

A unique predator in a unique ecosystem

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1 SHORT RUNNING PAGE HEADING: MODELLING THE APEX PREDATOR
2 FROM BRAZILIAN LATE CRETACEOUS

3

4 A UNIQUE PREDATOR IN A UNIQUE ECOSYSTEM: MODELLING THE APEX
5 PREDATOR WITHIN A LATE CRETACEOUS CROCODYLIFORM-DOMINATED
6 FAUNA FROM BRAZIL

7

8

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22 ABSTRACT

23 Theropod dinosaurs were relatively scarce in the Late Cretaceous ecosystems of
24 southeast Brazil. Instead, hypercarnivorous crocodyliforms known as baurusuchids
25 were abundant and probably occupied the ecological role of apex predators.
26 Baurusuchids exhibited a series of morphological adaptations hypothesised to be
27 associated with this ecological role, but quantitative biomechanical analyses of their
28 morphology have so far been lacking. Here, we employ a biomechanical modelling
29 approach, applying finite element analysis (FEA) to models of the skull and mandibles
30 of a baurusuchid specimen. This **allows** us to characterise the craniomandibular
31 apparatus of baurusuchids, as well as to compare the functional morphology of the
32 group to that of other archosaurian carnivores, such as theropods and crocodylians. Our
33 results support the ecological role of baurusuchids as specialised apex predators in the
34 continental Late Cretaceous ecosystems of South America. With a relatively weak bite
35 force (~600 N), the **predation strategies of baurusuchids** likely relied on other
36 morphological specializations, such as ziphodont dentition and strong cervical
37 musculature. Comparative assessments of the stress distribution and magnitude of
38 scaled models of other predators (the theropod *Allosaurus fragilis* and the living
39 crocodylian *Alligator mississippiensis*) consistently show different responses to
40 loadings under the same functional scenarios, suggesting distinct predatory behaviors
41 for these animals. The unique selective pressures in the arid to semi-arid Late
42 Cretaceous ecosystems of southeast Brazil, which were dominated by crocodyliforms,
43 possibly drove the emergence and evolution of the biomechanical features seen in
44 baurusuchids, which are distinct from those previously reported for other predatory
45 taxa.

46 Keywords: Finite Element Analysis; Baurusuchidae; Notosuchia

47 INTRODUCTION

48 In nearly all known continental Cretaceous ecosystems worldwide, the dominant
49 hypercarnivores and apex predators were theropod dinosaurs (Lloyd *et al.* 2008; Benson
50 *et al.* 2013; Zanno & Mackovicky 2013). However, in the Late Cretaceous ecosystems
51 of Brazil, theropods were exceptionally scarce. Instead, the putative dominant apex
52 predators were a group of large, terrestrial crocodyliforms, the baurusuchids (Riff &
53 Kellner 2011; Godoy *et al.* 2014). Baurusuchids are phylogenetically included within
54 Notosuchia, a group of highly diverse crocodyliforms which thrived mainly in
55 Gondwana during the Cretaceous (Pol & Leardi 2015; Mannion *et al.* 2015). Exhibiting
56 a wide range of morphological variation, from gracile omnivores to pug-nosed
57 herbivores, notosuchians **significantly contributed** to the highest peak of morphological
58 disparity experienced by crocodyliforms across their evolutionary history (Wilberg
59 2017; Godoy *et al.* 2019; Melstrom & Irmis 2019; Godoy 2020).

60 Although present in other parts of Gondwana, most baurusuchid species (ca.
61 80%) are found in the Late Cretaceous rocks of the Bauru Group, in southeast Brazil
62 (Carvalho *et al.* 2005; Godoy *et al.* 2014; Montefeltro *et al.* 2011). The Bauru Group
63 palaeoecosystem witnessed an extraordinary abundance of notosuchians, with nearly 30
64 species described so far. **While dinosaurs** were also present, their fossil record in this
65 rock sequence is relatively poor (Montefeltro *et al.* 2011; Godoy *et al.* 2014). Within
66 this crocodyliform-dominated ecosystem, baurusuchids **are** the likely apex predators.
67 Baurusuchids exhibited a series of morphological adaptations hypothesised to be
68 associated with their role as **terrestrial** hypercarnivores, possibly achieved via
69 heterochronic transformations, such as hypertrophied canines, a reduced number of
70 teeth, and dorsoventrally high skulls (Montefeltro *et al.* 2011; Riff & Kellner 2011;
71 Godoy *et al.* 2018; Wilberg *et al.* 2019). However, quantitative assessments of the

72 palaeobiology of baurusuchids are lacking, and the data supporting their role as apex
73 predators is primarily derived from broad generalizations and the faunal composition of
74 the Bauru palaeoecosystem (Riff & Kellner 2011; Godoy *et al.* 2014).

75 Here, we employ a biomechanical modelling approach **in a comparative**
76 **investigation of the functional morphology of a baurusuchid (*Baurusuchus*), one**
77 **analogue of a possible ecological competitor (*Allosaurus*), and an extant crocodyliform**
78 **(*Alligator*)**. Using finite element analysis (FEA), we characterize the baurusuchid skull
79 biomechanically and quantify functional similarities and differences between
80 baurusuchids, theropod dinosaurs and living crocodylians. We also calculate bite forces,
81 simulate functional scenarios, and conduct bending tests to reveal biomechanical
82 properties of the baurusuchid skull. **Our results shed light on key biomechanical aspects**
83 **that may have allowed this group to** dominated the unique ecosystems present during
84 the Cretaceous in Brazil.

85

86 METHODS

87 **Specimens.** The baurusuchid specimen modelled for the present study is a complete
88 skull with lower jaws, referred to *Baurusuchus pachecoi* (LPRP/USP 0697 Laboratório
89 de Paleontologia USP-RP, **Figure 1-A**) and collected in Jales, Brazil (Adamantina
90 Formation, Bauru Group; Montefeltro 2019). *Baurusuchus* is a typical baurusuchid,
91 **presenting the set of anatomical traits that characterizes Baurusuchidae and therefore**
92 **being representative of the clade as a whole (Montefeltro *et al.* 2011, Godoy *et al.***
93 **2014)**. The specimen used for this study has a basal skull length of 33.10 cm (see Table
94 **1 for more cranial measurements), and an estimated total body length of approximately**
95 **170 cm, based on the preserved portions of the skeleton (Montefeltro 2019). Compared**

96 to other relatively complete skeletons of adult baurusuchids, such as *Aplestosuchus*
97 *sordidus* and *Baurusuchus albertoi*, the specimen LPRP/USP 0697 represents a
98 medium-sized baurusuchid (Godoy et al. 2016), with the basal skull length being 70%
99 of that of the holotype of *Stratiotosuchus maxhechti* (one of the largest complete skulls
100 known among baurusuchids: Riff & Kellner, 2011; Godoy et al. 2016).

