1 **Title: Mandibular force profiles and tooth morphology in growth series of *Albertosaurus***

2 ***sarcophagus* and *Gorgosaurus libratus* (Tyrannosauridae: Albertosaurinae) provide**

3 **evidence for an ontogenetic dietary shift in tyrannosaurids.**

4

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19 **Abstract**

20 The albertosaurines *Albertosaurus sarcophagus* and *Gorgosaurus libratus* are among the best

21 represented tyrannosaurids, known from nearly complete growth series. These specimens

22 provide an opportunity to study mandibular biomechanical properties and tooth morphology in

23 order to infer changes in feeding behavior and bite force through ontogeny in tyrannosaurids.

24 Mandibular force profiles reveal that the symphyseal region of albertosaurines is consistently

25 stronger in bending than the middentary region, indicating that the anterior extremity of the jaws

26 played an important role in prey capture and handling through ontogeny. The symphyseal region

27 was better adapted to withstand torsional stresses than in most non-avian theropods, but not to

28 the extent seen in *Tyrannosaurus rex*, suggesting that albertosaurine feeding behavior may have

29 involved less bone crushing or perhaps relatively smaller prey than in *T. rex*. The constancy of

30 these biomechanical properties at all known growth stages indicates that although albertosaurines

31 maintained a similar feeding strategy through ontogeny, prey size/type had to change between

32 juvenile and mature individuals. This ontogenetic dietary shift likely happened when individuals

33 reached a mandibular length of ~58 cm, a size at which teeth shift from ziphodont to incrassate

34 in shape and bite force begins to increase exponentially. The fact that large albertosaurines were

35 capable of generating bite forces equivalent to similar-sized tyrannosaurines suggests that no

36 significant differences in jaw closing musculature existed between the two clades and that the

37 powerful bite of *T. rex* is the result of its large body size rather than of unique adaptations related

38 to a specialized ecology.

39 **Keywords**: Feeding behavior, paleoecology, biomechanics, mandibular force profile,

40 Tyrannosauridae, diet

41

Introduction

Tyrannosaurids were the apex predators of Late Cretaceous ecosystems in Asia and North America. Originating from small-bodied ancestors that lived during the Middle Jurassic through mid-Cretaceous, tyrannosaurids may have first evolved during the early Late Cretaceous (Loewen et al., 2013; Brusatte and Carr, 2016; Carr et al., 2017; Zanno et al., 2019). Although fragmentary fossil remains potentially referable to Tyrannosauridae have been recovered from upper Santonian (~83.5 Ma) deposits (e.g., Larson, 2008), tyrannosaurid specimens are best known from upper Campanian through upper Maastrichtian rock formations (~77-66 Ma).

In North America, the province of Alberta, Canada, preserves one of the best fossil records of tyrannosaurids for the Campanian-Maastrichtian time interval, with five known taxa: *Albertosaurus sarcophagus* Osborn, 1905, *Daspletosaurus torosus* Russell, 1970, *Gorgosaurus libratus* Lambe, 1914, *Thanatotheristes degrootorum* Voris et al., 2020, and *Tyrannosaurus rex* Osborn, 1905. Arguably, the best sampled tyrannosaurids are *Albertosaurus sarcophagus* from the uppermost Campanian-lower Maastrichtian Horseshoe Canyon Formation and *Gorgosaurus libratus* from the upper Campanian Dinosaur Park Formation, which together form the basal clade Albertosaurinae. These taxa are represented by nearly a dozen skeletons and abundant isolated elements, with specimens ranging in size from small juveniles (estimated skull length ~35 cm) to fully-grown adults (skull length ~100 cm). Such a large sample has allowed for numerous studies to document various aspects of the ontogeny of these tyrannosaurids (e.g., Russell, 1970; Carr, 1999; Currie, 2003a,b; Voris et al. 2019).

In his seminal work on Canadian tyrannosaurids, Dale Russell (1970) studied allometric trends in *Gorgosaurus libratus* using specimens available at the time (then referred to *Albertosaurus libratus*) and demonstrated that young individuals had dramatically different body

65   proportions than adults, trends that were later confirmed in other tyrannosaurid taxa (e.g., Carr,

66   1999, 2020; Currie, 2003a,b; Carr and Williamson, 2004, 2010; Tsuihiji et al., 2011; Voris et al

67   2019). Juveniles had long and slender hindlimbs, narrow skulls, and a ziphodont (i.e., blade-like)

68   dentition, whereas adults had robust builds with massive skulls and incrassate (i.e., inflated)

69   teeth. Such stark differences in morphology between juvenile and adult individuals suggest that

70   the diet, feeding behavior, and ecological niche of *Gorgosaurus*, and likely other tyrannosaurids,

71   changed during ontogeny (e.g., Holtz, 2004, accepted this volume; Paul, 2008; Tsuihiji et al.,

72   2011; Woodward et al., 2019).

73   Many studies have investigated aspects of tyrannosaurid feeding behavior, focusing

74   primarily on large or adult skull morphology, likely due to a paucity of juvenile specimens. The

75   skull and teeth of tyrannosaurids, particularly of *Tyrannosaurus rex*, have been shown to be

76   capable of delivering powerful bites and withstanding high torsional loads, induced by holding

77   onto prey and/or crushing bones (Erickson et al., 1996; Meers, 2002; Rayfield, 2004, 2005;

78   Molnar, 1998, 2008; Gignac and Erickson, 2017; Bates and Falkingham, 2018). Whereas

79   biomechanical properties of the dentary reveal that the symphyseal region of both juvenile and

80   adult tyrannosaurids was dorsoventrally buttressed and adapted to withstand torsional stresses

81   (Therrien et al., 2005), biomechanical properties and morphology of the nasal bones indicate that

82   the skull of juveniles was less apt at withstanding torsional stresses than that of adults (Snively et

83   al., 2006). Neck anatomy and musculature reconstructions indicate tyrannosaurids used

84   "puncture-and-pull" and shake strategies when feeding as opposed to the "rapid strikes" and

85   ventroflexion of the neck to increase bite force typical of other theropods (Snively and Russell,

86   2007). Tooth-marked bones, acid-etched bones, coprolites, and healed injuries indicate that large

87   or mature tyrannosaurids commonly fed on megaherbivores, such as hadrosaurids and

88   ceratopsids (e.g., Chin et al., 1998, 2003; Erickson et al., 1996; Erickson and Olson, 1996;

89   Jacobsen, 1998; Carpenter, 1998; Varricchio, 2001; Fowler and Sullivan, 2006; Hone and

90   Rauhut, 2010; Hone and Watabe, 2010; DePalma et al., 2013), but fossil evidence for diet in

91   juvenile tyrannosaurids is scarce (but see Peterson and Daus, 2019).

92   Although juveniles and ontogenetic series for tyrannosaurid species are rare, a large sample

93   of specimens is known for the albertosaurines *Albertosaurus sarcophagus* and *Gorgosaurus*

94   *libratus*, which allows for a thorough documentation of changes in feeding behavior and bite

95   force through ontogeny in this clade. In this study, we derive mandibular force profiles for

96   albertosaurines and amend the previous study of Therrien et al. (2005) by including many

97   specimens that have been discovered or prepared since and whose taxonomic identity has been

98   revised.

99

100   **Materials and Methods**

101   Insight into the feeding strategy of extinct animals can be gleaned from biomechanical

102   modeling. Numerous methods, involving muscle reconstructions and computer modeling, have

103   been employed in the past two decades to investigate the types of loads skulls can withstand and

104   the bite force of the predator, but these methods are time-consuming, complex, and often require

105   exquisitely-preserved specimens (i.e., complete and undistorted) or complex and expensive

106   computer software (e.g., Rayfield 2004, 2005; Barrett and Rayfield, 2006; Gignac and Erickson,

107   2017; Cost et al., 2020). In contrast, the principles of beam theory can be applied to dentaries

108   (isolated or in complete mandibles) in order to derive mandibular force profiles, which provide

109   information related to the feeding behavior and bite force of a predator. This method has the

110   benefits of being simple, efficient, and non-invasive, as it requires only external dimensions to be

111   measured on the mandible, and has been shown to produce results compatible with the more

112   complex finite-element analyses. Mandibular force profiles have previously been applied to a

113   variety of theropods (Therrien et al., 2005; Jasinski, 2011; Monfroy, 2017) as well as extant and

114   extinct carnivorous mammals (Biknevicius and Ruff, 1992; Therrien, 2005a,b; Christiansen,

115   2007; Blanco et al., 2011; Campbell and Santana, 2017).

116   As this method has been described in details elsewhere (Therrien et al., 2005, 2016, and

117   references therein), only a brief summary will be presented here. Using the external dimensions

118   of the dentary, the biomechanical properties of the mandible can be calculated by assuming that

119   it has a solid elliptical cross-section (i.e., the solid mandible model sensu Therrien et al., 2016).

