

## 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  $\mu$ 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/cm<sup>2</sup> (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/cm<sup>2</sup> and  $35$ N/cm<sup>2</sup>) 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

<b>LPRP/USP 0697</b>	
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.**

<b>Muscle</b>	<b>Total muscle force (N)</b>
<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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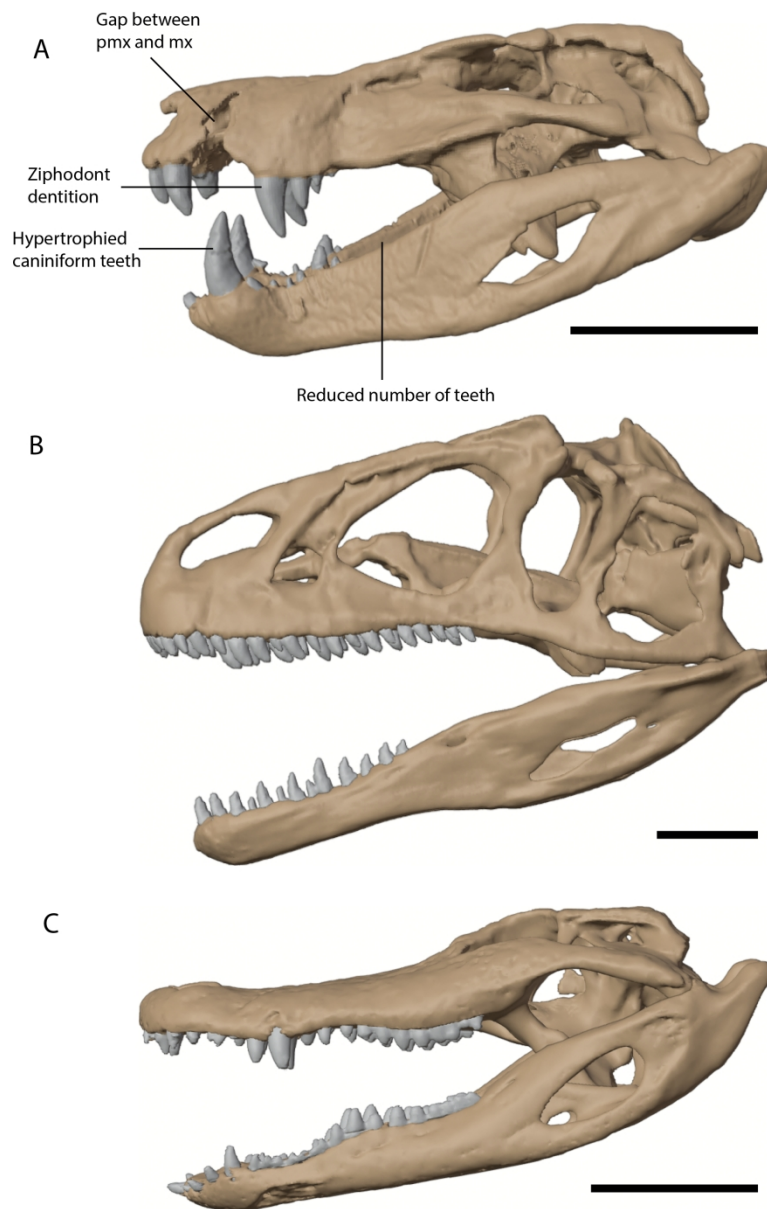


Figure 1. Digitally restored models of skulls used in this study. A- Baurusuchid (LPRP/USP 0697) in lateral view showing typical traits of the members of the clade. B- *Allosaurus fragilis* (MOR 693) in lateral view. C- *Alligator mississippiensis* (OUVC 9761) in lateral view.