101 For comparison, we modelled a specimen of the theropod dinosaur *Allosaurus*
102 *fragilis* (MOR 693, Museum of the Rockies, Bozeman, Figure 1-B) and one specimen
103 of *Alligator mississippiensis* (OUVC 9761, Ohio University Vertebrate Collections,
104 Figure 1-C) (see Rayfield et al. 2001, Witmer & Ridgely 2008 for scanning details).
105 *Allosaurus fragilis* was chosen based on its medium size when compared to other
106 theropods, which is equivalent to the putative size of the theropods from the
107 Adamantina Formation, for which no complete craniomandibular material is currently
108 known. Furthermore, *Allosaurus* has been proposed to be functionally similar to
109 abelisaurids, the most commonly found theropods in the Bauru Group (Sakamoto 2010).
110 The choice of *Alligator mississippiensis* (as a living representative of the crocodyliform
111 lineage) was made because this is a model organism for herpetological and functional
112 studies (Guillette et al. 2007; Farmer & Sanders 2010; Reed et al. 2011). For the
113 subsequent FEA, existing 3D models of *Allosaurus fragilis* and *Alligator*
114 *mississippiensis* from previous studies were used (Rayfield et al. 2001; Witmer &
115 Ridgely 2008; Lautenschlager 2015). The *Baurusuchus pachecoi* skull was scanned in a
116 Toshiba Aquilion Prime machine, at “Hospital das Clínicas de Ribeirão Preto”, Brazil.
117 The scan resulted in 1917 projections, generating 1,187 slices (thickness of 0.5 cm),
118 voltage of 120 kV, and current of 150 μ A. The segmentation of bones was performed
119 with Amira 5.3 (Thermo Fisher Scientific).

120 **FEA.** The 3D models of all specimens, including skulls and mandibles, were imported
121 into Hypermesh 11 (Altair Engineering) for the generation of solid tetrahedral meshes
122 (consisting of approximately 1,000,000 elements per model). For the *Alligator* and the
123 baurusuchid models, material properties for bone and teeth were assigned based on
124 values for *Alligator mississippiensis* (bone: $E = 15.0$ GPa, $\nu = 0.29$, teeth: $E = 60.4$ GPa,
125 $\nu = 0.31$; Porro *et al.* 2011; Sellers *et al.* 2017), whereas for the *Allosaurus* model,
126 values were derived from studies on theropods (bone: $E = 20.0$ GPa, $\nu = 0.38$, teeth: $E =$
127 60.4 GPa, $\nu = 0.31$; Rayfield *et al.* 2001, 2011). To exclude the possibility of different
128 results due to distinct material properties we also conducted an FEA on the *Allosaurus*
129 model using the same bone and teeth properties assigned to the crocodyliform models.
130 All material properties in the models were assigned in Hypermesh and treated as
131 isotropic and homogeneous.

132 Intrinsic scenarios for the baurusuchid, *Allosaurus fragilis* and *Alligator*
133 *mississippiensis*, were simulated for the skull and lower jaw models, using a simplified
134 jaw adductor muscle-driven biting. The adductor muscle forces of the baurusuchid were
135 estimated using the attachment area for each muscle (Figure 2), based on previous
136 works on extant and extinct crocodyliforms (Holliday & Witmer 2009; Holliday *et al.*
137 2013). The adductor chamber reconstruction of the dinosaur and crocodylian was based
138 on previously published data for the muscle arrangements for both taxa (Rayfield *et al.*
139 2001, 2011; Porro *et al.* 2011; Sellers *et al.* 2017). The attachment areas measured for
140 the three taxa were used as a proxy for physiological cross-section area, which was then
141 multiplied by an isometric muscle stress value of 25.0 N/cm² (Porro *et al.* 2011). Table
142 2 shows the total muscle force inferred for each muscle. Although this isometric muscle
143 stress is on the lower margin of the range of values reported for vertebrate muscles (e.g.
144 32 N/cm² and 35 N/cm²) it was selected here due to the relatively close phylogenetic

145 position of baurusuchids to modern crocodylians. However, the calculated bite force
146 would be only slightly (10-15%) higher using different values for isometric muscle
147 stress. Three intrinsic scenarios were analysed to estimate the muscle-driven biting force
148 in the baurusuchid, (1) a bilateral bite at the second maxillary and the fourth dentary
149 tooth, (2) a unilateral bite at the second maxillary and the fourth dentary tooth, and (3)
150 unilateral bite at the third premaxillary tooth. One intrinsic scenario was analysed for
151 both *Allosaurus fragilis* and *Alligator mississippiensis*: the maxillary and dentary
152 unilateral bite scenarios. For each intrinsic scenario in all taxa, constraints were placed
153 on nodes at the craniomandibular articular surfaces. Each node was constrained in all
154 directions (x, y, z). For the skulls, three nodes were constrained on the occipital
155 condyle, and two nodes on each quadrate articular surface. For the lower jaws, three
156 (baurusuchid) or four (*Allosaurus* and *Alligator*) nodes on each glenoid were
157 constrained. To estimate the biting force of the baurusuchid, nodes were constrained at
158 the tip of the teeth to measure the reaction force caused by the modelled adductor
159 muscles and the same approach was used for the other two taxa. In unilateral scenarios,
160 the tip of one tooth was constrained, while in bilateral scenarios the tip of the teeth on
161 both sides was constrained. For the baurusuchid, the constrained teeth were PM3, M2
162 and D4; for *Allosaurus fragilis*, M3 and D5; for *Alligator mississippiensis*, M4 and D4.
163 The intrinsic scenarios were all based on the same jaw adductor reconstructions for each
164 taxon, and aimed to emulate possible behaviours of baurusuchids, theropod dinosaurs
165 and crocodylians.

166 To investigate the craniomandibular biomechanical properties in alternative load
167 assignments, five bending scenarios were also tested for the baurusuchid skull and
168 mandible models: unilateral bending, bilateral bending, pull-back, head-shake, and
169 head-twist. The bending test scenarios were proposed as an additional investigation of

170 the skull properties in situations that approach behaviours during different types of
171 strikes, including biting (unilateral bending and bilateral bending) and supplementary
172 head movements allowed by postcranial musculature (pull-back, head-shake, and head-
173 twist). The loading applied for each scenario was based on the approximation of the
174 greatest bite force obtained from the intrinsic scenario (600 N; see results below). All
175 loadings in the unilateral bending scenario were applied to one node, perpendicular to
176 the occlusal planes on one of the following teeth: D1, D4, D9, PM2, PM3, M2 and M4.
177 Bilateral bending scenarios were tested with the same conditions as the unilateral ones,
178 but with two vectors of 300 N applied **symmetrically** to each canine at the M4 and the
179 D4. The head-shake scenario was tested with two vectors of 300 N pointing to the same
180 direction, one on one node on the labial surface of left M2/D4 and the other on one node
181 on the lingual surface of right M2/D4. For the pull-back, the load force of 600 N was
182 applied to one node at crown midheight over the distal carina of the caniniform teeth
183 (D4, PM3 and M2). For the head twist, the loadings were applied to two opposite
184 vectors of 300 N in each model. One loading vector was applied to one node at the tip
185 of the maxillary (M2) or dentary (D4) caniniform tooth, and another loading vector on
186 the opposite side on the dorsal surface of the maxilla, or ventral surface of the dentary
187 respectively.

