UNIVERSITY^{OF} BIRMINGHAM University of Birmingham Research at Birmingham

A unique predator in a unique ecosystem

Montefeitro, Felipe; Lautenschlager, Stephan; Godoy, Pedro; Ferreira, Gabriel; Butler, Richard

DOI: 10.1111/joa.13192

License: Other (please specify with Rights Statement)

Document Version Peer reviewed version

Citation for published version (Harvard):

Montefeitro, F, Lautenschlager, S, Godoy, P, Ferreira, G & Butler, R 2020, 'A unique predator in a unique ecosystem: modelling the apex predator within a Late Cretaceous crocodyliform-dominated fauna from Brazil', *Journal of Anatomy*, vol. 237, no. 2, pp. 323-333. https://doi.org/10.1111/joa.13192

Link to publication on Research at Birmingham portal

Publisher Rights Statement:

This is the peer reviewed version of the following article: Montefeltro, FC, Lautenschlager, S, Godoy, PL, Ferreira, GS, Butler, RJ. A unique predator in a unique ecosystem: modelling the apex predator within a Late Cretaceous crocodyliform-dominated fauna from Brazil. J. Anat. 2020; 00: 1–11., which has been published in final form at: https://doi.org/10.1111/joa.13192. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

•Users may freely distribute the URL that is used to identify this publication.

Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)

•User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?) •Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

SHORT RUNNING PAGE HEADING: MODELLING THE APEX PREDATOR 1 2 FROM BRAZILIAN LATE CRETACEOUS 3 A UNIQUE PREDATOR IN A UNIQUE ECOSYSTEM: MODELLING THE APEX 4 PREDATOR WITHIN A LATE CRETACEOUS CROCODYLIFORM-DOMINATED 5 FAUNA FROM BRAZIL 6 7 8 FELIPE C. MONTEFELTRO^{1,2}, STEPHAN LAUTENSCHLAGER², PEDRO L. GODOY³, 9 GABRIEL S. FERREIRA⁴, RICHARD J. BUTLER² 10 11 ¹Laboratório de Paleontologia e Evolução de Ilha Solteira, UNESP, Ilha Solteira, Brazil. 12 ²School of Geography, Earth and Environmental Sciences, University of Birmingham, 13 Birmingham, UK. ³Department of Anatomical Sciences, Stony Brook University, Stony Brook, USA. 14 ⁴Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, 15 Universidade de São Paulo, Ribeirão Preto, Brazil. 16 17 felipecmontefeltro@gmail.com, s.lautenschlager@bham.ac.uk, pedrolorenagodoy@gmail.com, 18 gsferreirabio@gmail.com, r.butler.1@bham.ac.uk 19 20

22 ABSTRACT

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

46 Keywords: Finite Element Analysis; Baurusuchidae; Notosuchia

47 INTRODUCTION

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

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

palaeobiology of baurusuchids are lacking, and the data supporting their role as apex 72 73 predators is primarily derived from broad generalizations and the faunal composition of the Bauru palaeoecosystem (Riff & Kellner 2011; Godoy et al. 2014). 74 75 Here, we employ a biomechanical modelling approach in a comparative investigation of the functional morphology of a baurusuchid (*Baurusuchus*), one 76 analogue of a possible ecological competitor (Allosaurus), and an extant crocodyliform 77 78 (*Alligator*). Using finite element analysis (FEA), we characterize the baurusuchid skull biomechanically and quantify functional similarities and differences between 79 baurusuchids, theropod dinosaurs and living crocodylians. We also calculate bite forces, 80 simulate functional scenarios, and conduct bending tests to reveal biomechanical 81 properties of the baurusuchid skull. Our results shed light on key biomechanical aspects 82 that may have allowed this group to dominated the unique ecosystems present during 83 elien the Cretaceous in Brazil. 84

85

86 **METHODS**

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

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	own 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).	

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

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

145	position of baurusuchids to modern crocodilians. 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 fo	
148	in the baurusuchid, (1) a bilateral bite at the second maxillary and the fourth dentary	
149	n, (2) a unilateral bite at the second maxillary and the fourth dentary tooth, and (3)	
150	ateral bite at the third premaxillary tooth. One intrinsic scenario was analysed for	
151	llosaurus 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.	

