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Mandibular force profiles and tooth morphology in growth series of *Albertosaurus sarcophagus* and *Gorgosaurus libratus* (Tyrannosauridae: Albertosaurinae) provide evidence for an ontogenetic dietary shift in tyrannosaurids

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

42 Introduction

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

50 In North America, the province of Alberta, Canada, preserves one of the best fossil records
51 of tyrannosaurids for the Campanian-Maastrichtian time interval, with five known taxa:

52 *Albertosaurus sarcophagus* Osborn, 1905, *Daspletosaurus torosus* Russell, 1970, *Gorgosaurus*
53 *libratus* Lambe, 1914, *Thanatotheristes degrootorum* Voris et al., 2020, and *Tyrannosaurus rex*
54 Osborn, 1905. Arguably, the best sampled tyrannosaurids are *Albertosaurus sarcophagus* from
55 the uppermost Campanian-lower Maastrichtian Horseshoe Canyon Formation and *Gorgosaurus*
56 *libratus* from the upper Campanian Dinosaur Park Formation, which together form the basal
57 clade Albertosaurinae. These taxa are represented by nearly a dozen skeletons and abundant
58 isolated elements, with specimens ranging in size from small juveniles (estimated skull length
59 ~35 cm) to fully-grown adults (skull length ~100 cm). Such a large sample has allowed for
60 numerous studies to document various aspects of the ontogeny of these tyrannosaurids (e.g.,
61 Russell, 1970; Carr, 1999; Currie, 2003a,b; Voris et al. 2019).

62 In his seminal work on Canadian tyrannosaurids, Dale Russell (1970) studied allometric
63 trends in *Gorgosaurus libratus* using specimens available at the time (then referred to
64 *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, $Z_x = \pi * (\text{dentary width}/2) * (\text{dentary depth}/2)^2/4$; (2) the section modulus or
126 maximum bending strength about the dorsoventral axis, $Z_y = \pi * (\text{dentary depth}/2) * (\text{dentary}$
127 $\text{width}/2)^2/4$; (3) the dorsoventral mandibular force, Z_x/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), Z_x/Z_y . By assuming that bone material property and safety factors are constant in the
130 mandible of vertebrates, Z_x/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 Z_x/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, Z_x/Z_y 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 (Z_x) profiles are similar in both *Albertosaurus* and *Gorgosaurus*, but
181 Z_x values at middentary undergo a dramatic 90-fold increase between the smallest and largest
182 specimens studied (Fig. 2a,b). The Z_x 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 Z_x 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 Z_x values and $p = 0.044$
192 for ratio of Z_x 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 (Z_x/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 $\sim 0.2-0.3$), 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 Z_x/Z_y 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 ($Z_x/Z_y \sim 2.0$) throughout ontogeny (Fig. 5). In
228 contrast, the mandible is much rounder near the symphysis in both albertosaurines, with Z_x/Z_y
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 (Z_x/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, Z_x/L values in *Albertosaurus* and *Gorgosaurus*
240 follow an exponential regression ($R^2 = 0.95$; Fig. 6b). Whereas Z_x/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 ($Z_x/L = 1.31$) on par with similar-sized individuals of
246 *Tyrannosaurus rex* (TMP 1981.6.1, jaw length ~106.4 cm, $Z_x/L = 1.33$). 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 Z_x values and 32-fold increase in
277 Z_x/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 Z_x and Z_x/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 Z_x 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 (Z_x/Z_y) is observed through ontogeny in *Albertosaurus* and *Gorgosaurus* (Fig. 5). With
307 Z_x/Z_y 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 Z_x/Z_y
311 values at middentary across the growth series suggest that this might not be the case (Fig. 5). The
312 Z_x/Z_y 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 $Z_x/Z_y = 1.5$) 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 Z_x/Z_y values (> 2) indicative of predominant dorsoventral
317 bending loads and slashing bites (Therrien et al., 2005). Even lower Z_x/Z_y 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 ($Z_x/Z_y = 0.44$), 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 Z_x/Z_y 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 Z_x/Z_y 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 Z_x/Z_y 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 Z_x/Z_y 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 (Z_x/Z_y)
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 Z_x/Z_y 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 (Z_x and Z_x/L) than the midentary 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 (Z_x/Z_y) 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 Z_x/Z_y 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 incassate 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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755

756 **Figure captions**

757 **Figure 1. Measurements taken on tyrannosaurid mandibles.** A) Mandibular depth and
758 distances measured at the 3rd alveolus and 9th alveolus landmarks. Depth at the 3rd alveolus
759 extends to the bottom of the “chin” even if it occurs slightly posterior to this landmark (see C).
760 B) Mandibular width measured at the landmarks. Width at the 3rd alveolus extends from the
761 posteriormost extent of the mandibular symphysis to the lateral aspect of the alveolus. C)
762 Dimensions of the mandibular symphysis (shaded gray) and depth at the 3rd alveolus. D) Crown
763 base length and width of alveoli. Dashed rectangles represent the boundaries of the alveoli.
764 Specimens illustrated are TMP 1991.36.500 (for A), TMP 2001.36.1 (for B and D), and TMP
765 2003.45.76 (for C).

766 **Figure 2. Bending strength (Zx) in albertosaurines.** Zx profiles in a growth series of
767 *Gorgosaurus libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the
768 landmarks in a given individual. In all albertosaurines, Zx values are higher in the symphyseal
769 region than at middentary. C) Reduced major axis regressions of the slopes of the Zx profiles in
770 *Gorgosaurus* and *Albertosaurus* against the distance between landmarks (a proxy for mandible
771 length) show that the slope of the Zx profiles becomes steeper as individuals get larger. D)
772 Reduced major axis regressions of the ratio of Zx values at the 3rd and 9th alveolus against the
773 distance between landmarks (a proxy for mandible length) show that bending strength at
774 middentary increases faster than at the 3rd alveolus through ontogeny. Asterisk indicates
775 incomplete *Albertosaurus* specimen that was not considered in the calculation of the regressions.
776 The low p-values in C and D show that albertosaurines follow highly similar trends.

777 **Figure 3. Estimation of mandible length in albertosaurines.** Ordinary least-squares
778 regressions of mandible length against the distance separating the two landmarks (A) and against
779 the distance between the 9th alveolus and the articular fossa (B). Both regressions are highly
780 accurate in predicting mandible length in albertosaurines. Whereas the accuracy of the first
781 regression is lower when applied to tyrannosaurids, the second regression is highly accurate for
782 all tyrannosaurids.