188 Four bending scenarios were also tested in the skull and lower jaws of
189 *Allosaurus fragilis* and *Alligator mississippiensis*, for comparison. Unilateral and
190 bilateral bending were simulated to the comparable positions of the tested in the
191 baurusuchid. Unilateral bending was tested in PM2, M3, M16, D1, D4 and D13 for
192 *Allosaurus fragilis*, and PM2, M4, M15, D2, D4 and D15 for *Alligator mississippiensis*.
193 Bilateral bending was also tested in M3 and D5 pairs for the theropod, and M4 and D4
194 pairs for the crocodylian. For meaningful comparisons of form and function

195 independent of size (Dumont et al., 2009), all models used in the bending tests were
196 scaled to the total surface of the baurusuchid specimen. For the bending scenarios,
197 constraints were placed on the same nodes as in the intrinsic scenarios. The
198 performances for the FEA models were assessed via contour plots of von Mises stress
199 distribution and mean von Mises stress and displacement values per element. To avoid
200 the influence of individual stress singularities, such as at the constrained or loaded
201 nodes, we used an averaging threshold of 99%.

202

203 RESULTS

204 During the bilateral bite scenario, the bite force estimate for the baurusuchid specimen
205 was 252 N for the skull and 578 N for the lower jaw. For the premaxillary unilateral bite
206 scenario, bite force was estimated as 199 N, whereas for both maxillary and lower jaw
207 unilateral bite scenarios, it was 450 N. The distribution and magnitude of the von Mises
208 stress showed little difference in the intrinsic scenarios for the skull and lower jaw of
209 the baurusuchid (Figure 3). Most of the elements in the skull remained relatively stress-
210 free in the three intrinsic scenarios simulated (mean von Mises stress of 0.46 MPa
211 during the bilateral maxillary biting, 0.50 MPa during the unilateral maxillary biting,
212 and 0.52 MPa during the premaxillary unilateral biting). The quadrate body, the body of
213 the ectopterygoid, and the posterior margin of the pterygoid are the main regions in
214 which stresses are present during those simulated scenarios (Figure 3). In the intrinsic
215 scenario for the premaxillary canine bite, there is also increased stress at the anterior
216 margin of the notch between the premaxilla and maxilla, which also extends medially
217 surrounding the notch at the secondary bony palate. As expected, the lower jaws
218 experienced more von Mises stress than the skull model (mean von Mises stress of 1.93

219 MPa in the bilateral biting, and 2.01 MPa in the unilateral biting). In both scenarios, the
220 symphyseal region surrounding the canine teeth, and the retroarticular process remained
221 relatively stress-free, and the greatest **von** Mises stress is observed on the dorsal surface
222 of the surangular and ventral surface of the angular.

223 Considerable differences were found between the **von** Mises stress magnitudes
224 of the skull and lower jaws of the baurusuchid among the different bending scenarios
225 tested (e.g. **mean** values of 0.4 MPa in the skull head twist and of 24.7 MPa in the
226 bilateral biting of the lower jaws). Although variable in magnitude, a general pattern is
227 discernable in the stress distribution in the skull and lower jaws of the baurusuchid
228 (Figure 4). The greatest **von** Mises stresses in the skull models are mostly present in the
229 posterior and median portions of the skull, with stress hotspots located on the ventral
230 and lateral regions of the quadrate body, ventral region of the infratemporal bar, and
231 preorbital region (anterior jugal, posterior maxillae, lacrimals, nasal, prefrontals, and
232 anterior frontal). In addition, the areas of maximum **von** Mises stress in the premaxillae
233 and maxillae are isolated from each other. This means that when loading is applied to
234 the premaxillary teeth, the maxillae remain relatively stress-free, whereas the dorsal
235 rostrum (premaxilla and nasals) is more stressed. When loading is applied to the
236 maxillary teeth, the premaxillae remain unstressed, and stress is concentrated on the
237 posterior portion of the skull (Figure 4).

238 The lower jaws also experienced more **von** Mises stress than the skull model
239 during the bending tests, and the stress hotspots are more homogeneously distributed,
240 located on the dorsal surface of the surangular, angular and retroarticular process. Two
241 exceptions are the jaw pull-back scenario, in which the stress hotspots are located
242 around the mandibular fenestra; and the bilateral bending scenario, in which most of the
243 lower jaw is highly stressed, and only the symphyseal region remains less stressed.

244 The areas around the maxillary and dentary canines remain relatively stress-free,
245 even during scenarios in which the loadings were applied to the canines (both in the
246 intrinsic scenarios and the bending tests). This is particularly evident for the dentary
247 canine, for which the surrounding bone remains unstressed in all scenarios, including
248 the least optimal scenario of the bilateral bending (Figure 4).

249 In general, the patterns of von Mises stress distribution obtained for *Allosaurus*
250 and *Alligator* (Figure 5 and Figure 6) were consistent with previous studies (Rayfield et
251 al. 2001; Porro et al. 2011). Even considering that the bone properties assigned to the
252 *Allosaurus* are slightly different from the other models, it did not substantially change
253 the results obtained from this taxon. Considering the intrinsic scenarios, the measured
254 mean von Mises stress is similar during maxillary unilateral biting (mean von Mises
255 stress of 0.72 MPa for *Allosaurus* and 0.62 MPa for *Alligator*). The pattern of stress
256 distribution observed in the models of the *Alligator* are much closer to the observed in
257 the baurusuchid than to the *Allosaurus*, perhaps related to the phylogenetic proximity
258 reflected in the cranial architecture of both crocodyliforms.

259 The two taxa retrieved greater differences in the lower jaw models during the
260 intrinsic scenarios (mean von Mises stress of 3.7 MPa for *Allosaurus* and 0.99 MPa for
261 *Alligator*). The discrepancies observed in the bending scenarios are also most evident in
262 the lower jaws, which for the baurusuchid remain consistently less stressed than those
263 of both the theropod and the crocodylian during the bending tests. When compared to
264 the baurusuchid, the theropod models obtained only slightly lower mean von Mises
265 stress values for the skull, but much higher values for the lower jaws (Figure 6). The
266 alligator model, in contrast, retrieved higher mean von Mises stress values in most
267 scenarios than both the baurusuchid and *Allosaurus*, even though differences in stress
268 values are less distinguishable between skull models of the analysed taxa (Figure 6).

