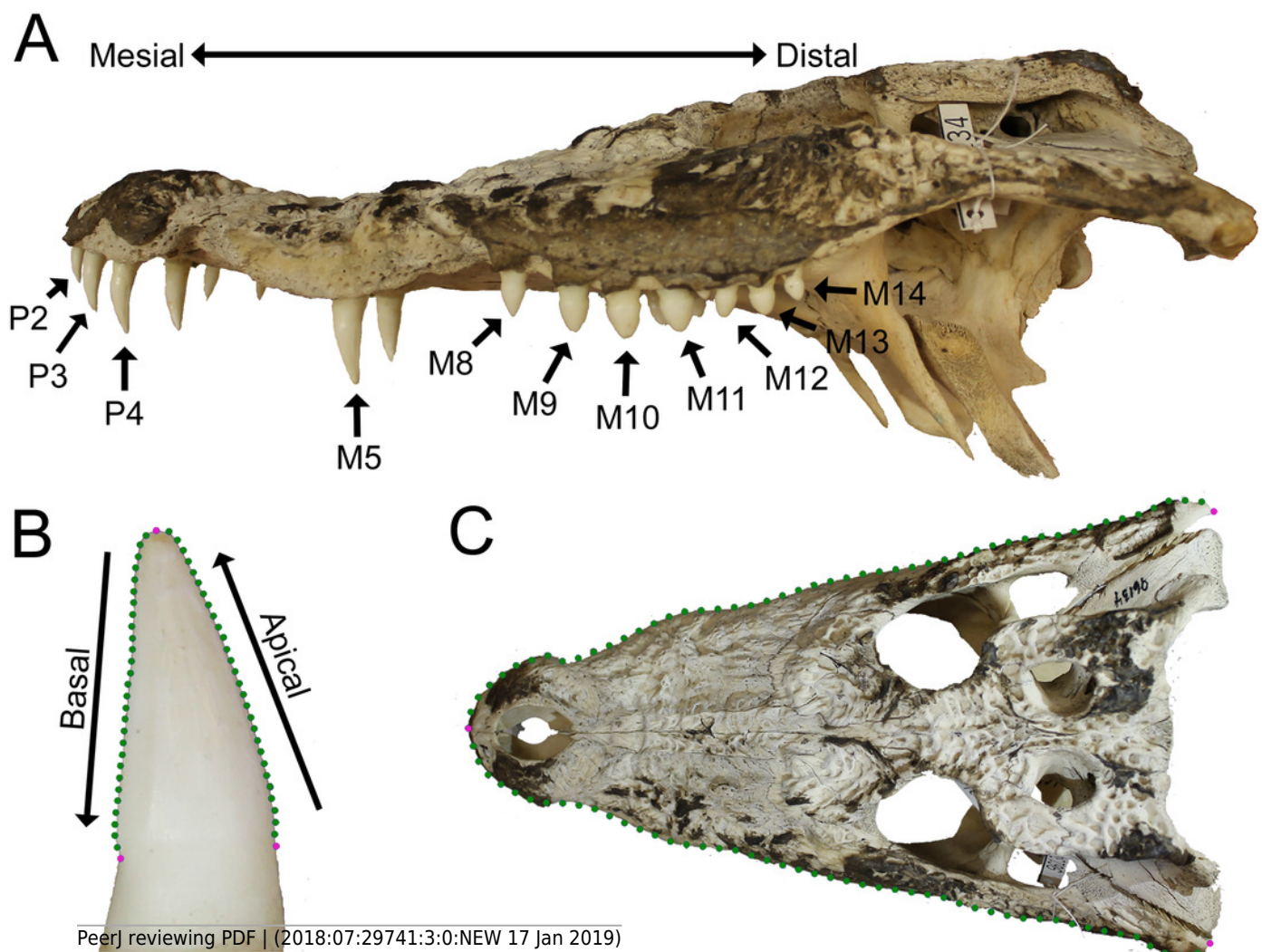
Figure 2

Variability within the first principal component for teeth.