783 **Figure 4. Bending force (Z_x/L) in albertosaurines.** Z_x/L profiles in a growth series of
784 *Gorgosaurus libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the
785 landmarks in a given individual. In nearly all albertosaurines, Z_x/L values are higher in the
786 symphyseal region than at midentary. C) Reduced major axis regressions of the slopes of the
787 Z_x/L profiles against mandible length in *Gorgosaurus* and *Albertosaurus*. The low R^2 values and
788 regression slopes near 0 indicate that Z_x/L profiles do not change through ontogeny. D) Reduced
789 major axis regressions of the ratio of Z_x/L values at the 3rd and 9th alveolus against mandible
790 length in *Gorgosaurus* and *Albertosaurus* show that bending force at midentary increases faster
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792 that was not considered in the calculation of the regressions. The low p-value in D show that
793 albertosaurines follow highly similar trends.

794 **Figure 5. Relative mandibular force (Z_x/Z_y) profiles in a growth series of *Gorgosaurus***
795 ***libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the landmarks in a**
796 **given individual.** In all albertosaurines, Z_x/Z_y values are lower in the symphyseal region (1.3-
797 1.7) than at midentary (~2.0). Asterisk indicates incomplete *Albertosaurus* specimen.

798 **Figure 6. Bite force estimation in tyrannosaurids.** A) Ordinary least-squares regression
799 between depth of the mandibular corpus and Zx/L values at middentary in albertosaurines. The
800 high R^2 values indicate a close fit between the two variables, making it possible to estimate the
801 bite force of specimens for which dentary width cannot be measured. B) Exponential regressions
802 through Zx/L values at middentary as a function of mandible length in albertosaurines (black)
803 and tyrannosaurids (gray). The overlapping 95%-confidence interval for the albertosaurine
804 regression (gray shade) and tyrannosaurid regression (gray dash lines) indicates the regressions
805 are not statistically significantly different and that albertosaurines and tyrannosaurines follow the
806 same trend. Asterisk indicates incomplete *Albertosaurus* specimen that was not considered in the
807 calculation of the regressions. C) Comparison of exponential regressions through Zx/L values at
808 middentary as a function of mandible length in tyrannosaurids (gray) and non-tyrannosaurid
809 theropods (black). Bite force estimates are greater in tyrannosaurids than in similar-sized non-
810 tyrannosaurid theropods once mandible length exceeds ~60 cm. Skull illustrations by J.T. Voris.

811 **Figure 7. Tooth crown base and symphyseal proportions in albertosaurines.** A) Tooth crown
812 base ratio (CBR) decreases as individuals become larger. Teeth are highly ziphodont (CBR >
813 2.1) in small individuals (mandible length < 40cm), moderately ziphodont (CBR 1.6-1.8) in
814 slightly larger individuals (mandible length = 40-58cm), and reach their adult incassate
815 morphology when individuals reach a mandible length of 58 cm. Asterisk indicates CBR ratio
816 derived from a single 3rd tooth, which has a rounder basal cross-section than more posterior
817 teeth. B) Reduced major axis regression of symphysis length/depth ratio against mandible length.
818 The low R^2 values and regression slopes near 0 indicate that symphyseal proportions do not
819 change through ontogeny.

820 **Figure 8. Hypothesized ontogenetic dietary shift in albertosaurines.** Changes in bite force
821 and tooth morphology through ontogeny suggest that albertosaurines underwent a dietary shift
822 when they reached a mandible length of ~58 cm. Whereas small albertosaurines likely preyed on
823 small animals/species, transition to feeding on megaherbivores likely occurred in the late
824 juvenile stage. Black line is the albertosaurine bite force regression; gray line is the
825 tyrannosaurid bite force regression. Skull illustrations by J.T. Voris.

826 **Appendix.** Mandibular, dental, and alveolar dimensions for tyrannosaurid and non-tyrannosaurid
827 theropods studied. Institutional abbreviations: AMNH, American Museum of Natural History,
828 New York City, New York, USA; BHI, Black Hills Institute of Geological Research Inc., Hill
829 City, South Dakota, USA; CM, Carnegie Museum, Pittsburgh, Pennsylvania, USA; FMNH PR,
830 Field Museum of Natural History, Chicago, Illinois, USA; LACM, Los Angeles County
831 Museum, Los Angeles, California, USA; MACN-CH, Museo Argentino de Ciencias Naturales
832 “Bernardino Rivadavia”, Buenos Aires, Argentina; MOR, Museum of the Rockies, Bozeman,
833 Montana, USA; MUCPv-CH, Museo de la Universidad Nacional del Comahue, El Chocón
834 collection, Neuquén, Argentina; NCSM, North Carolina State Museum of Natural Sciences,
835 Raleigh, North Carolina, USA; NMC, Canadian Museum of Nature, Ottawa, Ontario, Canada;
836 ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of
837 Palaeontology, Drumheller, Alberta, Canada; UCMP, University of California Museum of
838 Paleontology, Berkeley, California, USA; USNM, United States National Museum of Natural
839 History, Smithsonian Institution, Washington, D.C., USA; YPM, Yale Peabody Museum, New
840 Haven, Connecticut, USA.