269 The only scenario that does not follow this pattern is the unilateral bending at the back
270 of the upper tooth row, in which the **mean von Mises** stress value is similar for the
271 baurusuchid and *Alligator*, although both have higher stresses than the theropod. The
272 most divergent results are related to the mandibular anterior bending scenario, in which
273 the **mean** stress value in *Alligator* was more than nine times higher than in the
274 baurusuchid, and almost twice the **mean von Mises** stress recorded for the theropod.

275

276 DISCUSSION

277 The unexpectedly weak bite force estimated for the baurusuchid is much lower than that
278 measured for extant crocodylians of comparable size. For example, *Alligator sinensis*
279 has a similar total body length (150–200 cm) and can have a bite of up to 963 N
280 (measured at the caniniform tooth), **whereas *Paleosuchus* is the only living species with**
281 **comparable bite force values** (Erickson et al. 2012). The bite force estimated for the
282 baurusuchid is also only a fraction of the bite forces inferred for adult theropods, which
283 could potentially exceed 50,000 N (Gignac & Erickson 2017). **Furthermore, in order to**
284 **estimate the bite force of extinct crocodyliforms, previous studies have applied**
285 **equations based on regression data from extant crocodylians (e.g. Aureliano et al. 2015).**
286 **Although, this type of equation is likely to relatively correctly estimate the bite force for**
287 **fossil crocodyliforms phylogenetically close to the Crocodylia clade and sharing the**
288 **basic cranial architecture, it does not take into consideration the very different cranial**
289 **architectures present in more distantly related taxa, such as baurusuchids. As a result,**
290 **this equation may not be accurate for anatomically divergent taxa, and will overestimate**
291 **or underestimate the bite forces of those taxa. We applied the equations presented by**
292 **Aureliano et al. (2015), which uses data from living species (Verdade 2000; Erickson et**

293 al. 2012), to the craniomandibular measurements of the specimen studied here
294 (LPRP/USP 0697) and obtained a much higher bite force estimation (of nearly 4,000
295 N). This apparent overestimation demonstrates that the differences between the cranial
296 structures of living and extinct crocodyliforms may have important functional
297 implications, such as the disproportionately positive bite force increase previously
298 inferred for baurusuchids (Gignac & O'Brien 2016).

299 In this context, it is noteworthy that the bite force estimates from FEA vary
300 when using the skull or the mandible to obtain reaction forces. This is not surprising as
301 the geometry and architecture of the skull is more complex and subject to further
302 constraints than in the mandible. Validation tests have shown, however, that realistic
303 bite forces can be estimated from mandible models (Porro et al. 2011). Consequently,
304 we consider the higher bite force values obtained from the mandible as the more likely
305 for the baurusuchid.

306 This comparatively weak bite force in baurusuchids suggests that their role as
307 apex predators may have involved hunting strategies different from those of most
308 carnivorous theropods and living crocodylians, which mostly rely on muscle-driven
309 biting forces for killing (Rayfield 2004, 2005, 2011; D'Amore et al. 2011; Erickson et
310 al. 2012). As a consequence, the killing potential of baurusuchids could have been
311 enhanced by structural and behavioural traits, as in other weak-bite apex predators such
312 as troodontid and allosaurid theropods, varanid lizards, and felines, all of which harness
313 the postcranial musculature to supplement bite force (Rayfield 2001; D'Amore et al.
314 2011; Figueirido et al. 2018; Torices et al. 2018).

315 Alternatively, the apex predator role of baurusuchids could have been a
316 historical misinterpretation, and the group might be better interpreted as preying on

317 smaller and/or softer animals. However, a series of craniomandibular and postcranial
318 adaptations of baurusuchids indicate otherwise. For example, the presence of extensive
319 overengineered regions around the canines in both the skull and lower jaws (e.g. regions
320 that remain relatively stress-free in all tests) show that the baurusuchid
321 craniomandibular architecture could safely perform in much higher stress conditions
322 than imposed by muscle-driving biting forces. This is true even for our bending tests
323 that most likely overestimate the stress experienced by the skull of the baurusuchid. The
324 presence of overengineered regions in *Allosaurus* has been suggested as evidence that
325 this taxon also used mechanisms to enhance killing potential in its regular feeding
326 strategy (Rayfield *et al.* 2001).

327 Additionally, the tested pull-back, head-shake and head-twist scenarios were
328 designed to understand how the baurusuchid craniomandibular architecture would
329 perform during similar head movements employed by other weak- and strong-bite apex
330 predators (Rayfield 2001; D'Amore *et al.* 2011; Torices *et al.* 2018). For baurusuchids,
331 these movements would be possible given the robust cervical vertebrae, high neural
332 spines, and well-developed cervical ribs (particularly the first two), which provided
333 large attachment areas for the muscles responsible for head lift, head twist, and side-to-
334 side movements (Cleuren & De Vree 2000; Godoy *et al.* 2018). These tests show that
335 the baurusuchid skull and mandible worked optimally in scenarios simulating non-
336 orthal loads, suggesting that baurusuchids were well-suited for head movements during
337 predation, possibly even more so than living crocodylians. This can be explained by the
338 combination of three skull features that minimize skull stress during bites and torsion,
339 the oreinirostral morphology, the absence of the antorbital fenestra, and the extensively
340 ossified secondary palate. This combination of features is particularly efficient for stress
341 reduction during unilateral biting (Rayfield & Milner 2008).

342 Our tests also revealed that the well-developed gap between premaxillae and
343 maxillae is a unique specialization in the skull architecture of baurusuchids, very likely
344 related to predatory habits. This gap redirects the stress from the premaxillae to the
345 dorsal surface of the fused nasals during biting, preventing stress from traveling from
346 the occlusal region of one bone to the other, and implying a functional decoupling
347 between premaxillae and maxillae during bites. This gap at the premaxillae-maxillae
348 suture is absent in *Allosaurus* and *Alligator*, and in those taxa, the stress travels directly
349 from the premaxilla to the maxilla, especially during the unilateral premaxillary bending
350 scenarios. A similar stress redirection is observed in tyrannosaurids, in which the robust
351 and also fused nasals work as the main route for stress distribution, bypassing the less
352 robust maxilla-lacrimal contact (Rayfield 2005). We suggest that the gap observed in
353 baurusuchids, in combination with the robust and fused nasals, worked similarly to that
354 of tyrannosaurids, even though, the general cranial architecture presented by the
355 baurusuchid is closer to the *Alligator*. The gap could also allow repeated punctures to be
356 inflicted from biting at different positions of the tooth row, but concomitantly working
357 as a built-in safety factor, minimizing the risk of the skull yielding (Rayfield et al.,
358 2001). Finally, the presence of ziphodont dentition in baurusuchids is also in line with
359 the role of apex predator (Riff & Kellner 2011; Godoy et al. 2014). Knife-like teeth with
360 well-developed serrated cutting edges are a dental adaptation for optimal defleshing of
361 vertebrate carcasses (D'Amore et al. 2009) and are present in a series of unrelated apex
362 predators, including theropod dinosaurs and large monitor lizards (D'Amore et al. 2011;
363 Brink & Reisz 2014; Torices et al. 2018).