A) 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. B) Scores from the first and second principal components are plotted in a morphospace, with major taxonomic groupings labeled. [Full page width]
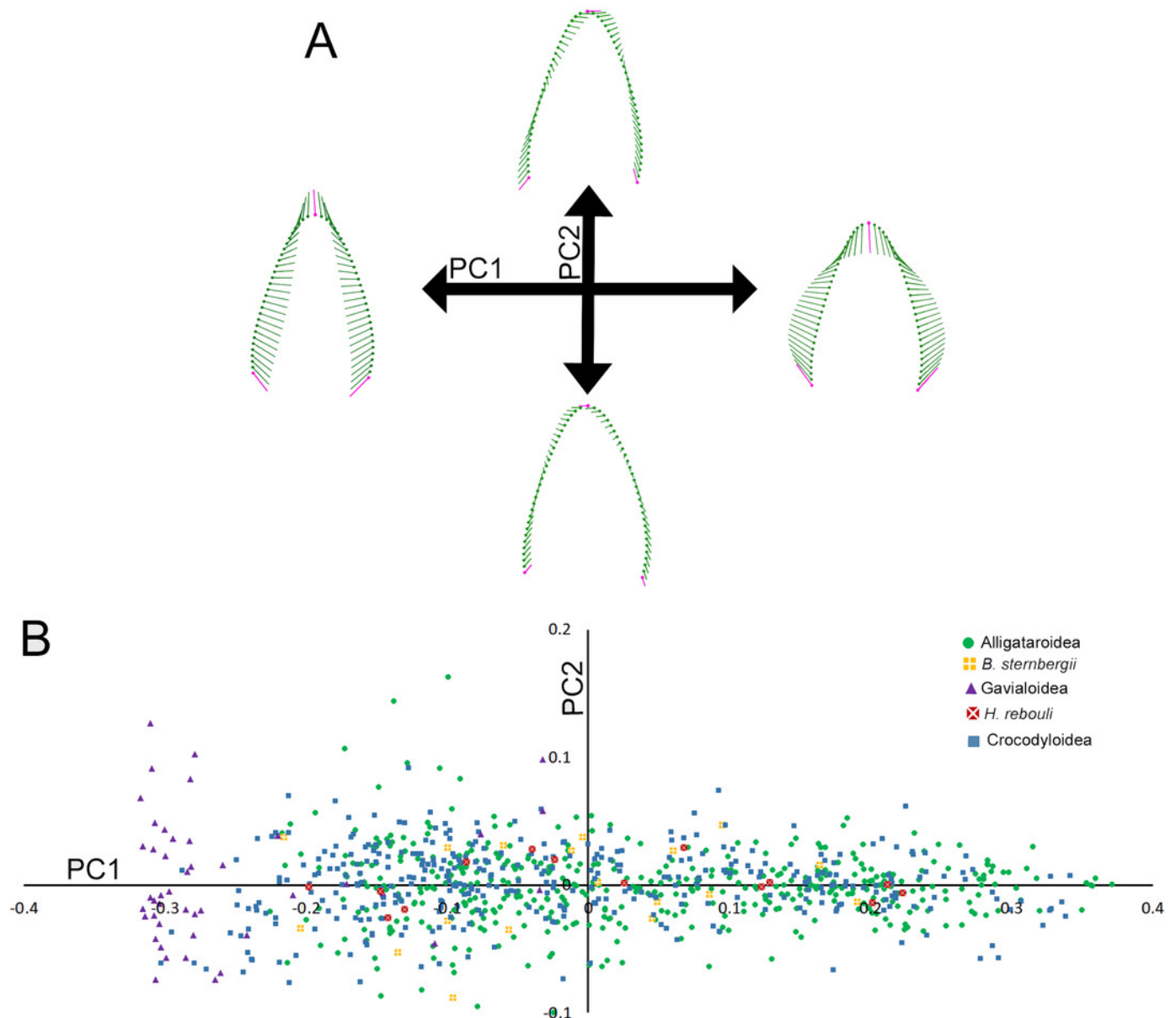
Figure 3