120   Although dentaries can be partly hollow and are not perfectly elliptical, the solid mandible model

121   has been shown to very closely approximate models that take into consideration the shape and

122   internal bone distribution of the dentary (see Therrien et al., 2016). Various biomechanical

123   properties of the dentary are evaluated at the symphyseal region (3rd alveolus) and middentary

124   region (9th alveolus): (1) the section modulus or maximum bending strength about the

125   mediolateral axis, $Zx = \pi*(\text{dentary width}/2)*(\text{dentary depth}/2)^2/4$; (2) the section modulus or

126   maximum bending strength about the dorsoventral axis, $Zy = \pi*(\text{dentary depth}/2)*(\text{dentary}$

127    $\text{width}/2)^2/4$; (3) the dorsoventral mandibular force, Zx/L, where L is the distance separating each

128   landmark from the articular fossa; and (4) the relative mandibular force (or overall mandibular

129   shape), Zx/Zy. By assuming that bone material property and safety factors are constant in the

130   mandible of vertebrates, Zx/L can be used as a measure of maximum force applied in the

131   dorsoventral plane, i.e., the plane of bite, at each landmark (for details, see Therrien, 2005a).

132   Consequently, the Zx/L value at the 9th alveolus can be used as a bite force proxy for each

133   specimen (Therrien et al., 2005). Although this approach has been argued to underestimate the

134   bite force necessary to produce tooth puncture marks left in bone by theropods (Gignac et al.,

135   2010), its results are comparable to other bite force estimation methods and even approximate *in*

136   *vivo* bite force measurements more accurately than other methods among carnivoran mammals

137   (Therrien et al., 2016). At the very least, bite force estimates derived from mandibular force

138   profiles can be used as proxies for comparison between taxa or individuals. Finally, Zx/Zy values

139   reflect mandibular adaptation to withstand the predominant loads applied at a specific landmark:

140   a ratio greater than 1 represents adaptation toward dorsoventral loads, a ratio lower than 1

141   represents adaptation toward mediolateral loads, and a ratio of 1 represents equal adaptation

142   toward dorsoventral and mediolateral loads, often reflecting the occurrence of torsional stresses

143   (see Therrien, 2005a,b and Therrien et al., 2005).

144   Isolated dentaries and complete mandibles of tyrannosaurids curated at the Royal Tyrrell

145   Museum of Palaeontology (TMP, Drumheller, Alberta, Canada) were considered in this study

146   (see Appendix). A large sample of the albertosaurines *Albertosaurus sarcophagus* (12

147   specimens) and *Gorgosaurus libratus* (23 specimens), representing ontogenetic series ranging

148   from the smallest known individual to the largest, was measured. For comparative purposes,

149   original specimens and casts of the tyrannosaurines *Daspletosaurus torosus* (two specimens) and

150   *Tyrannosaurus rex* (five specimens), and of various non-tyrannosaurid theropods present in the

151   RTMP collections were also measured (see Appendix). Although tyrannosaurid specimens are

152   also present at other institutions across North America, access was greatly limited due to the

153   COVID-19 pandemic; as such, few non-TMP specimens could be included in the study.

154   Various dimensions of dentaries, in situ teeth, and tooth alveoli (Fig. 1, Appendix) were

155   measured using calipers, except two specimens still partially embedded in matrix for which

156   dimensions were obtained from computed tomographic (CT) scans. After positioning the

157   mandible/dentary so the symphyseal surface is oriented vertically, the depth and width of the

158   mandibular corpus were measured at two landmarks, in the symphyseal region (3rd alveolus) and

159   in the middentary region (9th alveolus) (Fig. 1a,b). To determine mandibular width at the 3rd

160   alveolus, measurement was done diagonally from the posteroventral most extent of the

161   symphysis to the lateral side of the mid-3rd alveolus (Fig. 1b). The absence of the splenial bone

162   in most specimens represented by isolated dentaries introduces an error in the determination of

163   mandibular width at the 9th alveolus relative to specimens represented by complete lower jaws,

164   but this error is considered minimal due to the thinness of the splenial bone. Distance of each

165   landmark to the anterior extremity of the dentary and to the lateral expression of the articular

166   fossa (in the case of complete mandibles) was also measured (Fig. 1a). The length and depth of

167   the symphysis was measured in medial view (Fig. 1c). The crown base length and crown base

168   width of in situ teeth were measured at the enamel-dentine junction (whenever possible); if teeth

169   were absent, anteroposterior and mediolateral diameters of the alveoli were measured (Fig. 1d).

170   Teeth that were not fully erupted and alveoli that were incomplete or deformed were not

171   measured. Mean crown base ratios were calculated for each specimen based on the dimensions

172   of the 3rd through 15th tooth/alveolus.

173   Data were processed using a variety of software. Tabulation of measurements and

174   calculations were accomplished in Microsoft Excel. Bivariate plots, ordinary least-squares

175   regressions, and reduced major axis regressions were plotted and compared statistically using

176   PAST 4.03 (Hammer et al., 2001) and Golden Software Grapher 10. Statistical analyses were

177   conducted in PAST 4.03.

178

179 **Results**

180   The bending strength (Zx) profiles are similar in both *Albertosaurus* and *Gorgosaurus*, but

181   Zx values at middentary undergo a dramatic 90-fold increase between the smallest and largest

182   specimens studied (Fig. 2a,b). The Zx values are higher at the 3rd tooth than at middentary

183   regardless of ontogenetic stage (Fig 2a,b), although the difference between the two landmarks

184   changes through ontogeny. The gradient of change in bending strength along the tooth row (i.e.,

185   slope between the 3rd and 9th tooth) is minimal in juvenile individuals (slope ~ -0.2) and

186   increases gradually through ontogeny to become pronounced in adult individuals (slope < -1.0)

187   (Fig. 2c). Furthermore, the ratio between the Zx values at middentary and 3rd tooth increases

188   through ontogeny, from less than 0.5 in juveniles to nearly subequal (~0.8) in adults (Fig. 2d).

189   Neither of these ontogenetic trends differ significantly between the two albertosaurines, as their

190   slopes are within the 95% confidence interval of each other, and it is possible that the data for

191   both taxa could be pooled into a single regression (p = 0.18 for slope of Zx values and p = 0.044

192   for ratio of Zx values).

193   Because many specimens studied consist of isolated dentaries or incomplete mandibles,

194   total jaw length and distance to landmarks for these specimens had to be estimated from

195   complete mandibles in order to calculate bending force (Zx/L) and bite force estimates. Jaw

196   length was estimated from two least-squares regressions derived from measurements on

197   complete *Gorgosaurus* mandibles. The first regression documents the relationship between the

198   distance separating the 3rd from the 9th tooth and jaw length (Fig. 3a) and the second regression

199   documents the relationship between the distance separating the 9th tooth from the articular fossa

200   and jaw length (Fig. 3b); both exhibit very high determination coefficients (R^2 = 0.9891 and R^2 =

201   0.9928, respectively). The distance of each landmark to the articular fossa was subsequently

202   estimated from their mean relative position in the sample of complete *Gorgosaurus* mandibles

203   (73% and 94% of total jaw length for 9th tooth and 3rd tooth, respectively) and incorporated into

204   the calculation of bending force. The few *Albertosaurus* specimens with complete mandibles

205   known fall close to the regression, justifying its use to estimate jaw length in this taxon. When

206   the regressions are extrapolated to the size of *Daspletosaurus torosus* and *Tyrannosaurus rex*

207   specimens, the distance to the 9th alveolus is found to be a very good predictor of mandible

208   length in these taxa, whereas the distance between 3rd and 9th alveolus is a less accurate predictor

209   (Fig. 3a,b).

210   As is the case for bending strength, the bending force (Zx/L) profiles are similar in both

211   *Albertosaurus* and *Gorgosaurus*, but Zx/L values at middentary undergo a 32-fold increase

212   between the smallest and largest specimens studied (Fig. 4a,b). Except for one specimen, the

213   Zx/L values are higher at the 3rd tooth than at middentary at all ontogenetic stages (Fig 4a,b).

214   However, unlike what was observed for bending strength (Zx), there is no predictable change in

215   Zx/L related to ontogeny (regression slopes near 0 and $R^2 < 0.13$; Fig. 4c). Rather, the gradient

216   of change in bending force along the tooth row (i.e., slope between the 3rd and 9th tooth) remains

217   relatively constant through ontogeny (slope ~0.2-0.3), but with higher variation among larger

218   individuals (Fig. 4c). In contrast, the ratio between the Zx/L values at middentary and 3rd tooth

219   increases through ontogeny, from ~0.4 in juveniles to nearly subequal (~1.00) in adults (Fig. 4d).

220   Neither of these ontogenetic trends differ significantly between the two albertosaurines, as their

221   slopes are within the 95% confidence interval of each other, and it is possible that the data for

222   both taxa could be pooled into a single regression for the ratio of Zx/L values (p = 0.05).

223   The relative mandibular force (Zx/Zy) profiles for *Albertosaurus* and *Gorgosaurus* show

224   similar tendencies but with a lot of variation, likely due to either intraspecific differences or

225   subtle taphonomic deformation of the mandibular corpus. The Zx/Zy values are higher at

226   middentary than at the 3rd tooth, with values indicating that the mandibular corpus remains

227   nearly twice as deep as it is wide at middentary (Zx/Zy ~ 2.0) throughout ontogeny (Fig. 5). In

228   contrast, the mandible is much rounder near the symphysis in both albertosaurines, with Zx/Zy

229   values that vary between 1.3 and 1.7 throughout ontogeny (Fig. 5).