364 The discrepancy in the von Mises stress magnitude and distribution seen
365 between the mandibles of the three taxa during the intrinsic scenarios and during the
366 bending tests suggests that this structure is also pivotal in understanding the

367 palaeoecology of baurusuchids. The **von** Mises stress distribution shows that *Allosaurus*
368 and *Alligator* have, in general, higher and more homogeneously distributed **von** Mises
369 stress in the mandible, while in the baurusuchid the stress is concentrated at the
370 postsymphyseal region. This indicates that the robust symphysis in baurusuchids is
371 important for stabilizing the lower jaws.

372 The best example of the divergent responses among lower jaws is seen in the
373 bilateral bending scenario, for which the **mean von** Mises stress value for the
374 baurusuchid was approximately five times greater than any other scenario. Additionally,
375 this is the only scenario in which the **von** Mises stress approaches the higher values
376 presented by *Allosaurus* and *Alligator* (Figure 6). The baurusuchid response is also
377 different from *Allosaurus* and *Alligator* in the sense that the **mean von** Mises stress
378 values in the bilateral bending scenarios are distinct from the unilateral scenarios,
379 whereas the other two taxa show similar values in both scenarios. Based on our FEA
380 results, we propose that the bilateral biting is the least likely killing strategy for
381 baurusuchids, and the clamp-and-hold, employed by living crocodylians, and large
382 mammal predators, such as the lion (*Panthera leo*) (Figueirido *et al.* 2018), does not fit
383 the mechanical properties of the baurusuchid skull.

384 Our results also indicate that baurusuchids were well adapted for handling
385 struggling prey, which was possibly subdued by inflicting a series of bites using
386 premaxillary, maxillary and particularly the dentary canines, that combined with
387 ziphodonty would pierce repeatedly the skin of the prey. The puncture phase would be
388 followed by head-movements that would worsen the wounds caused by the punctures
389 and ultimately leading to the death of the prey.

390 Our results successfully characterise the exceptional suite of biomechanical
391 properties displayed by baurusuchids, which combine novel adaptations, features
392 similar to theropods, and others seen in living crocodylians. Such a combination has not
393 been reported previously for any predatory taxon, raising questions on the specific
394 evolutionary settings that allowed these features to emerge. Selective pressures from
395 extrinsic environmental factors seem to have an important influence during amniote
396 functional and biomechanical evolution (Sakamoto *et al.* 2019). In the case of
397 baurusuchids, the unique Late Cretaceous palaeoecosystems of southeast Brazil
398 exhibited a combination of playa-lake systems and transitory rivers which possibly
399 permitted life to flourish in semi-arid to arid conditions (Carvalho *et al.* 2010; Marsola
400 *et al.* 2016). These landmasses witnessed an extraordinary diversity of crocodyliforms
401 (especially notosuchians; Mannion *et al.* 2015), as well as other tetrapods (Godoy *et al.*
402 2014). This resulted in a diverse array of potential prey for baurusuchids among
403 terrestrial **tetrapods, including** crocodyliforms and **sauropods**, indicating that prey
404 selection could have played an important role in the evolution of the baurusuchid
405 craniomandibular apparatus.

406

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415 AUTHOR CONTRIBUTIONS

416 FCM, SL, and RJB conceived and designed the experiments. FCM, SL, PLG, GSF and

417 RJB analyzed the data. FCM, SL, and PLG wrote the paper. All authors read,

418 commented on and approved the final version of the article.

419

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544 FIGURE LEGENDS

545 **Figure 1.** Digitally restored models of skulls used in this study. A- Baurusuchid
 546 (LPRP/USP 0697) in lateral view showing typical traits of the members of the clade. B-
 547 *Allosaurus fragilis* (MOR 693) in lateral view. C- *Alligator mississippiensis* (OUVC
 548 9761) in lateral view.

549

550 **Figure 2.** Muscle attachment areas plotted on the 3D model of skull the baurusuchid
 551 LPRP/USP 0697. A, skull and lower jaws in lateral view; B, dorsal view of the left
 552 posterior of the skull; C, ventral view of the left posterior of the skull; D, posterolateral
 553 view of the skull; E, occipital view of the left portion of the skull; F, lateral view of the
 554 posterior portion of the left mandibular ramus; G, medial view of the posterior portion
 555 of the left mandibular ramus; H, occlusal view of the posterior portion of the left
 556 mandibular ramus; I, ventral view of the posterior portion of the left mandibular ramus.
 557 **MAMEM:** *m. adductor mandibulae externus medialis*; **MAMEP:** *m. adductor*
 558 *mandibulae externus profundus*; **MAMES:** *m. adductor mandibulae externus*
 559 *superficialis*; **MAMP:** *m. adductor mandibulae posterior*; **MDM:** *m. depressor*
 560 *mandibulae*; **MIRA:** *m. intramandibularis*; **MPSTPS:** *m. pseudotemporalis profundus*;
 561 **MPTD:** *m. pterygoideus dorsalis*; **MPTV:** *m. pterygoideus ventralis*.

562

563 **Figure 3.** Von Mises stress contour plots from finite elements analysis (FEA) of the
 564 baurusuchid specimen (LPRP/USP 0697) for the intrinsic scenarios. Arrows indicate the
 565 location of muscle-driven bite forces on models during each scenario, with respective
 566 estimated bite force values. **Mean von** Mises values per scenario are displayed on the
 567 bottom right. **JBMB.:** jaw bilateral muscle-driven bite; **JUMB.:** jaw unilateral muscle-
 568 driven bite; **SBMB.:** skull bilateral muscle-driven bite; **SUMB.:** skull unilateral muscle-
 569 driven bite; **UPMB.:** unilateral premaxillary muscle-driven bite.