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

A) Vector diagrams indicate shape variance of PLS1 for skull shape (Block 1) and average tooth shape (Block 2). B) PLS1 scores for both blocks were regressed, with colors and shapes representing species. Regression information is listed. [Full page width]
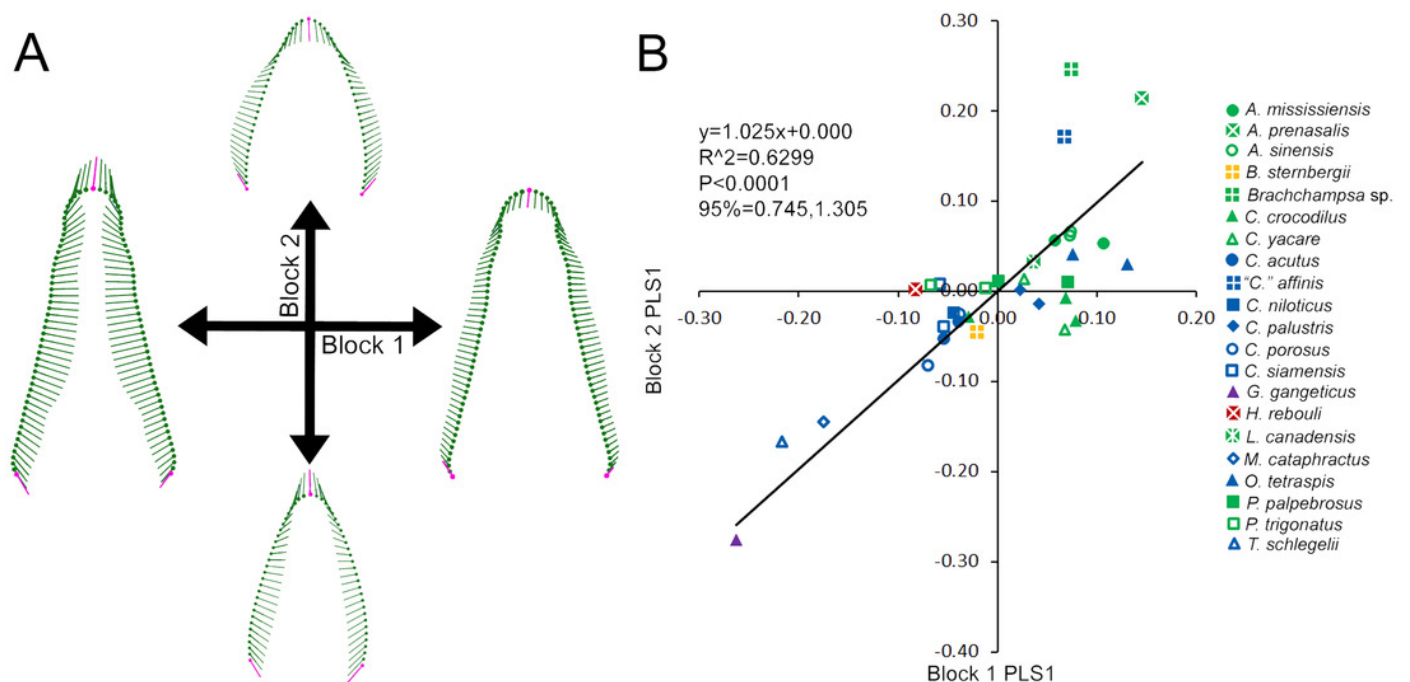
Figure 4

Heterodonty represented by Foote's morphological disparity

Ln scaling of Morphological Disparity (MD) for size (A) and shape (B) are plotted against the ln of skull length. Colors and shapes represent species, and regression information is listed. [Half page width]

A

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

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(Skull Length)