230   Given that bite force is usually estimated/compared at consistent locations along the

231   toothrow (e.g., at the most prominent maxillary tooth or at the molariform teeth) in extant

232   crocodylians (see Erickson et al. 2003, 2004, 2012 and Gignac and Erickson, 2015) and in non-

233   avian theropods (e.g., Rayfield, 2004; Gignac and Erickson, 2017), the use of bending force

234   (Zx/L) values at the 9th tooth (near the location of the most prominent maxillary tooth) as a proxy

235   for bite force in theropods is justifiable (see Therrien et al., 2005). A very close relationship (R^2

236   = 0.99) exists between depth of the mandibular corpus and bending force at middentary (Fig. 6a),

237   making it possible to estimate the bite force of specimens for which dentary width cannot be

238   measured, because they are either damaged or still enclosed in matrix or a field jacket. When

239   plotted as a function of estimated jaw length, Zx/L values in *Albertosaurus* and *Gorgosaurus*

240   follow an exponential regression (R^2 = 0.95; Fig. 6b). Whereas Zx/L values increase slowly

241   among small individuals (an increase of 0.09 over a 20-cm increase in jaw length), values start

242   increasing rapidly at a jaw length of ~58 cm (an increase five times greater over a similar jaw

243   length). An incomplete *Gorgosaurus* skull missing the anterior portion of the skull, TMP

244   1992.36.1220, is recovered as the largest known albertosaurines (estimated jaw length ~103 cm)

245   with an estimated bite force (Zx/L = 1.31) on par with similar-sized individuals of

246   *Tyrannosaurus rex* (TMP 1981.6.1, jaw length ~106.4 cm, Zx/L = 1.33). The inclusion of bite

247   force estimates for individuals of the tyrannosaurines *Daspletosaurus torosus* and *Tyrannosaurus*

248   *rex* produces a second exponential regression ($R^2 = 0.95$) that is not significantly different from

249   the albertosaurine regression (i.e., slopes within the 95% confidence interval of each other),

250   indicating that tyrannosaurines follow the same trend as albertosaurines (Fig. 6b). Comparison

251   with bite force estimates of non-tyrannosaurid theropods (Therrien et al., 2005) reveals that bite

252   force increases much faster in tyrannosaurids than in other theropods once individuals reach a

253   mandible length of ~60 cm and that subadult and adult tyrannosaurids were capable of

254   generating bite forces far greater than similar-sized or larger non-tyrannosaurid theropods (Fig.

255   6c).

256   Tooth crown base ratio changes during ontogeny in both *Albertosaurus* and *Gorgosaurus*

257   (Figs. 7a and 8). In the smallest individuals (mandible length < 40 cm), the dentition is highly

258   ziphodont, with a crown base ratio > 2.1. In slightly larger juveniles (mandible length 40-60 cm),

259   teeth are slightly wider relative to their mesiodistal diameter, with crown base ratios ~1.6-1.8.

260   Finally, teeth attain their widest cross-sectional proportions (crown base ratios ~1.3-1.5) in

261   individuals with a mandibular length of 58 cm and longer (i.e., late juvenile through adult

262   stages). The score for the *Albertosaurus* individual with the lowest crown base ratio is based on a

263   single 3rd tooth, a tooth that has a rounder cross-section than more posterior teeth.

264   The proportions of the mandibular symphysis do not appear to change through ontogeny in

265   *Albertosaurus* and *Gorgosaurus* as there is no correlation between symphysis length:depth ratio

266   and mandible length ($p = 0.66$; Fig. 7b). Despite a lot of intraspecific variation in length:depth

267   ratios in the studied specimens ($R^2 < 0.02$ for both regressions), the mandibular symphysis

268   remains of subequal proportion (~1) at all body sizes. This is congruent with the observations of

269   Therrien et al. (2005), who noted that the mandibular symphysis of all tyrannosaurids is strongly

270   inclined posteroventrally, with an anteroposterior extent nearly equal to its dorsoventral extent,

271   in contrast to that of most non-avian theropods where it is oriented subvertically.

272

273   **Discussion**

274   This study provides insights into the ontogenetic changes in feeding adaptations of the

275   mandible in the albertosaurines *Albertosaurus sarcophagus* and *Gorgosaurus libratus*. The

276   dramatic increase in resistance to bending (90-fold increase in Zx values and 32-fold increase in

277   Zx/L values) observed between the smallest and largest specimens studied clearly reflect the

278   effect of increase in body size through ontogeny. The symphyseal region of the mandible is

279   consistently stronger in bending (both Zx and Zx/L) than the middentary region at all ontogenetic

280   stages (Figs. 2a and 4a). A strong symphyseal region is found in predators that use the front of

281   their jaws to bite, seize and dismember prey (see Therrien, 2005a,b; Therrien et al., 2005, 2016)

282   in contrast to predators that deliver slashing bites (i.e., do not hold onto their prey), like varanids

283   (Therrien et al., 2005) and as inferred for many non-avian theropods (Therrien et al., 2005;

284   Jasinski, 2011). The fact that this relationship remains consistent through ontogeny indicates that

285   the hunting strategy of albertosaurines did not change as the animals grew and that the anterior

286   extremity of the jaws played an important role to bite, seize, and dismember prey at all growth

287   stages.

288   The relationship between the symphyseal and middentary region in albertosaurines is

289   different from the one observed in the only other large carnivorous theropod with a well-known

290   growth series , *Allosaurus fragilis* Marsh, 1877. Contrary to albertosaurines, the Zx values in the

291   symphyseal region of *A. fragilis* are lower than at middentary but gradually increase relative to

292   the latter as animals became larger (Therrien et al., 2005). This trend was interpreted to indicate

293   that a change in feeding behavior occurred through ontogeny, where juveniles either delivered

294   slashing bites (i.e., did not hold onto prey) or fed on small prey that did not require a

295   strengthened symphyseal region for capture. The role played by the anterior extremity of the

296   jaws became more important with age in *A. fragilis*, likely associated with capturing and

297   handling larger prey (Therrien et al., 2005). Although these authors mentioned that this

298   ontogenetic change in mandibular adaptations could reflect the existence of parental care in *A.*

299   *fragilis*, where parents brought food to young individuals as previously proposed by Bakker

300   (1997), they suggested that such changes could also be due to a gradual transition in the type/size

301   of prey hunted through ontogeny (e.g., from insects to amphibians, lizards, mammals, small

302   dinosaurs, and ultimately large dinosaurs), as occurs in extant Komodo dragons (*Varanus*

303   *komodoensis* Ouwens, 1912) and crocodylians (e.g., Cott, 1961; Auffenberg, 1981; Gignac and

304   Erickson, 2015; Grigg and Kirshner, 2015; Purwandana et al., 2016).

305   Similar to the patterns observed in bending strength, no change in relative mandibular

306   force (Zx/Zy) is observed through ontogeny in *Albertosaurus* and *Gorgosaurus* (Fig. 5). With

307   Zx/Zy values >2 at the middentary, the mandibular corpus is predominantly adapted for

308   dorsoventral bending loads associated with biting, as in other non-avian theropods (Therrien et

309   al., 2005). Although it had previously been suggested that the dentary became deeper than wide

310   during ontogeny in tyrannosaurids (Carr, 1999; Therrien et al., 2005), the nearly constant Zx/Zy

311   values at middentary across the growth series suggest that this might not be the case (Fig. 5). The

312   Zx/Zy values at the 3rd tooth vary between 1.3 and 1.7 at all growth stages in both

313   albertosaurines, which is similar to *Daspletosaurus torosus* (1.24-1.47) and *Allosaurus fragilis*

314   (mean Zx/Zy = 1.5) but much lower than in many non-avian theropods (e.g., dromaeosaurids,

315   *Ceratosaurus nasicornis* Marsh, 1884, *Giganotosaurus carolinii* Coria and Salgado, 1995).

316   These non-avian theropods have high Zx/Zy values (> 2) indicative of predominant dorsoventral

317   bending loads and slashing bites (Therrien et al., 2005). Even lower Zx/Zy values occur in

318   *Tyrannosaurus rex* (1.19-1.30, slightly higher than the mean of 0.94 reported in Therrien et al.

319   [2005]) and the spinosaurid *Suchomimus tenerensis* Sereno et al., 1998 (Zx/Zy = 0.44), which

320   have been interpreted to indicate that major torsional stresses occurred at the symphysis related

321   to holding onto prey or crushing bones (Therrien et al., 2005). The fact that albertosaurines

322   possess Zx/Zy values at the 3rd tooth that are intermediate between those of *T. rex* and those of

323   most non-avian theropods suggests that their symphysis underwent greater torsional stresses than

324   non-avian theropods that delivered slashing bites, but not as high as in *Tyrannosaurus rex*.

325   Because the latter is known to have been capable of crushing bones with its bite, a source of

326   significant torsional stresses (Erickson et al., 1996; Meers, 2002; Rayfield, 2004, 2005; Therrien

327   et al., 2005; Gignac and Erickson, 2017), it is possible the higher Zx/Zy values of albertosaurines

328   reflect a feeding behavior that involved less bone crushing or perhaps relatively smaller prey

329   than in *T. rex*. Although albertosaurines possess slenderer teeth and less robust skulls than

330   similar-sized tyrannosaurines (Carr, 1999; Paul, 2008), their feeding behavior likely still

331   involved activities that produced torsional stresses at the symphysis, such as capturing, holding,

332   and dismembering prey. This is reflected also by the posteroventral extension of their mandibular

333   symphysis, an adaptation to sustain torsional stresses (Hylander, 1984), and consistent with tooth

334   shape, multidirectional microwear, and neck musculature reconstructions, which indicate that

335   complex head shaking movements were involved in feeding (Farlow et al., 1991; Abler, 1992,

336   1997, 1999, 2001; Snively and Russell, 2007).