570

571 **Figure 4.** Von Mises stress contour plots from FEA of the baurusuchid specimen
 572 LPRP/USP 0697, comparing the stress distribution of skull and mandible models under
 573 distinct functional bending scenarios. Arrows indicate the location on the models of the

574 loading vectors for each scenario. **Mean von** Mises values per scenario are displayed on
575 the bottom right. **D.1:** jaw anterior unilateral bending; **D.4:** jaw canine unilateral
576 bending; **D.PB.:** dentary canine pull-back; **D.S.:** canine dentary shake; **HT.:** head-twist
577 (skull); **JBB.:** jaw canine bilateral bending; **JT.:** head-twist (jaw); **M.2:** maxilla canine
578 unilateral bending; **M.4:** maxilla posterior unilateral bending; **MBB.:** maxilla canine
579 bilateral bending; **M.PB.:** maxilla canine pull-back **PM.2:** premaxilla anterior unilateral
580 bending; **PM.3:** premaxilla canine unilateral bending; **PM.PB.:** premaxilla canine pull-
581 back; **S.S.:** canine skull shake.

582

583 **Figure 5.** Von Mises stress contour plots from FEA of *Allosaurus fragilis* and *Alligator*
584 *mississippiensis* for the intrinsic scenarios. **Mean von** Mises values per scenario for each
585 taxon are displayed on the right. **JUMB.:** jaw unilateral muscle-driven bite; **SUMB.:**
586 skull unilateral muscle-driven bite.

587

588 **Figure 6.** Comparison of **von** Mises stress distribution for scaled models of different
589 archosaurian carnivores: baurusuchid, *Allosaurus fragilis* and *Alligator mississippiensis*.
590 Stress contour plots displayed for the anterior bending scenario. On the right,
591 comparative **mean von** Mises values per scenario for each taxon. **DAB.:** jaw anterior
592 bending; **DCB.:** jaw canine unilateral bending; **DPB.:** jaw canine unilateral bending;
593 **JBB.:** jaw canine bilateral bending; **MBB.:** maxilla canine bilateral bending; **MCB.:**
594 maxilla canine unilateral bending, **MPB:** maxilla posterior unilateral bending; **PMB.:**
595 unilateral premaxillary bending.

596

597 TABLES

598 **Table 1.** Selected measurements (in cm) for the skull LPRP/USP 0697

LPRP/USP 0697	
Basal skull length (from tip of snout to occipital condyle along midline)	33.10
Length of skull (from posterior end of skull table to tip of snout, on midline)	30.20
Length of snout (from anterior end of orbit to tip of snout)	18.27
Greatest transverse width of skull (across quadratojugals)	17.99
Least transverse interorbital distance	4.65
Transverse width of skull at level of anterior ends of orbits	7.13
Transverse width of skull at level of postorbital bars	9.59
Transverse width of skull table anteriorly	10.16
Transverse width of skull table posteriorly	15.23

599

600

601 **Table 2. Total force inferred from cranial and lower jaw attachments for each**
602 **muscle modeled.**

Muscle	Total muscle force (N)
<i>m. adductor mandibulae externus medialis</i>	132.65
<i>m. adductor mandibulae externus profundus</i>	227.625
<i>m. adductor mandibulae externus superficialis</i>	157.875
<i>m. adductor mandibulae posterior</i>	249.475
<i>m. depressor mandibulae</i>	245.925
<i>m. intramandibularis</i>	87.775
<i>m. pseudotemporalis profundus</i>	61.25
<i>m. pterygoideus dorsalis</i>	235.94
<i>m. pterygoideus ventralis</i>	198.4

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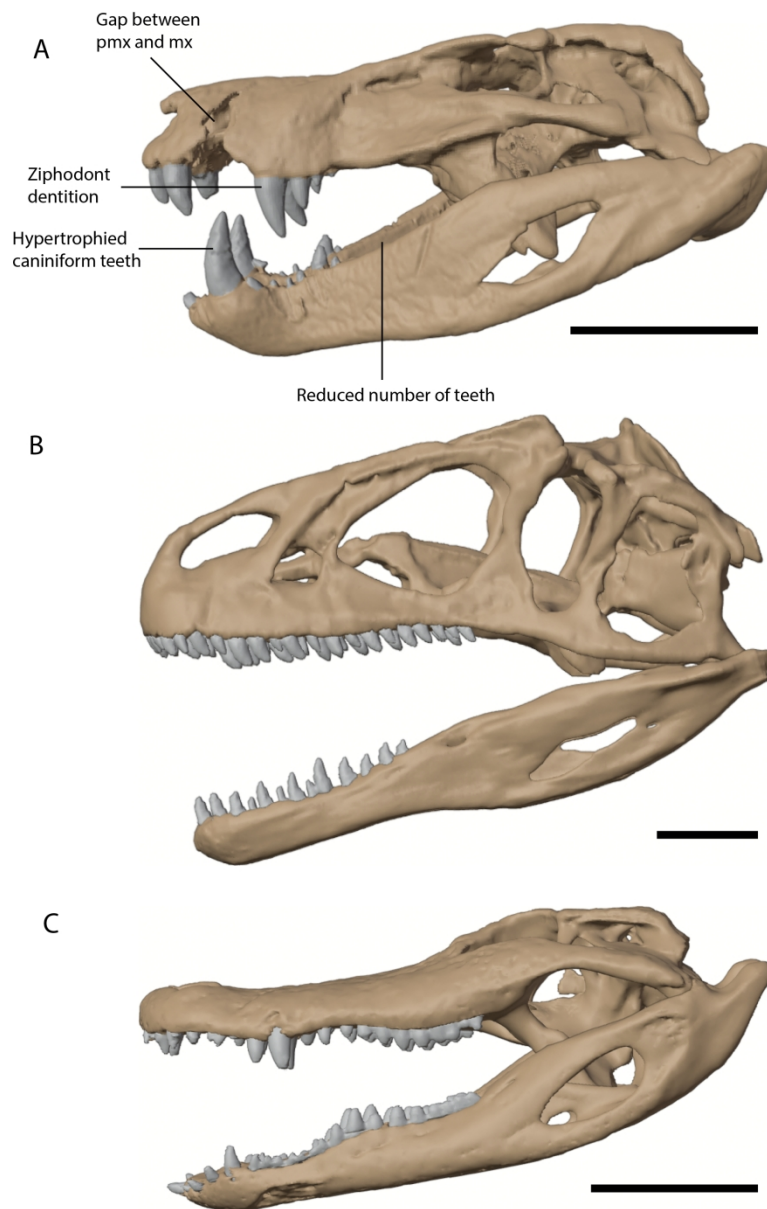


Figure 1. Digitally restored models of skulls used in this study. A- Baurusuchid (LPRP/USP 0697) in lateral view showing typical traits of the members of the clade. B- *Allosaurus fragilis* (MOR 693) in lateral view. C- *Alligator mississippiensis* (OUVC 9761) in lateral view.