● *A. mississiensis*	⊠ *A. prenasalis*	○ *A. sinensis*	⊞ *B. sternbergii*	▦ *Brachchampsa* sp.
▲ *C. crocodilus*	△ *C. yacare*	● *C. acutus*	▦ *"C." affinis*	■ *C. niloticus*
◆ *C. palustris*	○ *C. porosus*	□ *C. siamensis*	▲ *G. gangeticus*	⊠ *H. rebouli*
⊠ *L. pakistanensis*	▲ *M. cataphractus*	▲ *O. tetraspis*	■ *P. palpebrosus*	□ *P. trigonatus*
△ *T. schlegelii*				
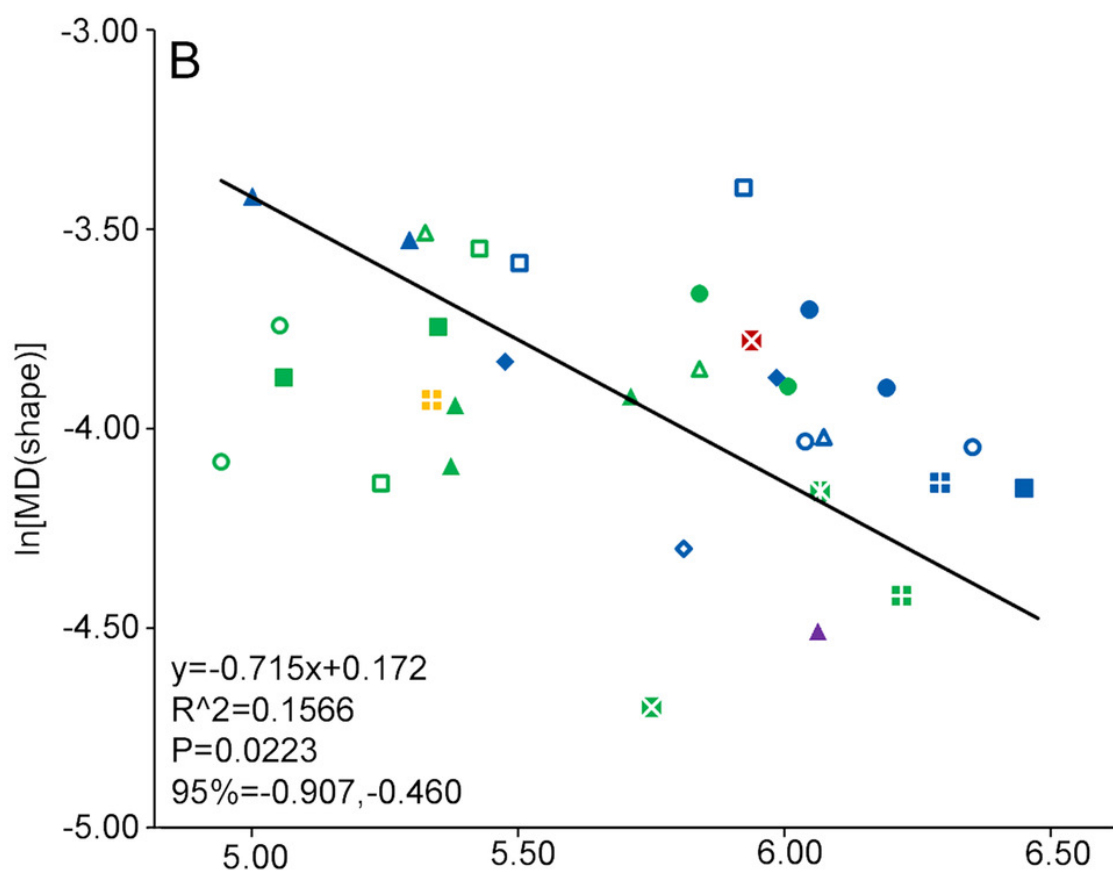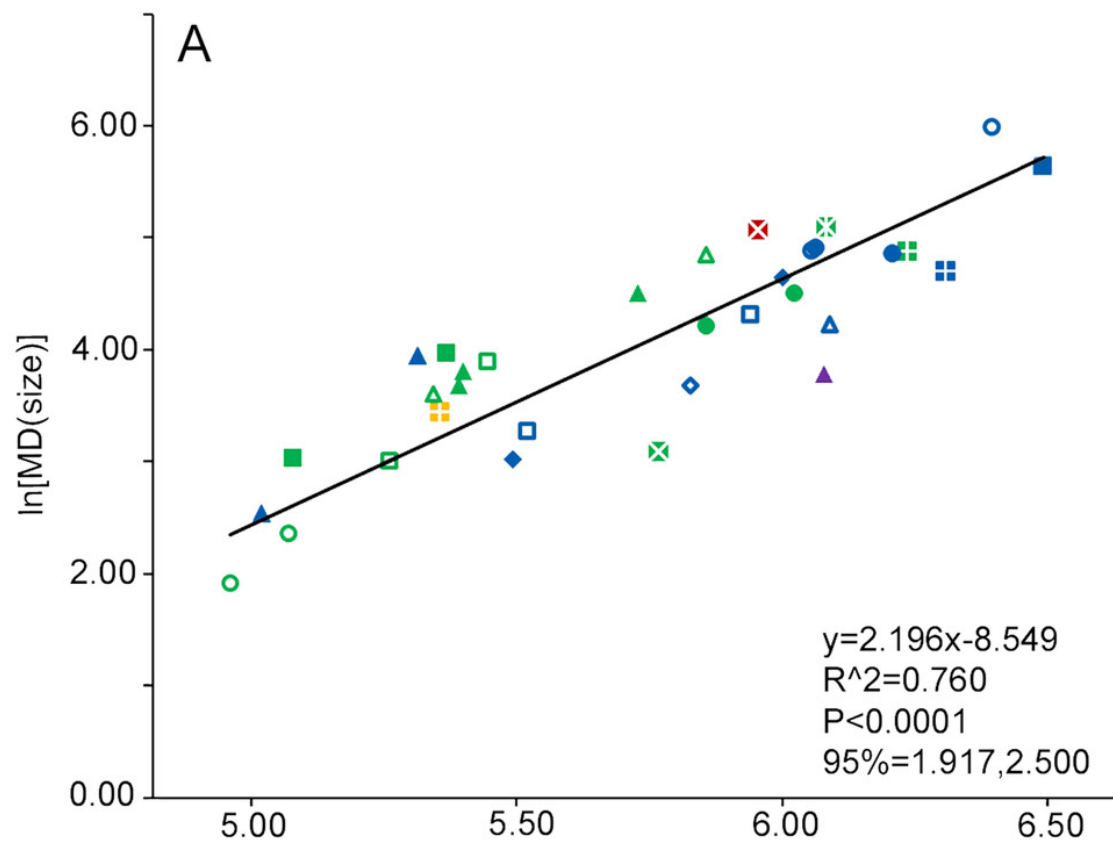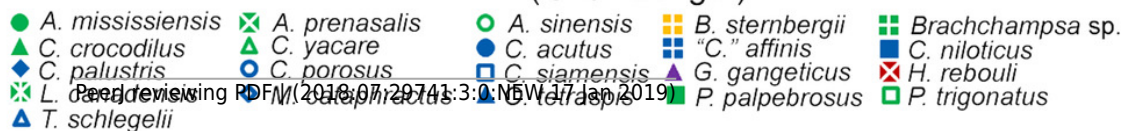
Figure 5