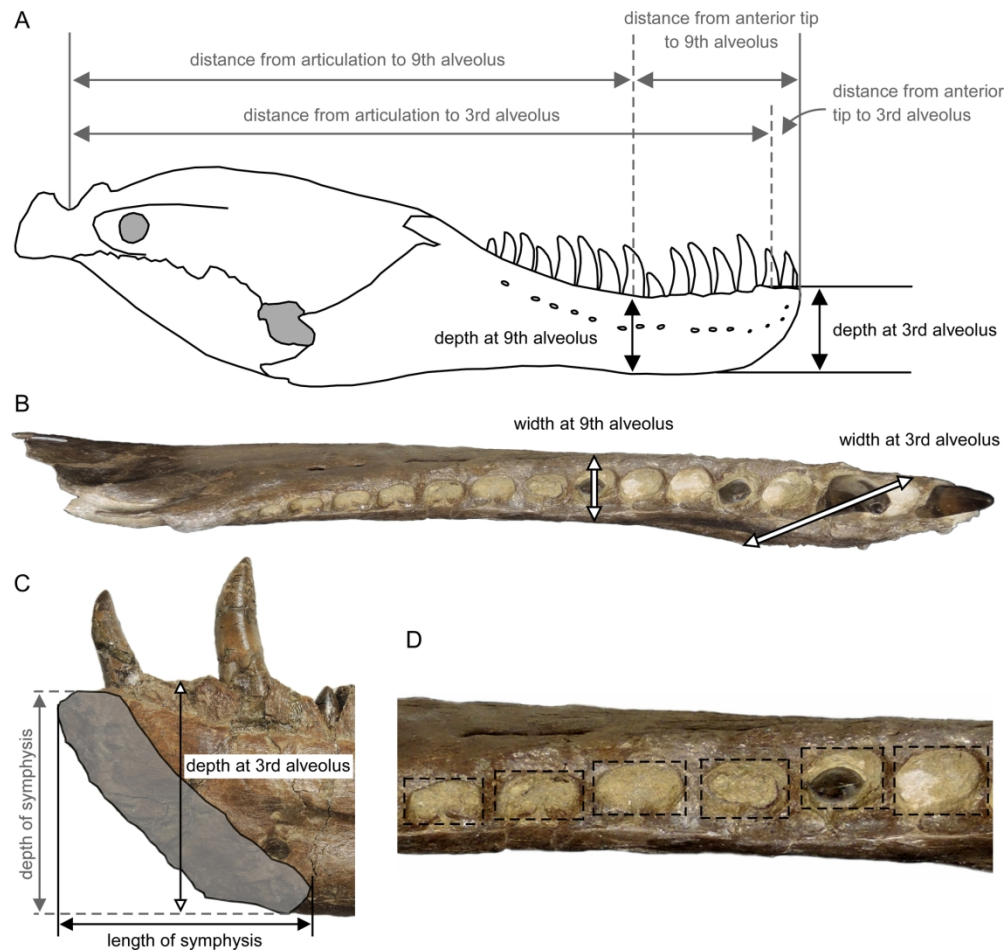


Figure 1. Measurements taken on tyrannosaurid mandibles. A) Mandibular depth and distances measured at the 3rd alveolus and 9th alveolus landmarks. Depth at the 3rd alveolus extends to the bottom of the “chin” even if it occurs slightly posterior to this landmark (see C). B) Mandibular width measured 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 base length and width of alveoli. Dashed rectangles represent the boundaries of the alveoli. Specimens illustrated are TMP 1991.36.500 (for A), TMP 2001.36.1 (for B and D), and TMP 2003.45.76 (for C).

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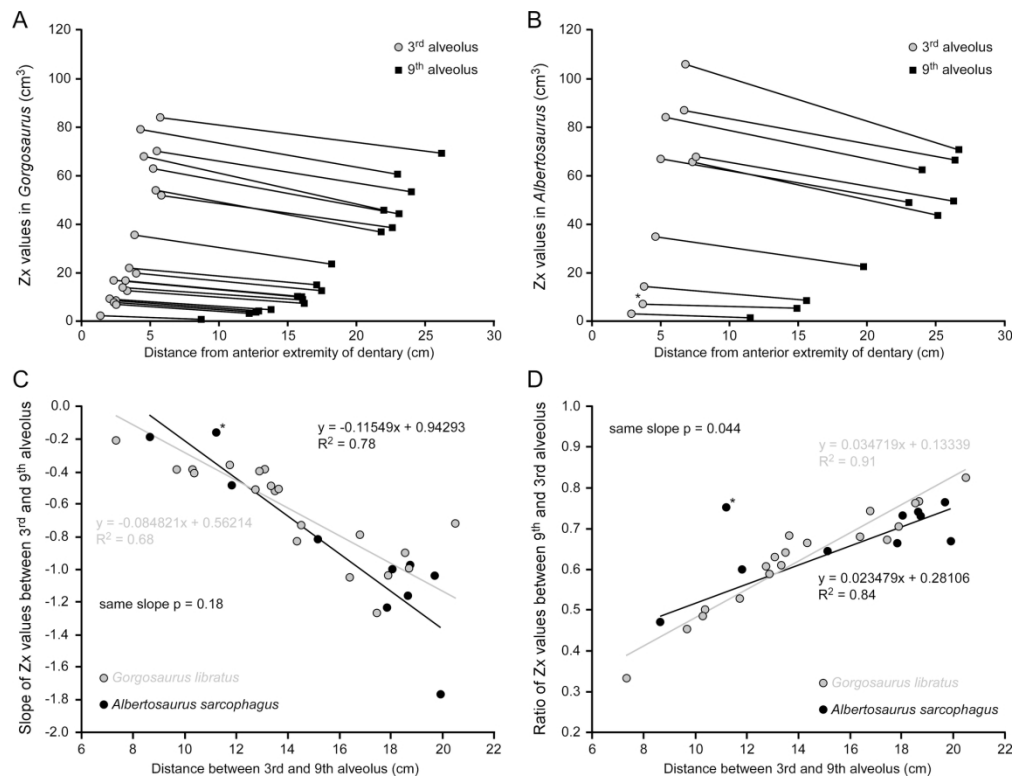


Figure 2. Bending strength (Zx) in albertosaurines. Zx profiles in a growth series of *Gorgosaurus libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the landmarks in a given individual. In all albertosaurines, Zx values are higher in the symphyseal region than at middentary. 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 distance between landmarks (a proxy for mandible length) show that bending strength at middentary increases faster than at the 3rd alveolus through ontogeny. Asterisk indicates incomplete *Albertosaurus* specimen that was not considered in the calculation of the regressions. The low p-values in C and D show that albertosaurines follow highly similar trends.