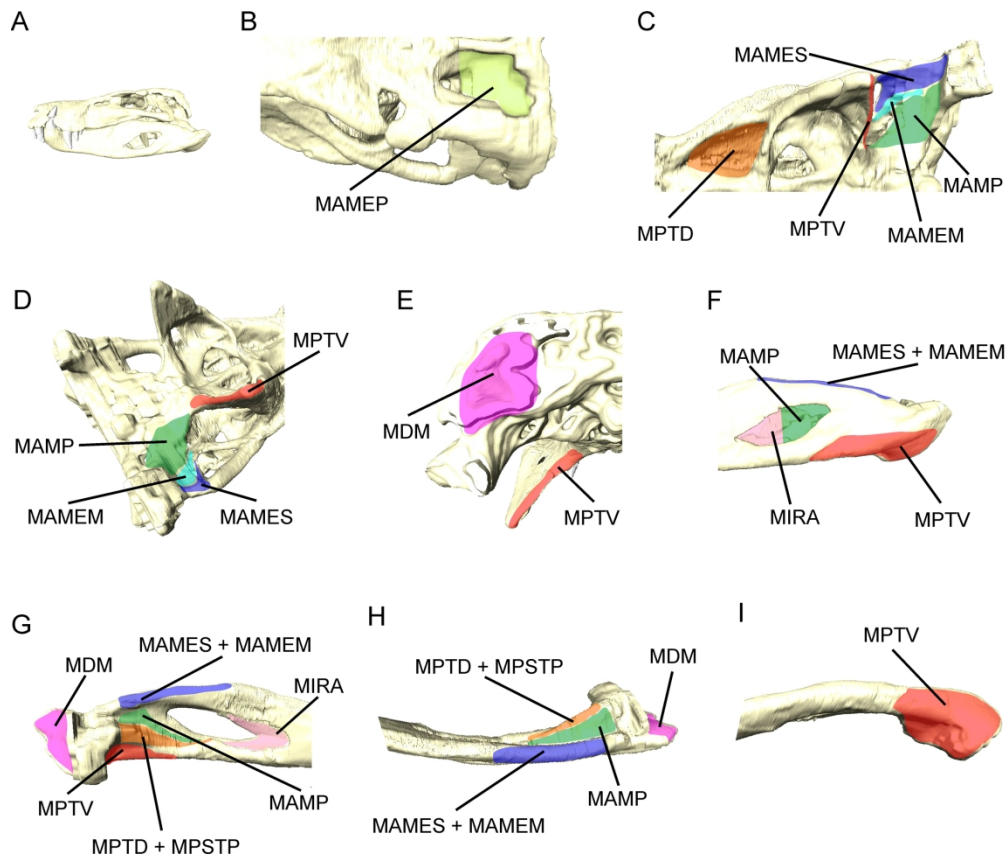


Figure 2. Muscle attachment areas plotted on the 3D model of skull the baurusuchid LPRP/USP 0697. A, skull and lower jaws in lateral view; B, dorsal view of the left posterior of the skull; C, ventral view of the left posterior of the skull; D, posterolateral view of the skull; E, occipital view of the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

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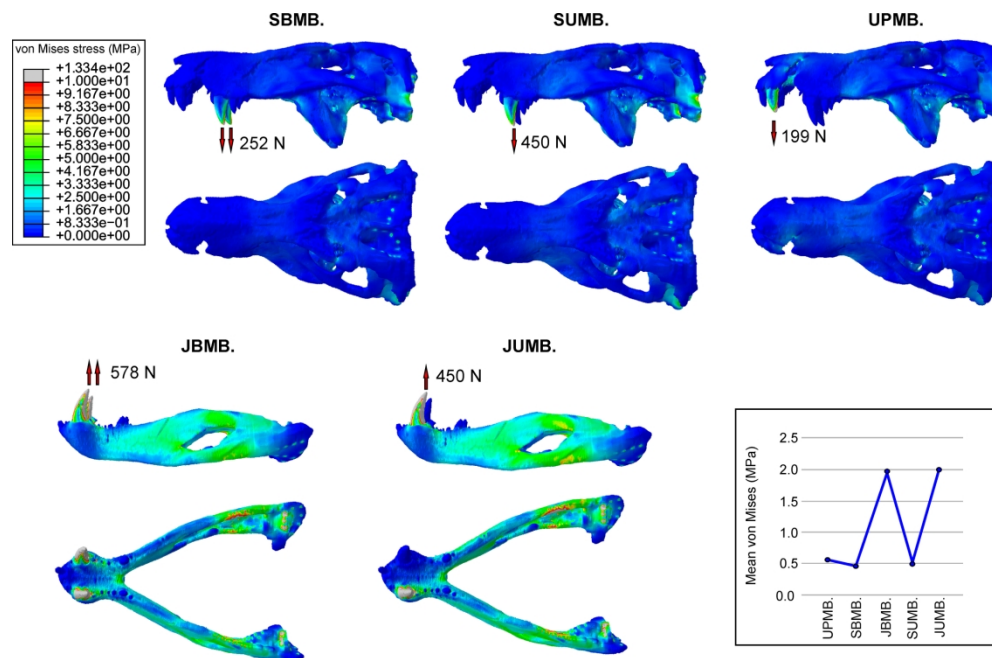