Heterodonty by tooth position

Centroid Size (CS) and principal component one (PC1) for extant Alligatoroidea (A,D), Crocodyloidea (B,E) , and remaining taxa (C,F), plotted against position along the arcade. Colors represent major taxonomic groups. See Figure 2 for a visual representation of shape change depicted by PC1 scores. [Full page width]
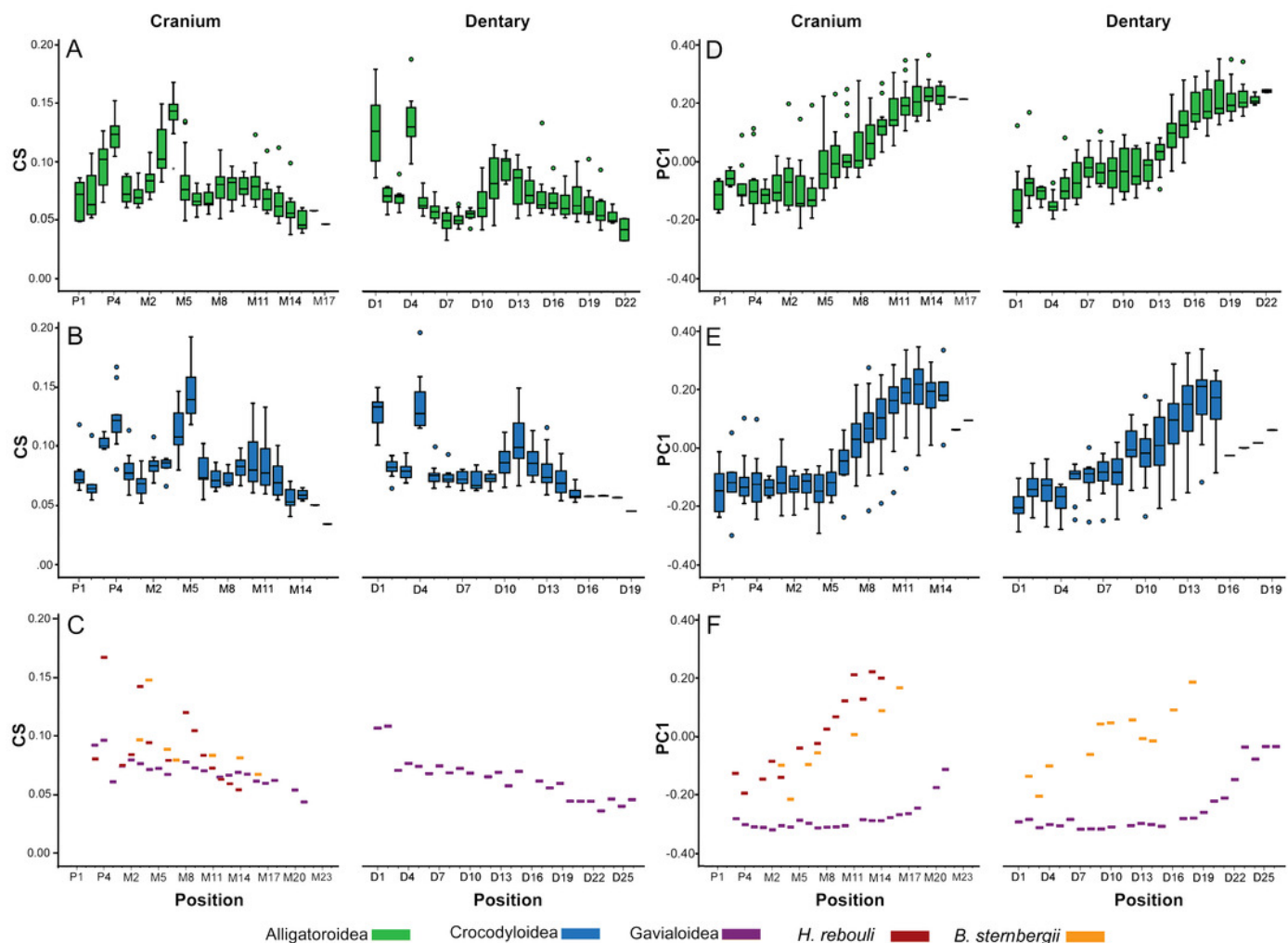
Figure 6