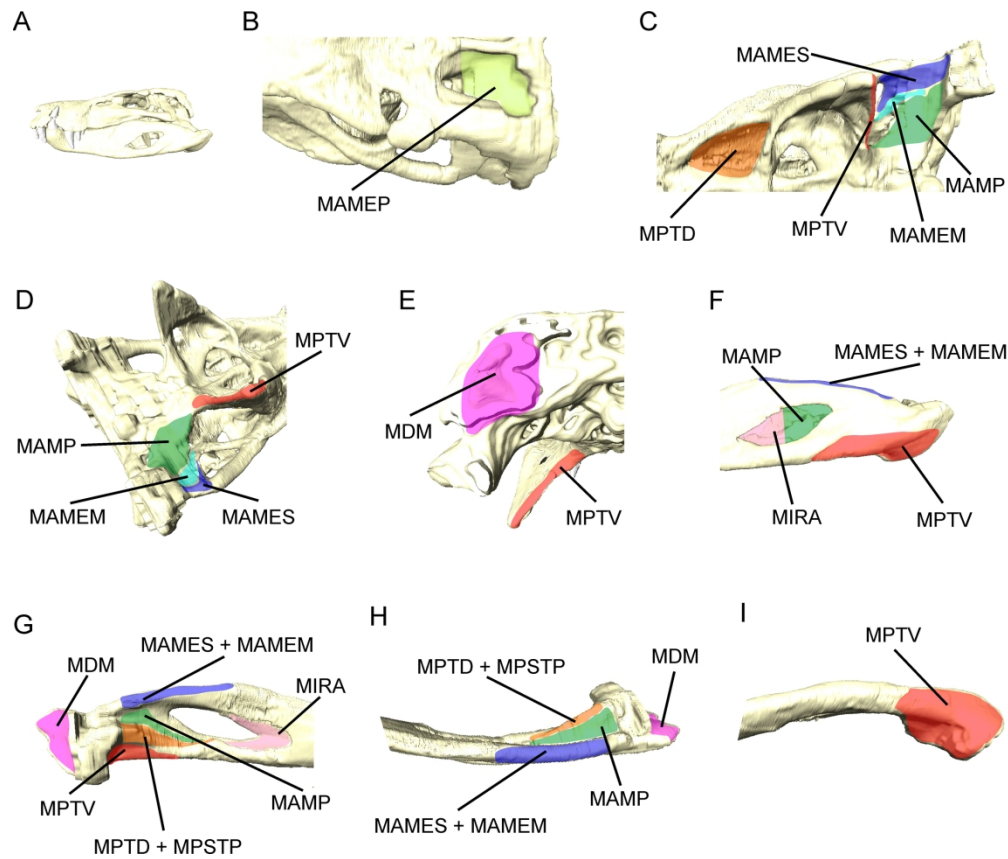


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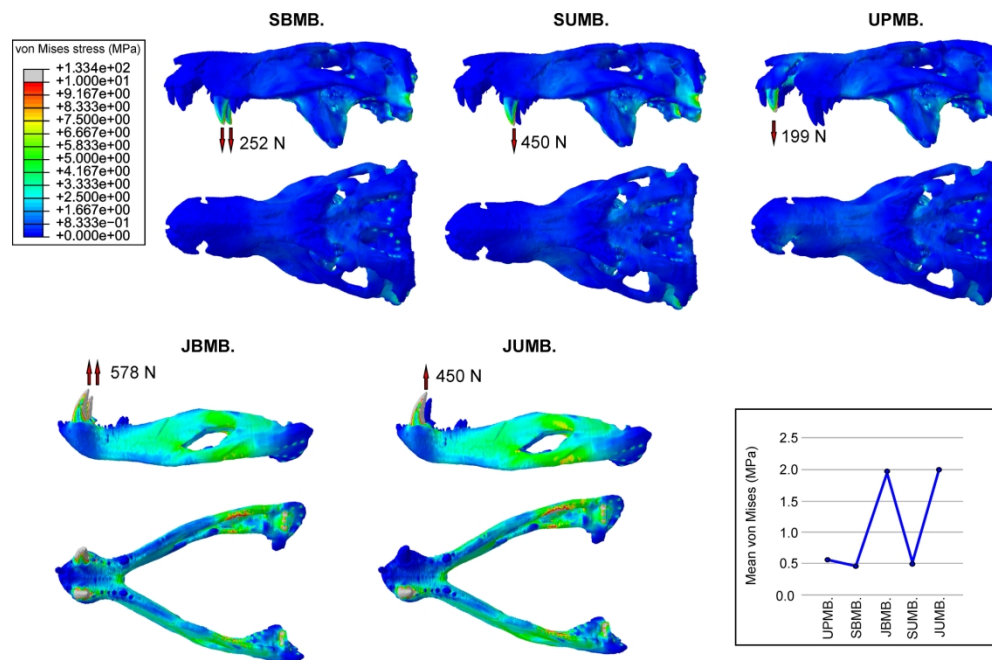


Figure 3. Von Mises stress contour plots from finite elements analysis (FEA) of the baurusuchid specimen (LPRP/USP 0697) for the intrinsic scenarios. Arrows indicate the location of muscle-driven bite forces on models during each scenario, with respective estimated bite force values. Mean von Mises values per scenario are displayed on the bottom right. JBMB.: jaw bilateral muscle-driven bite; JUMB.: jaw unilateral muscle-driven bite; SBMB.: skull bilateral muscle-driven bite; SUMB.; skull unilateral muscle-driven bite; UPMB.: unilateral premaxillary muscle-driven bite.