Figure 3. Von Mises stress contour plots from finite elements analysis (FEA) of the baurusuchid specimen (LPRP/USP 0697) for the intrinsic scenarios. Arrows indicate the location of muscle-driven bite forces on models during each scenario, with respective estimated bite force values. Mean von Mises values 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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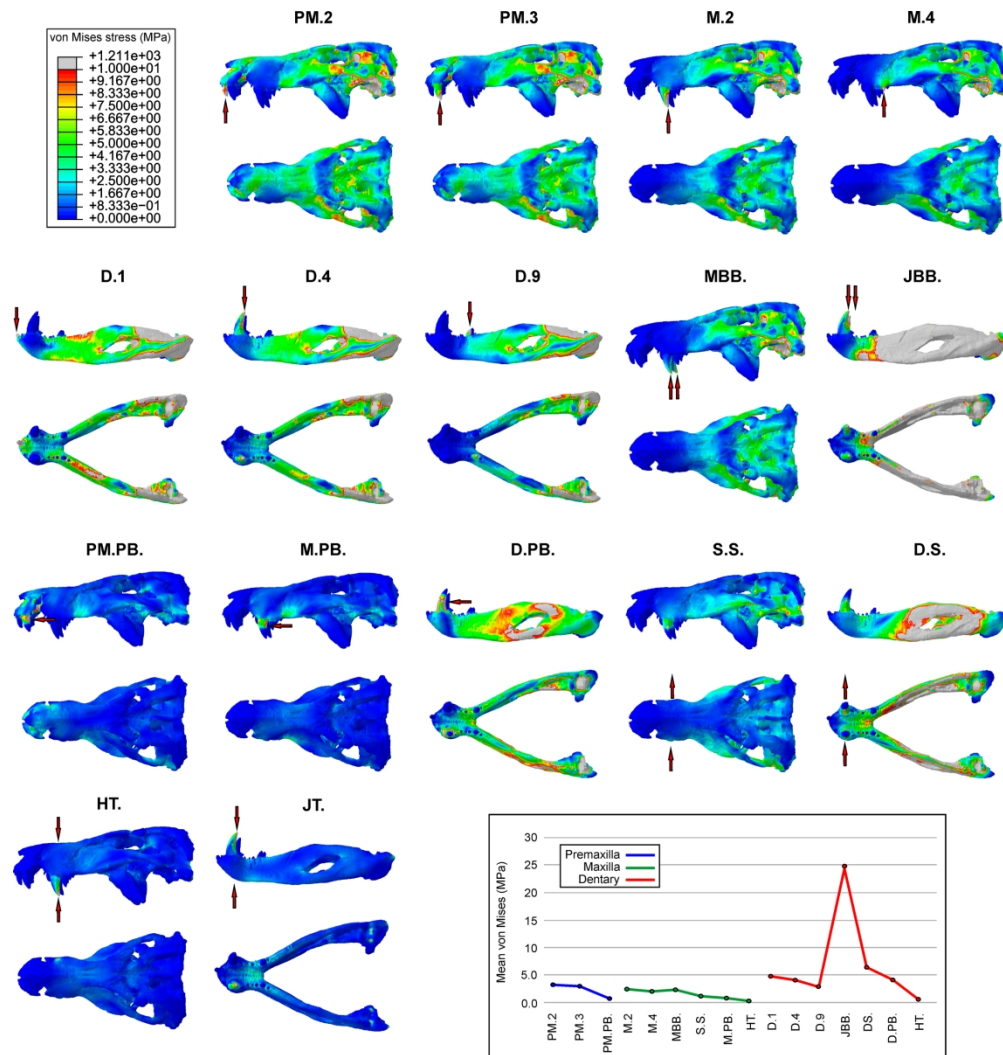


Figure 4. Von Mises stress contour plots from FEA of the baurusuchid specimen LPRP/USP 0697, comparing the stress distribution of skull and mandible models under distinct functional bending scenarios. Arrows indicate the location on the models of the loading vectors for each scenario. Mean von Mises 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.