Regression information for shape heterodonty

Slope (*m*) and y-intercept (*b*) data for regressions of the first principal component plotted against tooth position for individuals. Error bars indicate 95% confidence intervals, and colors and shapes represent species. Regression statistics are available in Table S2. [Full page width]
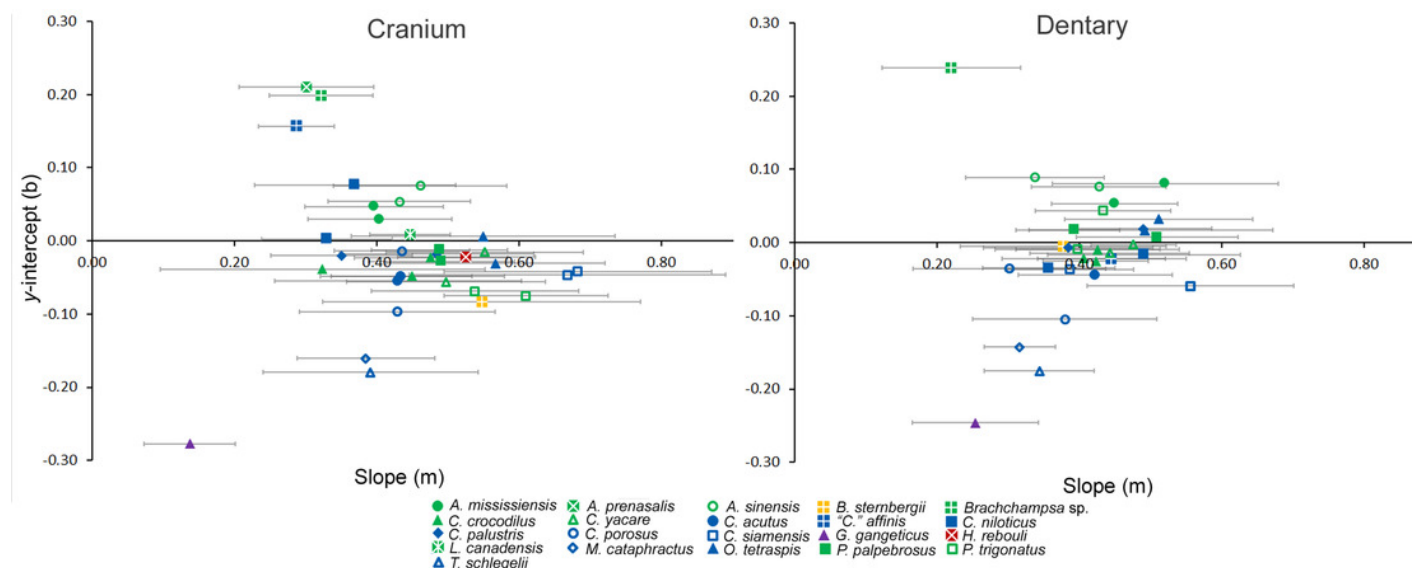
Figure 7

Direct comparisons between selected extant and extinct taxa

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