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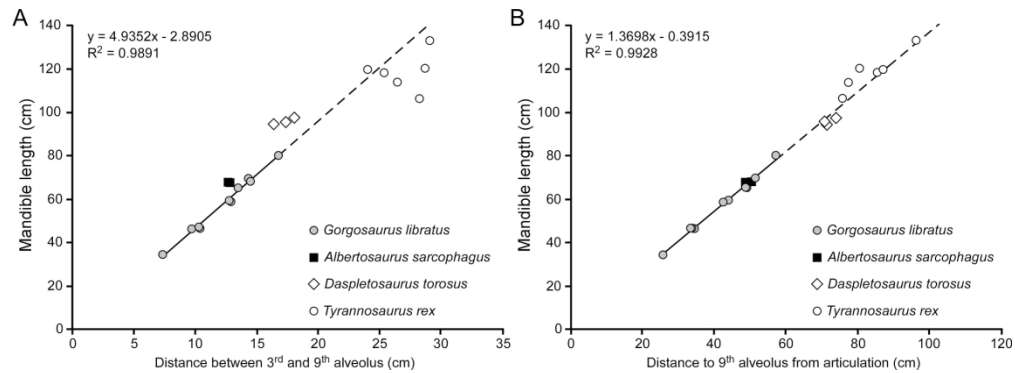


Figure 3. Estimation of mandible length in albertosaurines. Ordinary least-squares regressions of mandible length against the distance separating the two landmarks (A) and against the distance between the 9th alveolus and the articular fossa (B). Both regressions are highly accurate in predicting mandible length in albertosaurines. Whereas the accuracy of the first regression is lower when applied to tyrannosaurids, the second regression is highly accurate for all tyrannosaurids.

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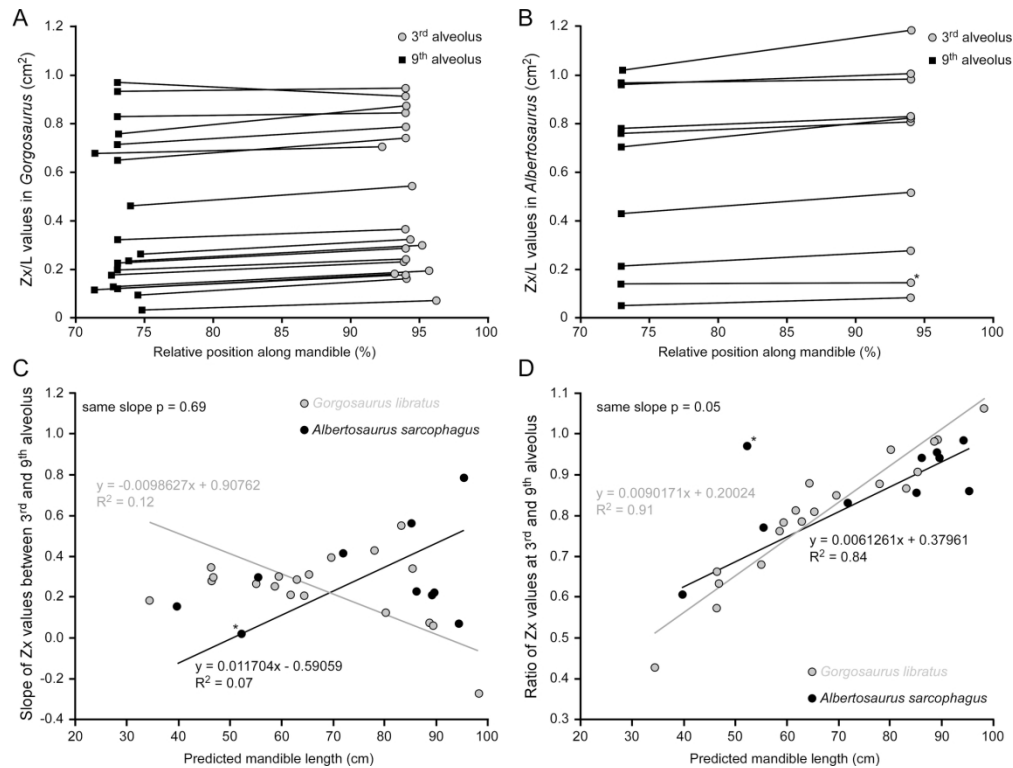


Figure 4. Bending force (Zx/L) in albertosaurines. Zx/L profiles in a growth series of *Gorgosaurus libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the landmarks in a given individual. In nearly all albertosaurines, Zx/L values are higher in the symphyseal region than at middentary. C) Reduced major axis regressions of the slopes of the Zx/L profiles against mandible length in *Gorgosaurus* and *Albertosaurus*. The low R² 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 that was not considered in the calculation of the regressions. The low p-value in D show that albertosaurines follow highly similar trends.

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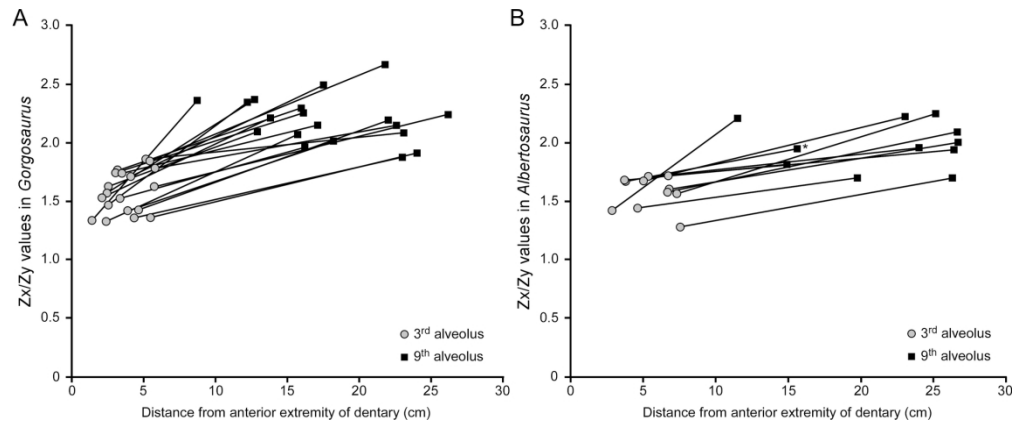


Figure 5. Relative mandibular force (Zx/Zy) profiles in a growth series of *Gorgosaurus libratus* (A) and *Albertosaurus sarcophagus* (B), where the lines connect the landmarks in a given individual. In all albertosaurines, Zx/Zy values are lower in the symphyseal region (1.3-1.7) than at middentary (~ 2.0). Asterisk indicates incomplete *Albertosaurus* specimen.