337   The lack of change in both relative mandibular force and symphyseal proportions through

338   ontogeny in albertosaurines (Figs. 5 and 7b) indicates that significant torsional stresses induced

339   while feeding were present at all known growth stages. Given the reduced nature of the forelimbs

340   in tyrannosaurids, prey capture would have been accomplished primarily with the jaws, hence

341   the need for the symphysis to be able to withstand torsional stresses. The fact that the mandible

342   of juvenile albertosaurines displays the same biomechanical properties as those of adult

343   individuals suggests that the anterior extremity of the jaw played an important role in prey

344   capture and handling throughout ontogeny in these animals. Although little is known about the

345   feeding behavior of very small individuals due to the lack of fossils, our results indicate that

346   juvenile albertosaurines were likely active predators at least by the time they reached a mandible

347   length of ~35 cm (the smallest individual examined in this study), capable of capturing their own

348   prey, like adult individuals, rather than being limited to feeding on prey previously killed by

349   conspecifics (either through extended parental care or by members of a pack) or scavenging

350   carcasses. Indeed, juvenile carnivoran mammals that feed on prey killed by parents or pack

351   members possess different symphyseal adaptations than adult conspecifics, where Zx/Zy values

352   are significantly higher (i.e., symphysis undergoes less torsional loads) than those of adults

353   because they do not need to seize or restrain their prey (Therrien, 2005a). In contrast, juvenile

354   carnivorans that actively participate in the capture and killing of prey do not have significantly

355   different Zx/Zy values than adults, as their jaws are subjected to similar torsional loads as those

356   of adults (Therrien, 2005a). Thus, it can be concluded that juvenile albertosaurines actively

357   captured their prey, otherwise their mandibular adaptations would have differed from those of

358   adults.

359　　　　　Given the constancy of mandibular force profiles through ontogeny, prey species/size

360　　　　selection must have changed from small juveniles to multi-ton adult albertosaurines. Compared

361　　　　to adults, juvenile individuals would likely have preyed upon smaller species/individuals (e.g.,

362　　　　small ornithischians/theropods) in order to maintain *relatively* similar torsional loads on their

363　　　　jaws (i.e., similar Z_x/Z_y values in juveniles and adults). Otherwise, the capture of large prey

364　　　　would have induced *relatively* greater loads on the jaws of juveniles than adults and thus would

365　　　　have resulted in different mandibular adaptations (i.e., lower Z_x/Z_y values in juveniles reflecting

366　　　　resistance to greater torsional stresses at the symphysis) (see Therrien et al., 2005). Feeding

367　　　　traces (e.g., tooth-marked bones, coprolites) show that mature tyrannosaurids commonly fed on

368　　　　megaherbivorous dinosaur taxa, such as hadrosaurs and ceratopsids (e.g., Chin et al., 1998, 2003;

369　　　　Erickson et al., 1996; Erickson and Olson, 1996; Jacobsen, 1998; Carpenter, 1998; Fowler and

370　　　　Sullivan, 2006; Hone and Rauhut, 2010; Hone and Watabe, 2010; DePalma et al., 2013), and

371　　　　occasionally practiced cannibalism (Bell and Currie, 2010; Longrich et al., 2010; Hone and

372　　　　Tanke, 2015; Mclain et al., 2018), but little is known in regards to the diet of juvenile

373　　　　individuals. Although small, closely-spaced tooth marks are occasionally observed on small

374　　　　ornithischian bones (e.g., ossified tendons, ribs; pers. obs.), it is impossible to determine if they

375　　　　were produced by juvenile tyrannosaurids or by any of the small-bodied theropods (e.g.,

376　　　　dromaeosaurids, troodontids) that lived in the same ecosystems. To date, tooth marks left on a

377　　　　subadult individual of the dromaeosaurid *Saurornitholestes langstoni* and a juvenile individual of

378　　　　the hadrosaurine *Edmontosaurus annectens* are the only feeding traces that have been ascribed to

379　　　　juvenile tyrannosaurids, a small juvenile tyrannosaurid in the former case (Jacobsen, 2001) and a

380　　　　late juvenile stage individual in the latter (Peterson and Daus, 2019). Nevertheless, the similarity

381　　　　in mandibular adaptations at all known growth stages in albertosaurines reveals that the method

382   of prey capture must not have changed greatly and that juveniles must have fed on relatively

383   smaller prey or else the biomechanical properties of their symphyseal region would have differed

384   from those of adults.

385   The disproportionate increase in bending resistance of the middentary region relative to the

386   symphyseal region observed through ontogeny in albertosaurines (Figs. 2c,d and 4c,d) is likely

387   an adaptation to the increasing bite force as animals grew. Since the amount of force that can be

388   generated during a bite increases posteriorly along the toothrow due the lever advantage

389   provided by the proximity to the jaw joint (e.g., Greaves, 1995), the mandibular corpus at

390   middentary needs to become more resistant against dorsoventral bending than the symphyseal

391   region to withstand increases in bite force. Given that relative mandibular force profiles (Zx/Zy)

392   remain constant through ontogeny (Fig. 5), the disproportionate increase in bending resistance of

393   the middentary region relative to the symphyseal region is not due to a decrease of feeding-

394   related torsional stresses through ontogeny, contrary to Therrien et al.'s (2005) hypothesis.

395   Rather, it is solely due to the increase in bite force, otherwise the Zx/Zy values would have

396   increased through ontogeny.

397   Bite force changes dramatically through ontogeny in albertosaurines, undergoing a 40-fold

398   increase between the smallest (TMP 1994.12.155, ~35 cm mandibular length) and largest (TMP

399   1992.36.1220, ~103 cm mandibular length) specimens studied (Figs. 6 and 8). Bite force

400   increases slowly among small individuals but begins an exponential increase in late juvenile

401   stage individuals (mandible length ~58 cm, body length ~ 5.5 m based on TMP 1991.36.500).

402   The fact that large albertosaurines follow the same trend as and even overlap with specimens of

403   *Daspletosaurus torosus* and *Tyrannosaurus rex* indicates that both albertosaurines and

404   tyrannosaurines were capable of generating similar bite forces, suggesting that no major

405   differences in jaw closing musculature existed between the two clades. A similar pattern is

406   observed in crocodylians, where ontogenetic trends in bite force are similar among different

407   species due to similarity in jaw-closing musculature and mechanical leverage (Erickson et al.,

408   2012). Since the largest albertosaurine known (*Gorgosaurus libratus* TMP 1992.36.1220) and

409   the similar-sized *T. rex* specimen TMP 1981.6.1 are recovered here as having similar bite forces,

410   the previously-published bite force estimates of 12,197-21,799 N for the latter specimen (Gignac

411   and Erickson, 2017) can be hypothesized to represent the maximum bite force producible by

412   adult albertosaurines. Furthermore, our results indicate that the high bite forces predicted for *T.*

413   *rex* (e.g., Erickson et al., 1996; Meers, 2002; Rayfield, 2004, 2005; Gignac and Erickson, 2017;

414   Bates and Falkingham, 2018) can be explained by the extrapolation of the tyrannosaurid trend to

415   extremely large body size rather than as the result of unique adaptation(s) in *T. rex* for a

416   specialized ecology (e.g., bone crushing). Reported differences in craniodental robusticity

417   between similar-sized albertosaurines and tyrannosaurines (e.g., Carr, 1999; Currie, 2003a,b;

418   Paul, 2008) are likely not related to differences in bite force but could reflect taxonomic

419   differences or differences in feeding behavior (i.e., adaptations to higher torsional stresses).

420   The exceptional bite force of tyrannosaurids is apparent when compared to that of non-

421   tyrannosaurid theropods (Fig. 6c). The exponential regression describing the ontogenetic

422   increase in bite force among tyrannosaurids is far steeper than that describing bite force among

423   non-tyrannosaurid theropods, indicating that bite force increased much faster as a function of

424   body size in tyrannosaurids than in other theropods. Whereas very young through late juvenile

425   tyrannosaurid individuals (up to mandible length ~60 cm) had a bite force comparable to that of

426   similar-sized subadult/adult individuals of several non-tyrannosaurid theropods (e.g.,

427   dromaeosaurids, *Allosaurus fragilis*, *Ceratosaurus nasicornis*), the bite force of subadult and

428   adult tyrannosaurids far surpassed that of similar-sized non-tyrannosaurid theropods. For

429   example, subadult tyrannosaurids had a bite force on par with *Acrocanthosaurus atokensis*

430   Stovall and Langston, 1950, a theropod with a mandible 30-40 cm longer, whereas *T. rex* could

431   generate bite forces three to five times greater than the similar-sized *Acrocanthosaurus* and the

432   larger *Giganotosaurus*. The significantly higher bite force of subadult and adult tyrannosaurids

433   relative to similar-sized theropods supports previously-published inferences that tyrannosaurids

434   had a dramatically different feeding behavior, where prey was captured and subdued primarily (if

435   not exclusively) through powerful bites whereas other theropods relied on slashing attacks

436   delivered with their jaws and claws (e.g., Holtz, 2003; Rayfield, 2004, 2005; Therrien et al.,

437   2005; Snively et al., 2006).