210x220mm (300 x 300 DPI)



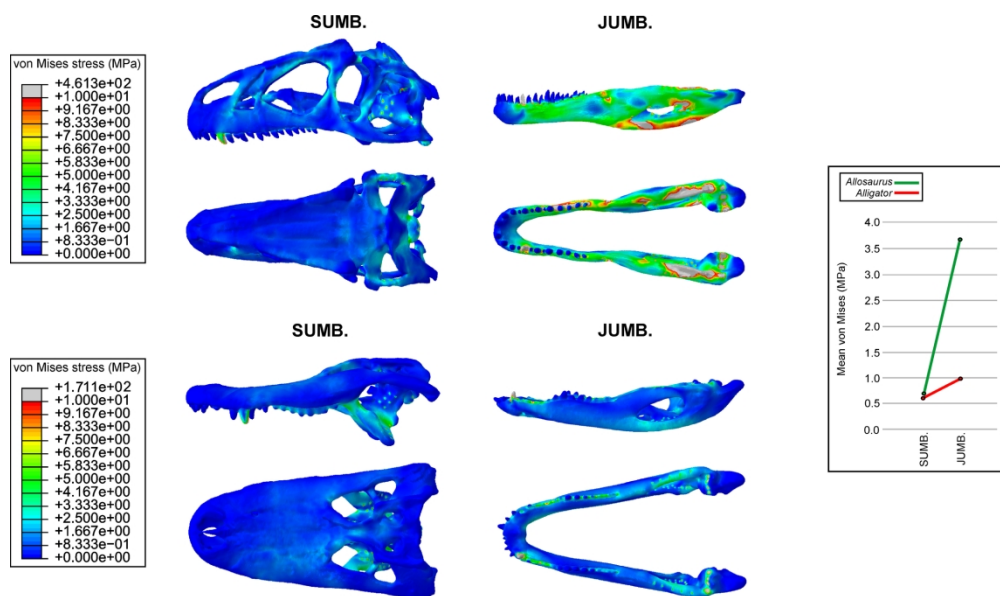


Figure 5. Von Mises stress contour plots from FEA of *Allosaurus fragilis* and *Alligator mississippiensis* for the intrinsic scenarios. Mean von Mises values per scenario for each taxon are displayed on the right. JUMB.: jaw unilateral muscle-driven bite; SUMB.: skull unilateral muscle-driven bite.

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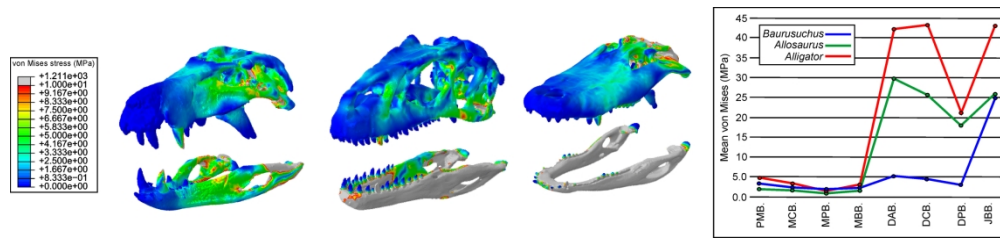


Figure 6. Comparison of von Mises stress distribution for scaled models of different archosaurian carnivores: baurusuchid, *Allosaurus fragilis* and *Alligator mississippiensis*. Stress contour plots displayed for the anterior bending scenario. On the right, comparative mean von Mises values per scenario for each taxon. DAB.: jaw anterior bending; DCB.: jaw canine unilateral bending; DPE.: 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)