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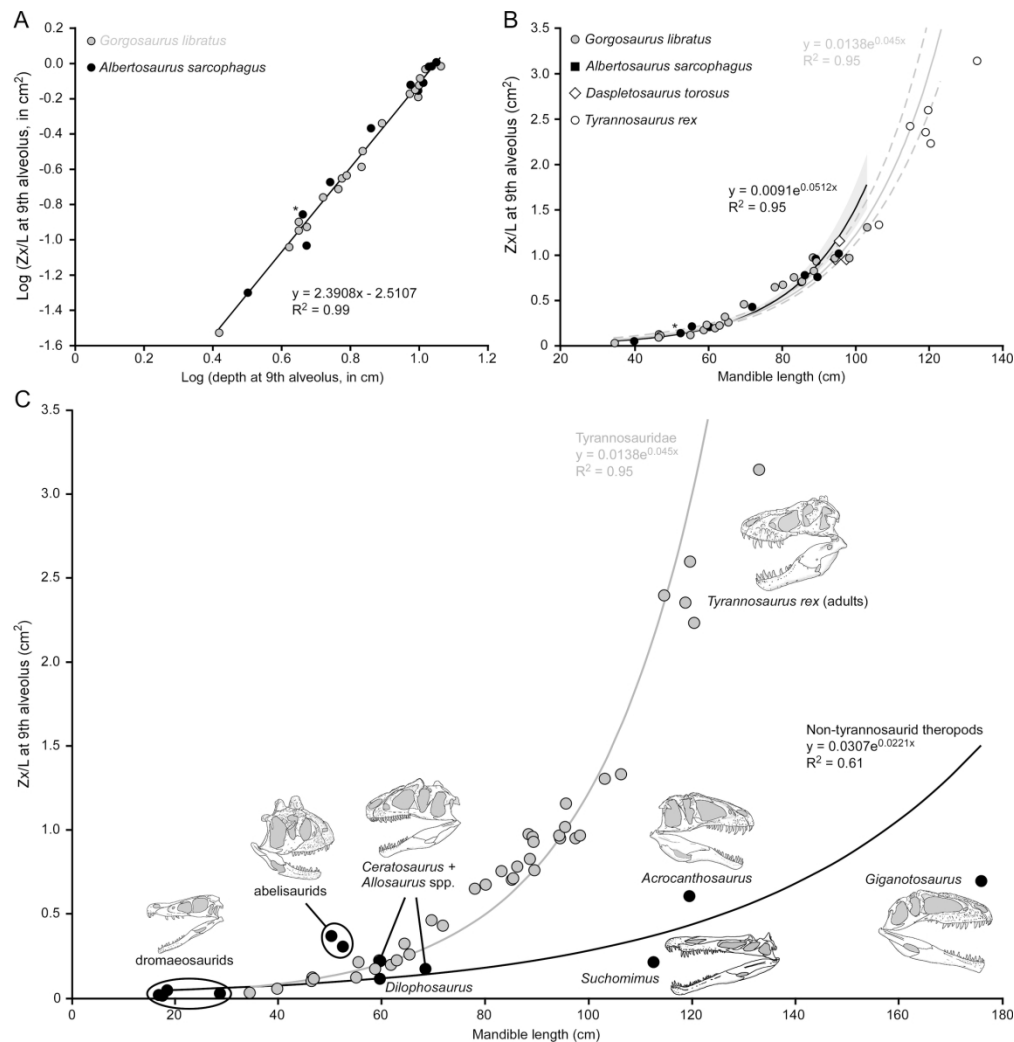


Figure 6. Bite force estimation in tyrannosaurids. A) Ordinary least-squares regression between depth of the mandibular corpus and Zx/L values at middentary in albertosaurines. The high R^2 values indicate a close fit between the two variables, making it possible to estimate the bite force of specimens 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) and tyrannosaurids (gray). The overlapping 95%-confidence interval for the albertosaurine regression (gray shade) and tyrannosaurid regression (gray dash lines) indicates the regressions are not statistically significantly different and that albertosaurines and tyrannosaurines follow the same trend. Asterisk indicates incomplete *Albertosaurus* specimen that was not considered in the calculation of the regressions. C) Comparison of exponential regressions through Zx/L values at middentary as a function of mandible length in tyrannosaurids (gray) and non-tyrannosaurid theropods (black). Bite force estimates are greater in tyrannosaurids than in similar-sized non-tyrannosaurid theropods once mandible length exceeds ~ 60 cm. Skull illustrations by J.T. Voris.

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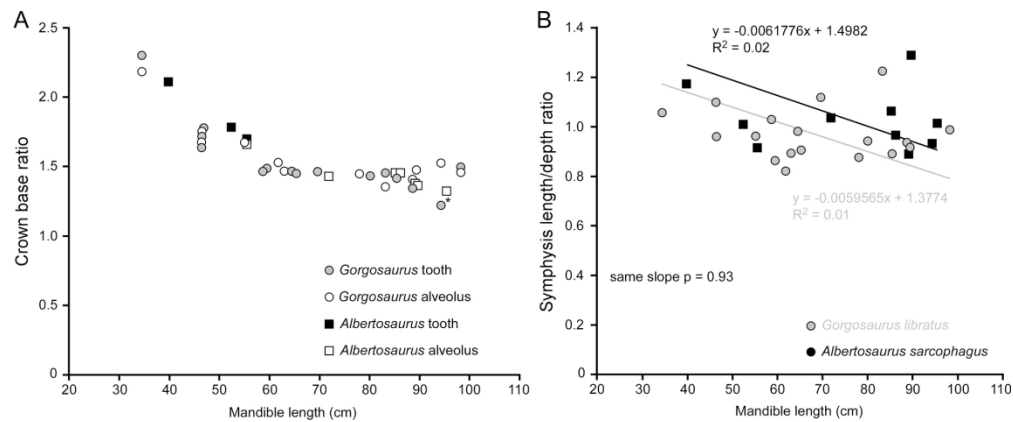


Figure 7. Tooth crown base and symphyseal proportions in albertosaurines. A) Tooth crown base ratio (CBR) decreases as individuals become larger. Teeth are highly ziphodont (CBR > 2.1) in small individuals (mandible length < 40cm), moderately ziphodont (CBR 1.6-1.8) in slightly larger individuals (mandible length = 40-58cm), and reach their adult incassate morphology when individuals reach a mandible length of 58 cm. Asterisk indicates CBR ratio derived from a single 3rd tooth, which has a rounder basal cross-section than more posterior teeth. B) Reduced major axis regression of symphysis length/depth ratio against mandible length. The low R2 values and regression slopes near 0 indicate that symphyseal proportions do not change through ontogeny.