438   A few non-tyrannosaur theropod taxa appear as outliers on the bite force regression and

439   warrant a brief discussion. The abelisaurids *Carnotaurus sastrei* Bonaparte et al., 1990 and

440   *Majungasaurus crenatissimus* (Depéret, 1896) plot well above both regressions, but this is likely

441   due to their short skull (and hence short mandible), equivalent to that of a juvenile albertosaurine

442   (~50 cm); if bite force estimates could be presented as a function of body mass, abelisaurids

443   would likely plot closer to the non-tyrannosaur theropod regression. In contrast, the spinosaurid

444   *Suchomimus* and the carcharodontosaurid *Giganotosaurus* both fall well below the regression.

445   The weak bite force of *Suchomimus*, equivalent to that of a theropod nearly half its size and less

446   than 10% the bite force of a similar-sized *T. rex*, is consistent with a diet consisting

447   predominantly of small prey and fish hypothesized for spinosaurids (e.g., Holtz, 2003; Therrien

448   et al., 2005; Amiot et al., 2010; Cuff and Rayfield, 2013; Vullo et al., 2016). As for

449   *Giganotosaurus*, its weak bite could either reflect a potential plateau in the bite force as

450   theropods reach large body size or be related to inaccuracies in the reconstruction of the

451   mandible due to the incomplete nature of the holotype (see Coria and Salgado, 1995); only the

452   study of additional taxa and discovery of more complete *Giganotosaurus* specimens will shed

453   light on this issue.

454   Interestingly, changes in tooth morphology through ontogeny appear to correlate with

455   change in bite force in albertosaurines. Teeth are ziphodont in small juveniles, become gradually

456   wider through ontogeny, and reach their incrassate adult morphology in individuals with a

457   mandible length of ~58 cm (i.e., late juvenile stage), concurrent with the onset of the rapid

458   increase in bite force (Fig. 8). Because the method of prey capture and feeding behavior likely

459   remained similar through ontogeny in albertosaurines, the correspondence between tooth

460   morphology and bite force is hypothesized to indicate that an ontogenetic dietary shift (i.e.,

461   selected prey size/species) occurred once they reached this size. Because incrassate teeth are

462   better suited than ziphodont teeth to withstand torsional stresses due to their rounder cross-

463   section (e.g., Farlow et al., 1991), the transition to an incrassate dentition likely reflects the onset

464   of higher torsional stresses induced by struggling large prey and bone contact during bite. Thus

465   whereas small juveniles likely preyed on small animals (e.g., small ornithischians/theropods; see

466   Jacobsen, 2001), late juvenile stage individuals reached a body size that allowed them to prey on

467   the same large dinosaur species as mature albertosaurines, namely megaherbivores (e.g.,

468   hadrosaurs, ceratopsids). This interpretation is consistent with reports that feeding on

469   megaherbivores began by the late juvenile stage in *Tyrannosaurus rex* (Peterson and Daus, 2019;

470   Carr, 2020).

471

472   **Conclusions**

473   Beam theory can be used to shed light on changes in feeding behavior that occurred in

474   albertosaurine tyrannosaurids during ontogeny. The similarity in mandibular force profiles

475   between *Albertosaurus sarcophagus* and *Gorgosaurus libratus* reveals that the feeding behaviors

476   of these two albertosaurines did not differ dramatically. The symphyseal region is more

477   dorsoventrally-buttressed for bending (Zx and Zx/L) than the middentary region at all growth

478   stages, indicating that the anterior extremity of the jaws played an important role in prey capture

479   and handling through ontogeny, consistent with the inability of tyrannosaurids to use their

480   reduced forelimbs to grasp prey. The relative mandibular force (Zx/Zy) at the 3rd tooth of

481   albertosaurines indicates that the symphyseal region was better adapted to withstand torsional

482   stresses than most non-avian theropods, but not to the extent of *Tyrannosaurus rex*. These

483   intermediate Zx/Zy values could indicate that the feeding behavior of albertosaurines may have

484   involved less bone crushing, an action that generates significant torsional stresses at the

485   symphysis (see Therrien et al., 2005), or relatively smaller prey than in *T. rex*.

486   Contrary to the allosaurid *Allosaurus fragilis*, which underwent a change in feeding

487   behavior with increase in body size (Therrien et al., 2005), albertosaurines appear to have

488   maintained a similar feeding strategy through ontogeny, where prey was seized and

489   dismembered with the anterior portion of the jaws. As adaptation of the symphysis toward

490   torsional stresses did not change through ontogeny, the size of the prey hunted likely changed

491   between juvenile and mature individuals. Small albertosaurines must have hunted small prey and

492   transitioned to feeding on megaherbivores as they increased in body size. This ontogenetic

493   dietary shift likely happened when individuals reached a mandibular length of ~58 cm (late stage

494   juvenile), size at which teeth shift from being ziphodont to incrassate and bite force begins to

495   increase exponentially. Large albertosaurines were capable of generating bite forces equivalent

496   to similar-sized *Daspletosaurus torosus* and *Tyrannosaurus rex* individuals (12,197-21,799 N),

497   suggesting that no significant differences in jaw closing musculature existed between

498   albertosaurines and tyrannosaurines and that the powerful bite of *T. rex* was the result of its large

499   body size rather than a unique adaptation related to a specialized ecology.

500

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511

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Figure captions
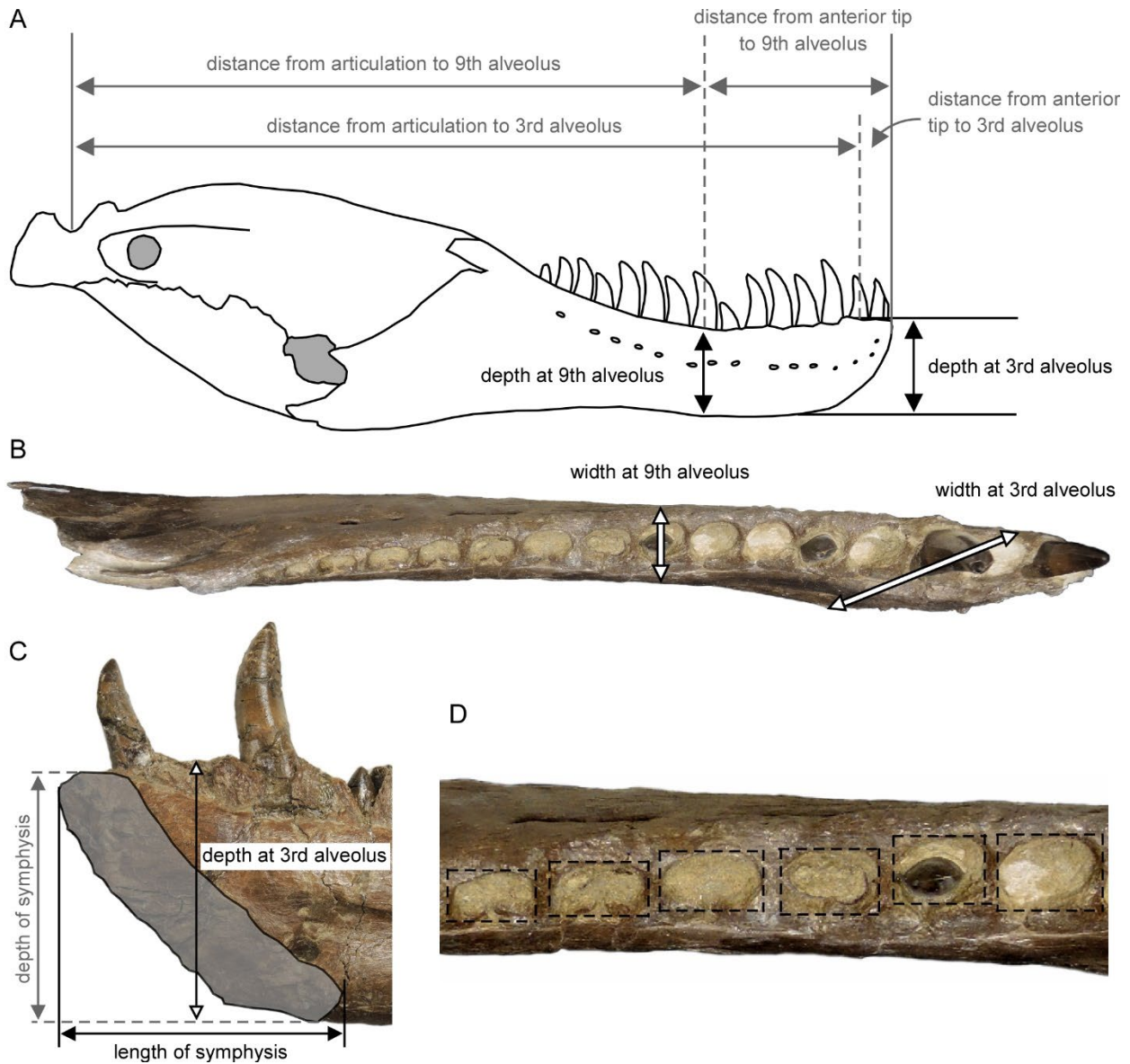
Figure 1. Measurements taken on tyrannosaurid mandibles. A) Mandibular depth and distances measured at the 3rd alveolus and 9th alveolus landmarks. Depth at the 3rd alveolus extends to the bottom of the "chin" even if it occurs slightly posterior to this landmark (see C). B) Mandibular width measured at the landmarks. Width at the 3rd alveolus extends from the posteriormost extent of the mandibular symphysis to the lateral aspect of the alveolus. C) Dimensions of the mandibular symphysis (shaded gray) and depth at the 3rd alveolus. D) Crown

764　　base length and width of alveoli. Dashed rectangles represent the boundaries of the alveoli.