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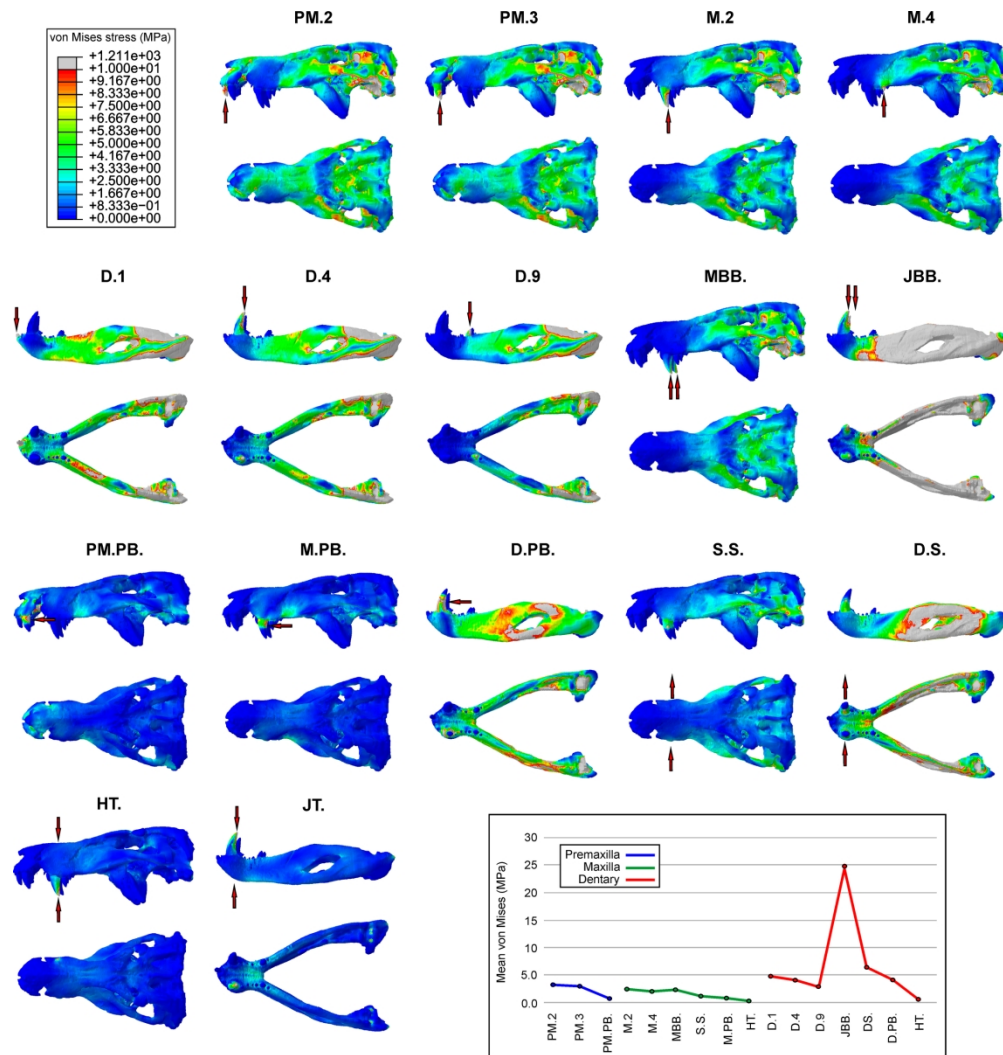


Figure 4. Von Mises stress contour plots from FEA of the baurusuchid specimen LPRP/USP 0697, comparing the stress distribution of skull and mandible models under distinct functional bending scenarios. Arrows indicate the location on the models of the loading vectors for each scenario. Mean von Mises values per scenario are displayed on the bottom right. D.1: jaw anterior unilateral bending; D.4: jaw canine unilateral bending; D.PB.: dentary canine pull-back; D.S.: canine dentary shake; HT.: head-twist (skull); JBB.: jaw canine bilateral bending; JT.: head-twist (jaw); M.2: maxilla canine unilateral bending; M.4: maxilla posterior unilateral bending; MBB.: maxilla canine bilateral bending; M.PB.: maxilla canine pull-back; PM.2: premaxilla anterior unilateral bending; PM.3: premaxilla canine unilateral bending; PM.PB.: premaxilla canine pull-back; S.S.: canine skull shake.

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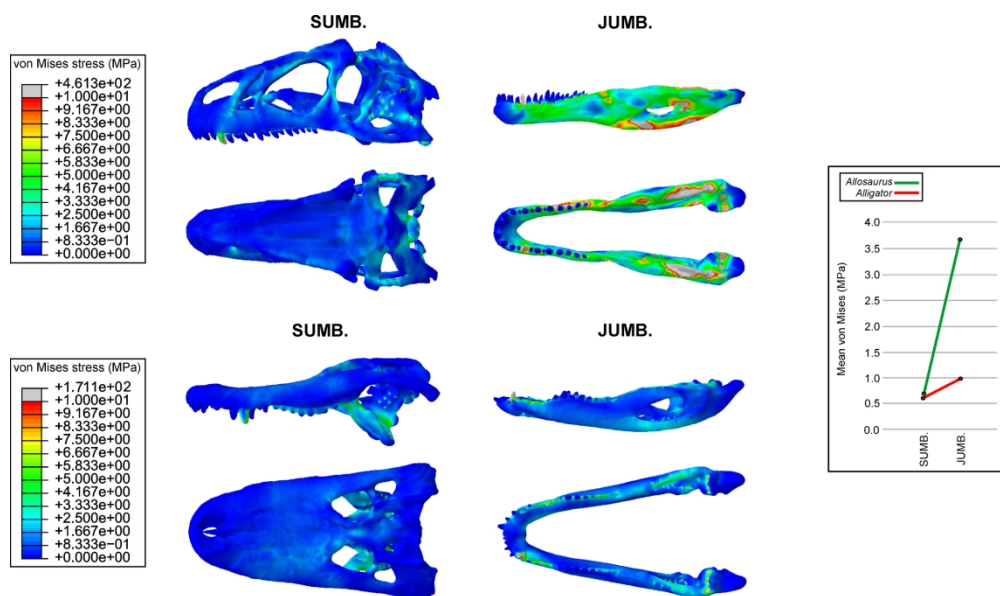


Figure 5. Von Mises stress contour plots from FEA of *Allosaurus fragilis* and *Alligator mississippiensis* for the intrinsic scenarios. Mean von Mises values per scenario for each taxon are displayed on the right. JUMB.: jaw unilateral muscle-driven bite; SUMB.: skull unilateral muscle-driven bite.

200x117mm (300 x 300 DPI)

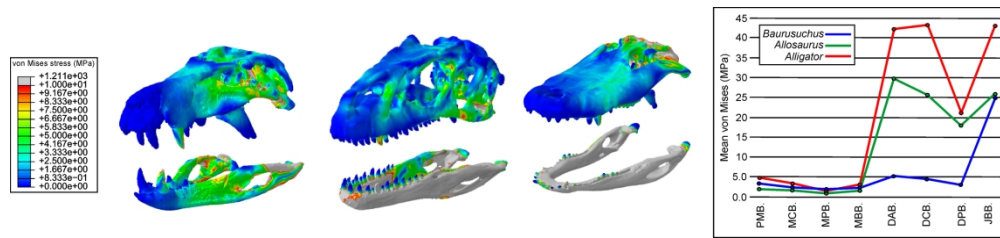


Figure 6. Comparison of von Mises stress distribution for scaled models of different archosaurian carnivores: baurusuchid, *Allosaurus fragilis* and *Alligator mississippiensis*. Stress contour plots displayed for the anterior bending scenario. On the right, comparative mean von Mises values per scenario for each taxon. DAB.: jaw anterior bending; DCB.: jaw canine unilateral bending; DPB.: jaw canine unilateral bending; JBB.: jaw canine bilateral bending; MBB.: maxilla canine bilateral bending; MCB.: maxilla canine unilateral bending, MPB: maxilla posterior unilateral bending; PMB.: unilateral premaxillary bending.

237x54mm (300 x 300 DPI)