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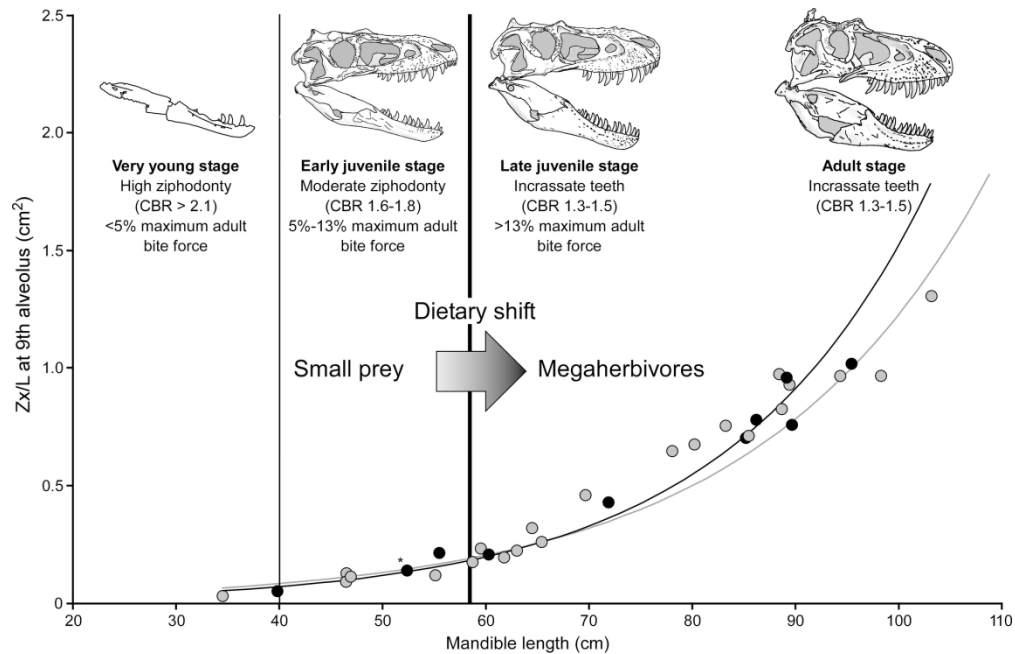


Figure 8. Hypothesized ontogenetic dietary shift in albertosaurines. Changes in bite force and tooth morphology through ontogeny suggest that albertosaurines underwent a dietary shift when they reached a mandible length of ~58 cm. Whereas small albertosaurines likely preyed on small animals/species, 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.

181x119mm (300 x 300 DPI)

	Depth at 9 th tooth (cm)	Width at 9 th tooth (cm)	Distance from tip (cm)	Distance to articulation (cm)	Depth at 3rd tooth (cm)	Width at 3rd tooth (cm)	Distance from tip (cm)	Distance to articulation (cm)	Length of mandible (cm)	Predicted mandible length from regression (cm)	Symphysis length (cm)	Symphysis depth (cm)
<i>Gorgosaurus libratus</i>												
TMP 1994.12.155	2.641	1.119	8.7	25.8	3.15	2.363	1.35	33.2	34.5		3.331	3.15
TMP 1986.144.1	4.5	2.15	12.9	33.8	5.2	3.2	2.5	44.5	46.5		4.8	5
TMP 2016.14.1 - left side	4.22	1.8	12.2	34.6	4.7	3.2	2.5	43.7	46.45		5.5	5
TMP 2009.12.14 - left side	4.5	1.9	12.7	33.45	4.99	3.18	2.4	43.7	46.9		~3.87	~4.8
TMP 1987.46.1	~4.75	2.15	13.8	?	5.2	3.4	2.05	?	?	55.10	5.2	5.4
TMP 1994.143.1	5.29	2.7	16.2	42.6	5.8	3.81	3.3	55.1	58.7		5.8	5.64
TMP 2012.12.29	5.86	2.6	16.1	?	6.27	3.6	3	3.85	?	61.76	5.35	6.52
TMP 1992.36.749	6	2.9	15.7	?	6.1	4.6	2.35	?	?	62.99	5.81	6.5
TMP 1995.5.1	7.85	3.9	18.2	51.5	8	5.65	3.85	65.8	69.65		8.05	7.2
TMP 1984.9.4 (cast of ROM 1247) – right side	?	?	18.65	50.35	?	?	4.13	64.95	68.2		?	?
TMP 1991.163.1	6.85	2.75	17.5	48.85	7	4.1	4	61.6	65.4		5.8	6.4
TMP 1999.55.170	6.9	3.21	17.1	?	7.3	4.2	3.45	?	?	64.47	6.54	6.65
TMP 1986.49.29	10	3.75	21.8	?	10.05	5.45	5.4	?	?	78.05	8.68	9.9
TMP 1983.36.134	10.13	5.3	24	?	9.9	7.28	5.45	?	?	88.66	9.05	9.66
TMP 1994.12.602	10.07	4.6	22	?	9.95	7	4.55	?	?	83.23	10.3	8.4
TMP 1982.28.1	9.8	4.7	23.1	?	10.6	5.7	5.2	?	?	85.45	9.2	10.32
TMP 1967.9.164	11.65	5.2	26.2	?	11.15	6.88	5.7	?	?	98.28	10.58	10.7
TMP 1975.11.3	10.5	5.6	23	?	10.3	7.6	4.3	?	?	89.40	9.87	10.75
TMP 1991.36.500	6.2	2.7	15.95	44	6.7	3.8	3.2	56.65	59.5		5.7	6.6
TMP 1999.33.1	?	?	16.8	49.1	?	?	4.1	61.75	65.25		?	?
TMP 1992.36.1220	12.55	?	?	75.6	?	?	?	?	?	103.17	?	?
TMP 2000.12.11	11.1	?	25.75	?	11.64	?	7.25	?	?	88.41	?	?
TMP 2004.3.4	9.45	4.4	22.6	57.23	9.8	5.5	5.8	74	80.2		8.3	8.8
<i>Albertosaurus sarcophagus</i>												
TMP 1997.58.1 - combination measurements from both sides	3.2	1.45	11.5	?	3.55	2.5	2.85	?	?	39.80	4.35	3.75
TMP 2007.7.1 (specimen with damaged alveolar margin indicated by asterisk in manuscript)	4.62	2.55	14.9	?	4.95	2.95	3.7	?	?	52.38	4.7	4.65
TMP 1999.50.40	5.55	2.85	15.6	?	6.25	3.75	3.77	?	?	55.49	5.4	5.9
TMP 1999.50.20	7.3	4.3	19.75	?	8	5.55	4.6	?	?	71.88	7.2	6.95
TMP 1994.25.6	10.35	4.66	23.05	?	10.45	6.25	5	?	?	86.19	8.21	8.5
TMP 1996.25.61	10.75	5.5	24	?	11.35	6.65	5.35	?	?	89.15	9.25	10.4
TMP 1997.25.53	10	4.45	25.15	?	10.15	6.5	7.3	?	?	85.20	9.9	9.3
TMP 2002.45.21	9.5	5.6	26.3	?	9.6	7.5	7.55	?	?	89.64	11.15	8.65
TMP 2003.45.84	11.3	5.65	26.62	?	12	7.5	6.7	?	?	95.42	10.8	10.65
TMP 1985.98.1	?	?	17.7	50.4	?	?	5	63.6	68.05		?	?
TMP 1986.64.1	5.8	~4	18.55	48.8	~6.82		5.75	61.35	?	60.28	?	?
TMP 1986.205.1	10.95	5.65	26.4	?	11.5	6.7	6.7	?	?	94.33	9.6	10.3