765　　Specimens illustrated are TMP 1991.36.500 (for A), TMP 2001.36.1 (for B and D), and TMP

766　　2003.45.76 (for C).

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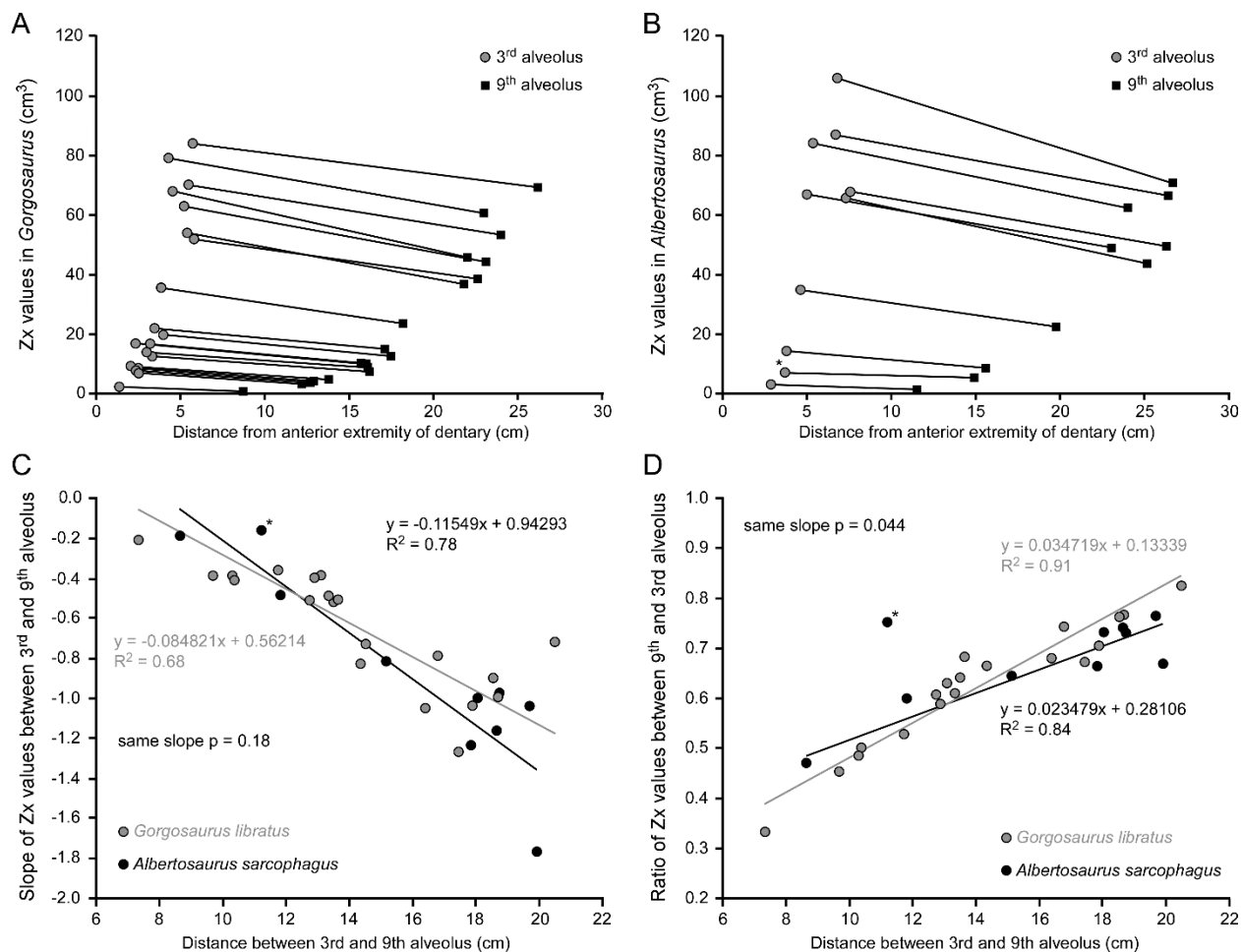
Figure 2. Bending strength (Zx) in albertosaurines. Zx profiles in a growth series of

Gorgosaurus libratus (A) and *Albertosaurus sarcophagus* (B), where the lines connect the

landmarks in a given individual. In all albertosaurines, Zx values are higher in the symphyseal

region than at middentary. C) Reduced major axis regressions of the slopes of the Zx profiles in

Gorgosaurus and *Albertosaurus* against the distance between landmarks (a proxy for mandible

length) show that the slope of the Zx profiles becomes steeper as individuals get larger. D)

Reduced major axis regressions of the ratio of Zx values at the 3rd and 9th alveolus against the

775   distance between landmarks (a proxy for mandible length) show that bending strength at

776   middentary increases faster than at the 3rd alveolus through ontogeny. Asterisk indicates

777   incomplete *Albertosaurus* specimen that was not considered in the calculation of the regressions.

778   The low p-values in C and D show that albertosaurines follow highly similar trends.
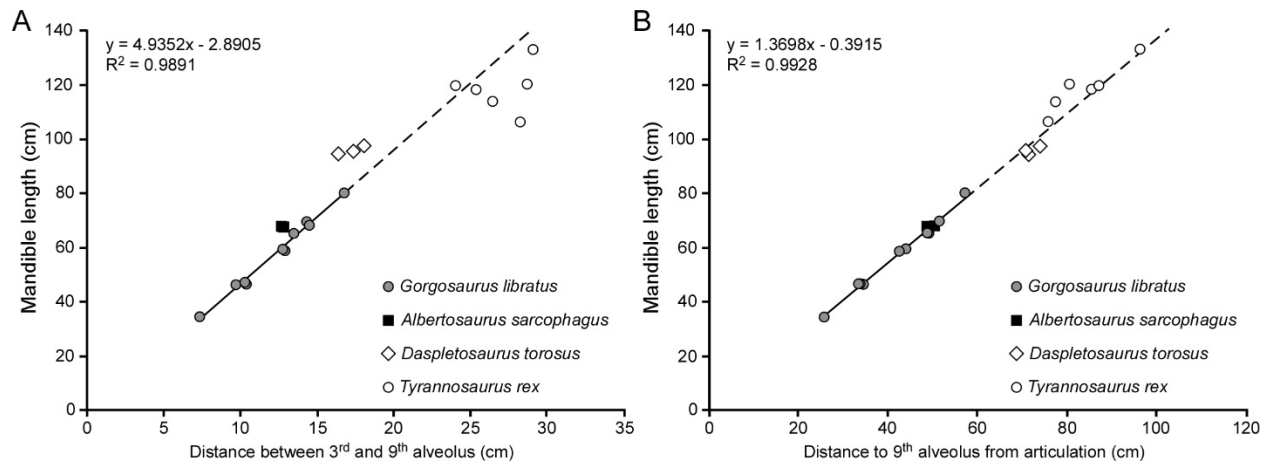

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780   **Figure 3. Estimation of mandible length in albertosaurines.** Ordinary least-squares

781   regressions of mandible length against the distance separating the two landmarks (A) and against

782   the distance between the 9th alveolus and the articular fossa (B). Both regressions are highly

783   accurate in predicting mandible length in albertosaurines. Whereas the accuracy of the first

784   regression is lower when applied to tyrannosaurids, the second regression is highly accurate for
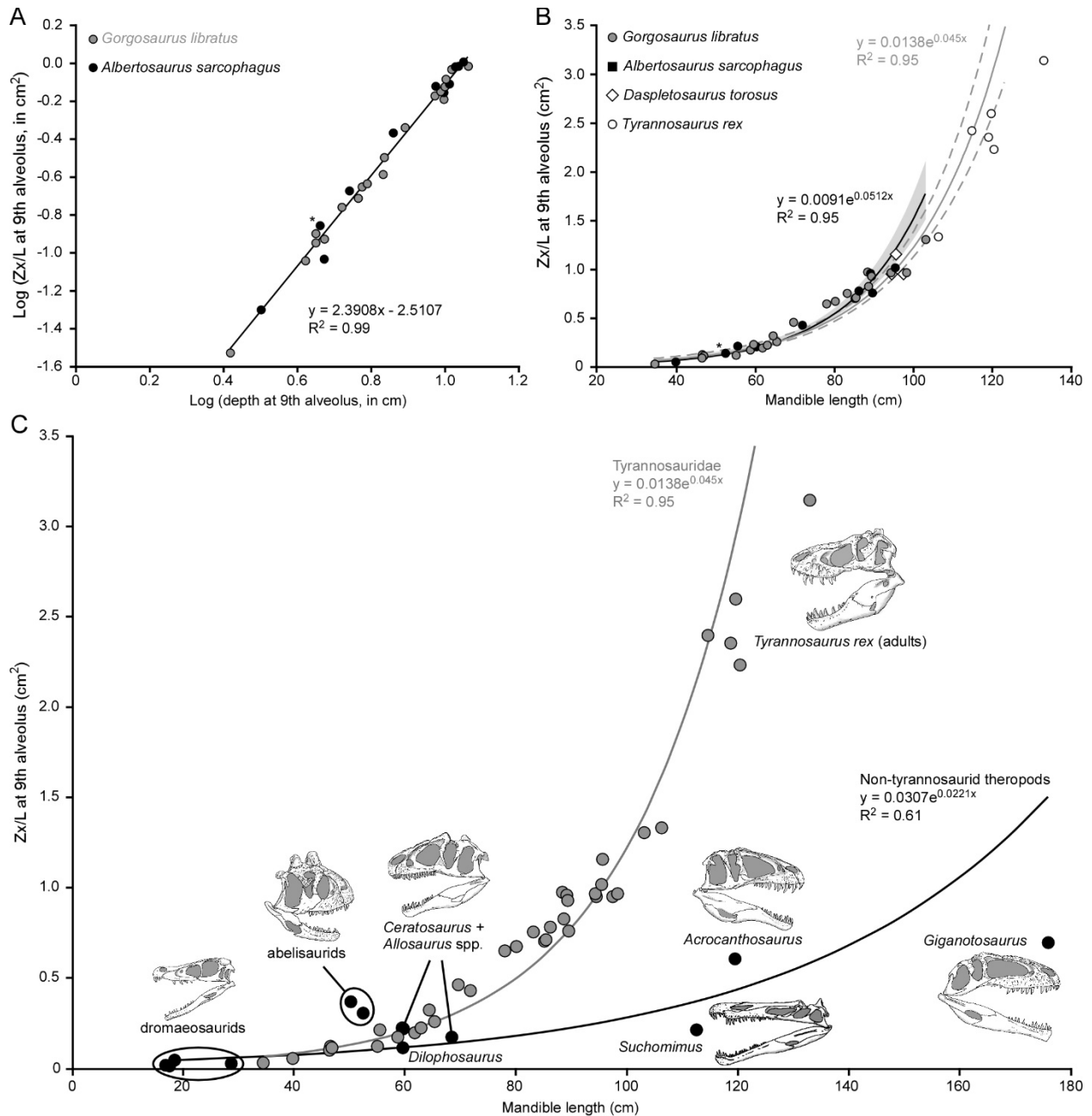
785   all tyrannosaurids.
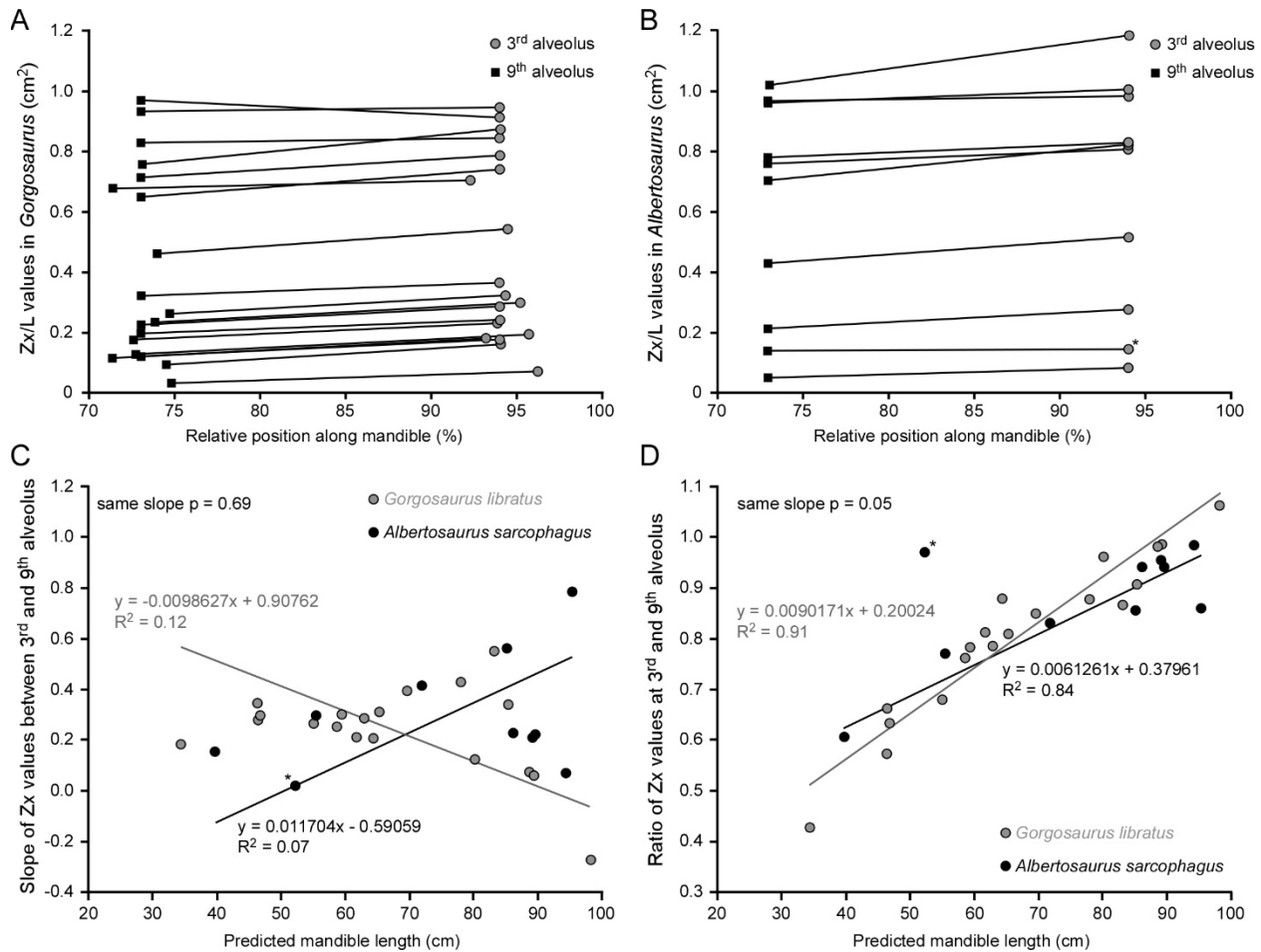
Figure 4. Bending force (Zx/L) in albertosaurines. Zx/L profiles in a growth series of *Gorgosaurus libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the landmarks in a given individual. In nearly all albertosaurines, Zx/L values are higher in the symphyseal region than at middentary. C) Reduced major axis regressions of the slopes of the Zx/L profiles against mandible length in *Gorgosaurus* and *Albertosaurus*. The low R^2 values and regression slopes near 0 indicate that Zx/L profiles do not change through ontogeny. D) Reduced major axis regressions of the ratio of Zx/L values at the 3rd and 9th alveolus against mandible length in *Gorgosaurus* and *Albertosaurus* show that bending force at middentary increases faster than at the 3rd alveolus through ontogeny. Asterisk indicates incomplete *Albertosaurus* specimen

796   that was not considered in the calculation of the regressions. The low p-value in D show that

797   albertosaurines follow highly similar trends.
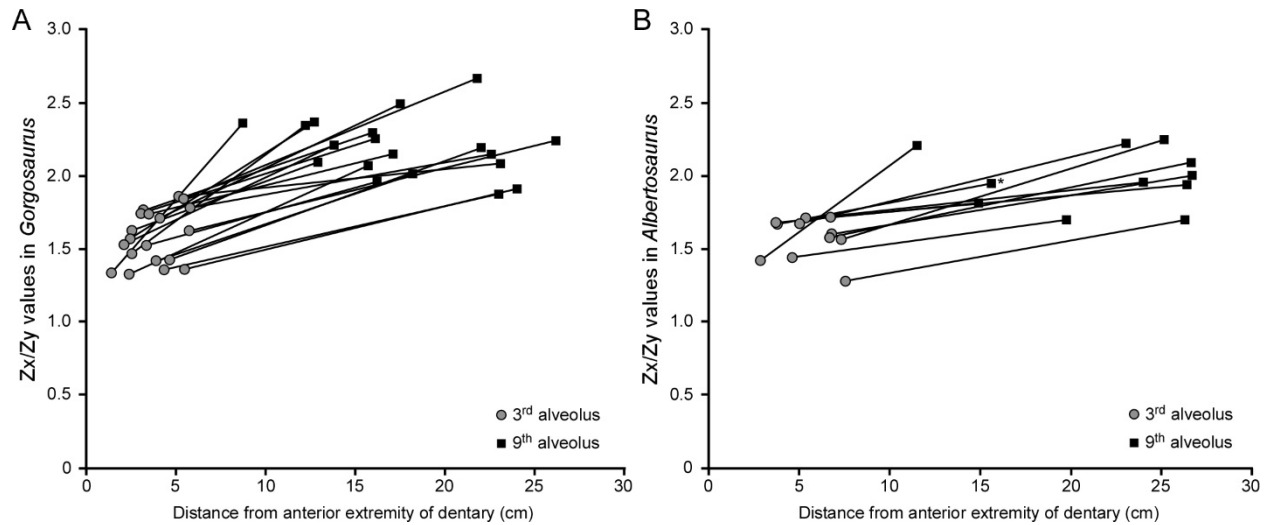
799   **Figure 5. Relative mandibular force (Zx/Zy) profiles in a growth series of *Gorgosaurus***

800   ***libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the landmarks in a**

801   **given individual.** In all albertosaurines, Zx/Zy values are lower in the symphyseal region (1.3-

802   1.7) than at middentary (~2.0). Asterisk indicates incomplete *Albertosaurus* specimen.