	Crown length/crown width = crown base ratio (all measurements in mm)													
	3 rd tooth	4 th tooth	5 th tooth	6 th tooth	7 th tooth	8 th tooth	9 th tooth	10 th tooth	11 th tooth	12 th tooth	13 th tooth	14 th tooth	15 th tooth	Crown base ratio average
<i>Gorgosaurus libratus</i>														
TMP 1994.12.155			9.66/4.41 =2.19	9.9/4.68 =2.12	10.18/4.18 =2.44	9.47/4.67 =2.03		10.49/4.35 =2.41			9.99/3.83 =2.61			2.30
TMP 1986.144.1		13.79/8.39 =1.64	14.81/8.85 =1.67					14.09/7.68 =1.83						1.72
TMP 2016.14.1	12.8/8.4 =1.52		13.7/8.1 =1.69		13.1/7.7 =1.70		12.8/8.1 =1.58	11.5/6.6 =1.74		12.6/7.2 =1.75		10.1/6.9 =1.46		1.64
TMP 2009.12.14	8.1/6.7 =1.21	13.6/8.2 =1.66	15.5/8.5 =1.82		15.1/8 =1.89		13.9/8.3 =1.67	14.7/7.1 =2.07	13.9/8 =1.74	14.7/6.8 =2.16		10.5/5.4 =1.94	6.9/4.3 =1.60	1.78
TMP 1994.143.1	14.64/11.5 =1.27		18.39/11.9 =1.55	15.9/11.11 =1.43				18.31/11.39 =1.61						1.46
TMP 1995.5.1		16.61/10.18 =1.63	20.32/15.37 =1.32	19.45/11.71 =1.66	19.37/14.41 =1.34			19.12/13.53 =1.41	17.3/10.71 =1.62	18.89/13.14 =1.44	17/12.42 =1.37	14.2/7.85 =1.81	13.55/8.75 =1.55	1.46
TMP 1991.163.1	16.82/10.44 =1.61	19.21/14.02 =1.37	17.78/12.14 =1.46		20.34/12.18 =1.67						16.88/10.84 =1.56			1.45
TMP 1999.55.170		17.75/14.29 =1.24	18.7/12.37= 1.51		17.9/11.5 =1.56		17.23/11.77 =1.46		17.23/10.44 =1.65			14.53/9.28 =1.57	13.34/8.02 =1.66	1.47
TMP 1983.36.134							25.79/17.65 =1.46	20.7/13.21 =1.57	23.13/19.56 =1.18	21.09/16.35 =1.29	13.21/10.86 =1.22			1.34
TMP 1994.12.602			31.1/19.05 =1.63						22.57/17.69 =1.28					1.45
TMP 1982.28.1	24.04/19.16 =1.25	22.72/17.06 =1.33	26.25/16.83 =1.56	24.94/16.64 =1.50		28.16/22.64 =1.24	23.33/14.85 =1.57		24.77/17.12 =1.45					1.42
TMP 1967.9.164					25.31/17.75 =1.43			25.62/16.34 =1.57						1.5
TMP 1991.36.500	15.16/13.83 =1.10	17.19/11.89 =1.45	16.71/11.12 =1.50	17.17/11.2 =1.53	16.25/10.51 =1.55		18.13/10.91 =1.66	16.55/9.78 =1.69	16.79/10.39 =1.62	17.04/10.16 =1.68	14.04/7.66 =1.83	13.41/7.88 =1.70	11.63/7.25 =1.60	1.49
TMP 2004.3.4	18.52/11.97 =1.55	23.37/17.44 =1.34	20.14/13.39 =1.50	21.41/15.74 =1.36	21.43/15.06 =1.42	23.18/15.6 =1.49	21.73/13.67 =1.59		19.4/14 =1.39	17.59/12.23 =1.44		15.18/12.15 =1.25		1.43
<i>Albertosaurus sarcophagus</i>														
TMP 1997.58.1	9.92/4.88 =2.03	11.4/5.64 =2.02	9.5/4.18 =2.27											2.11
TMP 2007.7.1		14.1/7.91 =1.78												1.78
TMP 1999.50.40									14.34/8.44 =1.70					1.7
TMP 1986.205.1	25.3/20.71 =1.22													1.22

	Alveolus length/alveolus width = alveolus ratio (all measurements in mm)													
	3 rd alveolus	4 th alveolus	5 th alveolus	6 th alveolus	7 th alveolus	8 th alveolus	9 th alveolus	10 th alveolus	11 th alveolus	12 th alveolus	13 th alveolus	14 th alveolus	15 th alveolus	Alveolus ratio average
<i>Gorgosaurus libratus</i>														
TMP 1994.12.155							11.87/5.44 =2.18							2.18
TMP 1986.144.1	11.84/7.47 =1.59			15.88/9.01 =1.76		15.56/8.78 =1.77			14.95/7.9 =1.89					1.75
TMP 2016.14.1		13.8/7.2 =1.92		11.2/6.9 =1.62		10.6/7.7 =1.38					10.7/6 =1.78			1.67
TMP 1987.46.1				17.98/10.74 =1.67										1.67
TMP 2012.12.29	18.11/13.63 =1.33	19.76/13.22 =1.49	20.38/14.52 =1.40	20.69/13 =1.59	19.65/13.38 =1.47	19.14/11.36 =1.68								1.53
TMP 1992.36.749		19.25/13.12 =1.47	20.15/14.38 =1.40	20.31/13.99 =1.45	20.25/14.26 =1.42	20.16/13.15 =1.53	18.49/13.51 =1.37	18.03/12.62 =1.43		16.11/9.65 =1.67				1.47
TMP 1986.49.29			23.75/16.41 =1.45											1.45
TMP 1983.36.134		30.82/22.56 =1.37	30.96/21.67 =1.43	26.53/18.56 =1.43										1.41
TMP 1994.12.602		29.06/20.58 =1.41				22.88/15.48 =1.48		24.42/19.09 =1.28	23.66/18.91= 1.25					1.36
TMP 1967.9.164				30.07/19.53 =1.54		28.55/20.74 =1.38		26.27/18.03 =1.46						1.46
TMP 1975.11.3		26.08/19.06 =1.37	28.56/18.25 =1.56	29.37/16.71 =1.76	29.56/17.3 =1.71	27.24/19.45 =1.40	28.79/18.85 =1.53	32.39/21.69 =1.49	27.34/22.58 =1.21	25.16/19.67 =1.28	25.89/17.09 =1.51	22.76/16.13 =1.41		1.48
<i>Albertosaurus sarcophagus</i>														
TMP 1999.50.40						18.61/11.2 =1.66								1.66
TMP 1999.50.20		19.03/14.32 =1.33	17.84/12.52 =1.42	18.5/13.51= 1.37	23.55/14.75 =1.60									1.43
TMP 1994.25.6	23.98/16.03 =1.50	30.07/21.61 =1.39	28.21/19.2 =1.47	31.21/21.08 =1.48	28.35/17.53 =1.62	27.34/17.83 =1.53					20.76/17.27 =1.20			1.46
TMP 1996.25.61	25.29/18.14 =1.39		25.18/18.46 =1.36											1.38
TMP 1997.25.53									24.16/17.11 =1.41	26.69/17.61 =1.52	20.47/16.81 =1.22	17.48/10.43 =1.68		1.46
TMP 2002.45.21	28.95/18.69 =1.55	31.31/23.21 =1.35	31.12/24.91 =1.25	30.1/22.86 =1.32	30.21/22.26 =1.36									1.36
TMP 2003.45.84							26.76/20.38 =1.31							1.32
TMP 1986.205.1		33.77/22.14 =1.53												1.53

Other tyrannosaurids	Depth at middentary (cm)	Width at middentary (cm)	Distance from tip (cm)	Distance to articulation (cm)	Depth at 3rd tooth (cm)	Width at 3rd tooth (cm)	Distance from tip (cm)	Distance to articulation (cm)	Length of mandible (cm)
<i>Daspletosaurus torosus</i> PR 308 (cast TMP 1981.3.6)	11.95	4.85	22.84	71.5	4.85	?	6.15	87.9	94.5
<i>Daspletosaurus torosus</i> NMC 8506	11.5	6.3	?	70.8	10.8	8.7	?	88.2	95.6
<i>Daspletosaurus torosus</i> TMP 2001.36.1	11.7	5.25	24.6	74	12.5	8.5	6.15	92.1	97.47
<i>Tyrannosaurus rex</i> TMP 1981.6.1	13.2	5.91	37.92	75.8	13	10	9.23	104.07	106.35
<i>Tyrannosaurus rex</i> AMNH 5027 (cast TMP 1987.149.1)	15.4	8.65	33.2	85.5	17.15	14.45	7.55	110.77	118.37
<i>Tyrannosaurus rex</i> LACM 23844 (cast TMP 1992.15.1)	15.94	9.04	34.3	86.8	20.35	16.27	10.7	110.83	119.72
<i>Tyrannosaurus rex</i> FMNH PR 2081	18.51	9.00	?	96.35	14.48	18.55	?	125.46	133.03
<i>Tyrannosaurus rex</i> BHI 3033 (cast TMP 1998.86.1)	16.85	6.45	41.1	80.57	18.00	13.80	11.24	109.30	120.42
<i>Tyrannosaurus rex</i> CM 8390 (cast TMP 2009.3.49)	16.45	6.95	38.65	75.40	19.30	15.78	10.75	103.56	113.92

Non-tyrannosaurid theropods (from Therrien et al., 2005)	Depth at midentary (cm)	Width at midentary (cm)	Distance to articulation (cm)	Length of mandible (cm)	Zx/L at midentary (cm²)
<i>Allosaurus fragilis</i> USNM 4734	6.90	2.20	46.19	59.80	0.22
<i>Allosaurus jimmdaseni</i> MOR 693 (cast UCMP 147068)	6.02	2.56	53.00	68.45	0.17
<i>Ceratosaurus nasicornis</i> USNM 4735	6.20	2.55	44.15	59.60	0.22
<i>Suchomimus tenerensis</i> (cast at Chicago Children's Museum)	7.11	3.48	81.32	112.58	0.21
<i>Giganotosaurus carolinii</i> MUCPv-CH-1 (cast TMP 2000.25.1)	13.40	5.75	143.52	175.97	0.70
<i>Acrocanthosaurus atokensis</i> NCSM 14345 (cast at Academy of Natural Sciences –Philadelphia)	10.48	5.10	90.69	119.56	0.61
<i>Majungasaurus crenatissimus</i> FMNH PR 2100 (cast)	5.82	3.51	38.25	52.48	0.31
<i>Carnotaurus sastrei</i> MACN-CH 894 (cast TMP 1997.27.1)	6.30	3.48	36.76	50.30	0.37
<i>Dilophosaurus wetherilli</i> UCMP 77270	4.95	2.06	43.59	59.66	0.11
<i>Dromaeosaurus albertensis</i> AMNH 5356 (cast TMP 1984.8.1)	2.40	1.02	13.05	18.54	0.04
<i>Deinonychus antirrhopus</i> YPM 41147	2.54	0.86	21.70	28.71	0.03
<i>Saurornitholestes langstoni</i> TMP 1988.121.39	1.80	0.74	12.40	16.96	0.02
<i>Velociraptor mongoliensis</i> (Utah Geological Survey cast of privately-owned specimen)	1.75	0.53	12.45	17.61	0.01

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