Figure 6. Bite force estimation in tyrannosaurids. A) Ordinary least-squares regression

between depth of the mandibular corpus and Zx/L values at middentary in albertosaurines. The

high R^2 values indicate a close fit between the two variables, making it possible to estimate the

bite force of specimens for which dentary width cannot be measured. B) Exponential regressions

through Zx/L values at middentary as a function of mandible length in albertosaurines (black)

809 and tyrannosaurids (gray). The overlapping 95%-confidence interval for the albertosaurine

810 regression (gray shade) and tyrannosaurid regression (gray dash lines) indicates the regressions

811 are not statistically significantly different and that albertosaurines and tyrannosaurines follow the

812 same trend. Asterisk indicates incomplete *Albertosaurus* specimen that was not considered in the

813 calculation of the regressions. C) Comparison of exponential regressions through Zx/L values at

814 middentary as a function of mandible length in tyrannosaurids (gray) and non-tyrannosaurid

815 theropods (black). Bite force estimates are greater in tyrannosaurids than in similar-sized non-

816 tyrannosaurid theropods once mandible length exceeds ~60 cm. Skull illustrations by J.T. Voris.
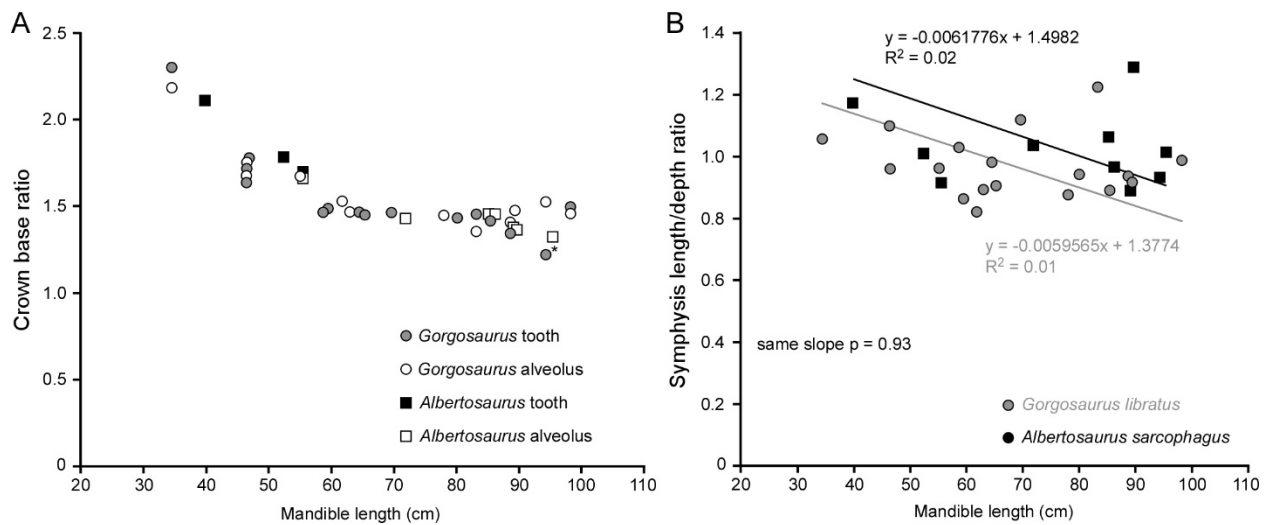
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818 **Figure 7. Tooth crown base and symphyseal proportions in albertosaurines.** A) Tooth crown

819 base ratio (CBR) decreases as individuals become larger. Teeth are highly ziphodont (CBR >

820 2.1) in small individuals (mandible length < 40cm), moderately ziphodont (CBR 1.6-1.8) in

821 slightly larger individuals (mandible length = 40-58cm), and reach their adult incrassate

822 morphology when individuals reach a mandible length of 58 cm. Asterisk indicates CBR ratio

823 derived from a single 3rd tooth, which has a rounder basal cross-section than more posterior

824 teeth. B) Reduced major axis regression of symphysis length/depth ratio against mandible length.

825   The low R^2 values and regression slopes near 0 indicate that symphyseal proportions do not

826   change through ontogeny.

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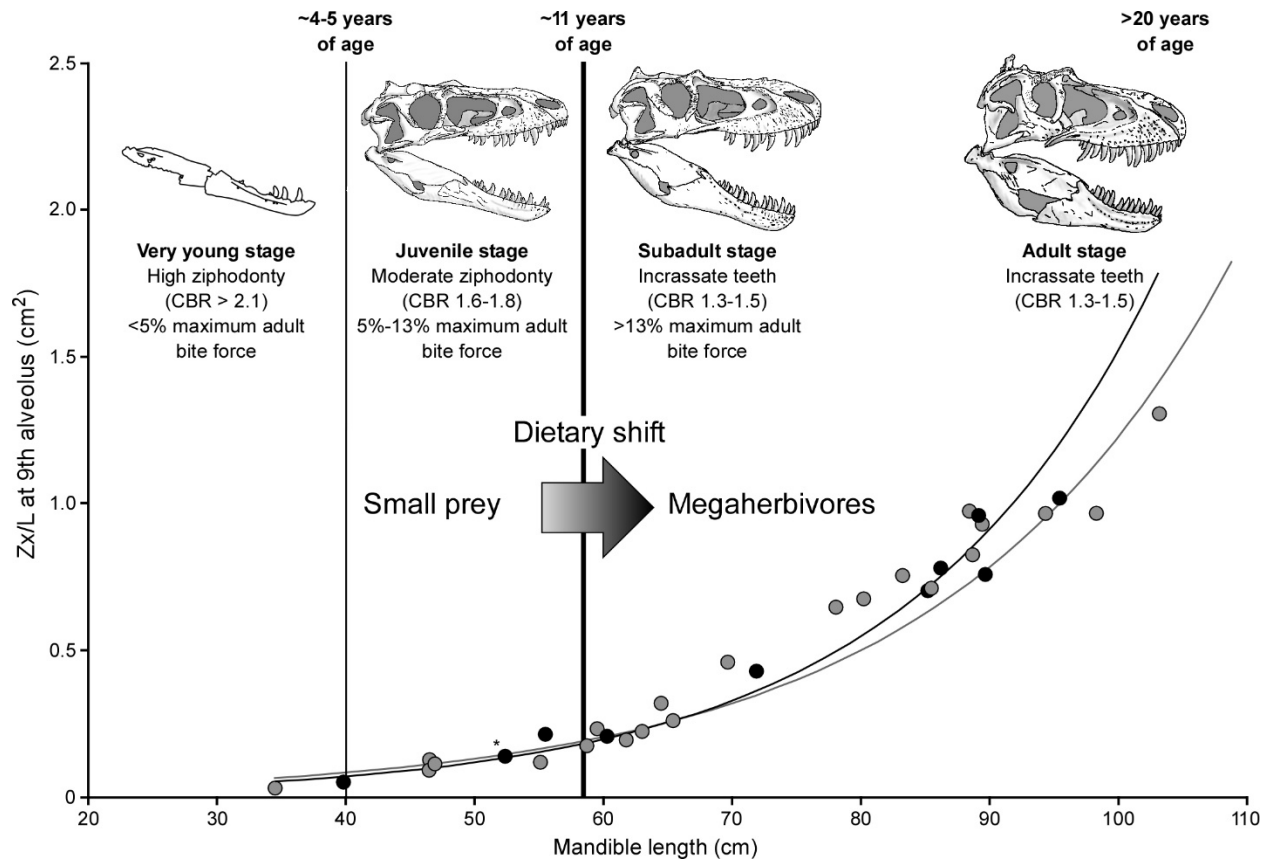
Figure 8. Hypothesized ontogenetic dietary shift in albertosaurines. Changes in bite force

and tooth morphology through ontogeny suggest that albertosaurines underwent a dietary shift

when they reached a mandible length of ~58 cm. Whereas small albertosaurines likely preyed on

small animals/species, transition to feeding on megaherbivores likely occurred in the late

juvenile stage. Black line is the albertosaurine bite force regression; gray line is the

tyrannosaurid bite force regression. Skull illustrations by J.T. Voris.

Appendix. Mandibular, dental, and alveolar dimensions for tyrannosaurid and non-tyrannosaurid

theropods studied. Institutional abbreviations: AMNH, American Museum of Natural History,

New York City, New York, USA; BHI, Black Hills Institute of Geological Research Inc., Hill

837   City, South Dakota, USA; CM, Carnegie Museum, Pittsburgh, Pennsylvania, USA; FMNH PR,

838   Field Museum of Natural History, Chicago, Illinois, USA; LACM, Los Angeles County

839   Museum, Los Angeles, California, USA; MACN-CH, Museo Argentino de Ciencias Naturales

840   "Bernardino Rivadavia", Buenos Aires, Argentina; MOR, Museum of the Rockies, Bozeman,

841   Montana, USA; MUCPv-CH, Museo de la Universidad Nacional del Comahue, El Chocón

842   collection, Neuquén, Argentina; NCSM, North Carolina State Museum of Natural Sciences,

843   Raleigh, North Carolina, USA; NMC, Canadian Museum of Nature, Ottawa, Ontario, Canada;

844   ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of

845   Palaeontology, Drumheller, Alberta, Canada; UCMP, University of Califormia Museum of

846   Paleontology, Berkeley, California, USA; USNM, United States National Museum of Natural

847   History, Smithsonian Institution, Washington, D.C., USA; YPM, Yale Peabody Museum, New

848   Haven, Connecticut, USA.