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

Page 8 of 33

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

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

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

202

203 RESULTS

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

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

Considerable differences were found between the von Mises stress magnitudes 223 of the skull and lower jaws of the baurusuchid among the different bending scenarios 224 225 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 discernable in the stress distribution in the skull and lower jaws of the baurusuchid 227 228 (Figure 4). The greatest von Mises stresses in the skull models are mostly present in the posterior and median portions of the skull, with stress hotspots located on the ventral 229 and lateral regions of the quadrate body, ventral region of the infratemporal bar, and 230 preorbital region (anterior jugal, posterior maxillae, lacrimals, nasal, prefrontals, and 231 232 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 rostrum (premaxilla and nasals) is more stressed. When loading is applied to the 235 236 maxillary teeth, the premaxillae remain unstressed, and stress is concentrated on the posterior portion of the skull (Figure 4). 237

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

244	44 The areas around the maxillary and dentary canines remain relatively stress	
245	even during scenarios in which the loadings were applied to the canines (both in th	
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).	

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

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

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

- 275
- 276 DISCUSSION

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

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

In this context, it is noteworthy that the bite force estimates from FEA vary when using the skull or the mandible to obtain reaction forces. This is not surprising as the geometry and architecture of the skull is more complex and subject to further constraints than in the mandible. Validation tests have shown, however, that realistic bite forces can be estimated from mandible models (Porro et al. 2011). Consequently, we consider the higher bite force values obtained from the mandible as the more likely 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 carnivorous theropods and living crocodylians, which mostly rely on muscle-driven 308 biting forces for killing (Rayfield 2004, 2005, 2011; D'Amore et al. 2011; Erickson et 309 310 al. 2012). As a consequence, the killing potential of baurusuchids could have been enhanced by structural and behavioural traits, as in other weak-bite apex predators such 311 as troodontid and allosaurid theropods, varanid lizards, and felines, all of which harness 312 313 the postcranial musculature to supplement bite force (Rayfield 2001; D'Amore et al. 2011; Figueirido et al. 2018; Torices et al. 2018). 314

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

Page 14 of 33

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

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

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

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

palaeoecology of baurusuchids. The von Mises stress distribution shows that *Allosaurus*and *Alligator* have, in general, higher and more homogeneously distributed von Mises
stress in the mandible, while in the baurusuchid the stress is concentrated at the
postsymphyseal region. This indicates that the robust symphysis in baurusuchids is
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, this is the only scenario in which the von Mises stress approaches the higher values 375 376 presented by Allosaurus and Alligator (Figure 6). The baurusuchid response is also different from *Allosaurus* and *Alligator* in the sense that the mean von Mises stress 377 values in the bilateral bending scenarios are distinct from the unilateral scenarios, 378 whereas the other two taxa show similar values in both scenarios. Based on our FEA 379 results, we propose that the bilateral biting is the least likely killing strategy for 380 381 baurusuchids, and the clamp-and-hold, employed by living crocodylians, and large mammal predators, such as the lion (Panthera leo) (Figueirido et al. 2018), does not fit 382 the mechanical properties of the baurusuchid skull. 383

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

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

406

407 ACKNOWLEDGEMENTS

This work was supported in part by a Rutherford Fund Strategic Partner Grant to the
University of Birmingham, which funded the travel of FCM to Birmingham. This
research was supported by a National Science Foundation grant (NSF DEB 1754596) to
PLG and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP
2019/10620-2) to GSF. We thank two reviewers for their comments which improved the
final version of this manuscript.

to per Review only

AUTHOR CONTRIBUTIONS 415

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

420 REFERENCES

421 422 423	 Aureliano T, Ghilardi AM, Guilherme E, Souza-Filho JP, Cavalcanti M, Riff D (2015) Morphometry, bite-force, and paleobiology of the Late Miocene Caiman Purussaurus brasiliensis. <i>PLOS ONE</i>, 10, e0117944.
424 425 426 427	 Benson RBJ, Mannion PD, Butler RJ, Upchurch P, Goswami A, Evans SE (2013) Cretaceous tetrapod fossil record sampling and faunal turnover: implications for biogeography and the rise of modern clades. <i>Palaeogeogr Palaeoclimatol Palaeoecol</i>, 372, 88–107.
428 429	Brink KS, Reisz RR (2014) Hidden dental diversity in the oldest terrestrial apex predator <i>Dimetrodon</i> . <i>Nat Commun</i> , 5 , 3269.
430 431 432	Carvalho IS, Campos ACA Nobre PH (2005) <i>Baurusuchus salgadoensis</i> , a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. <i>Gondwana Res</i> , 8 , 11–30.
433 434 435	Carvalho IS, Gasparini ZB, Salgado L, Vasconcellos FM, Marinho TS (2010) Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. <i>Palaeogeogr Palaeoclimatol Palaeoecol</i> , 297 , 252–262.
436 437 438	Cleuren J, De Vree F (2000) Feeding in Crocodilians. In: <i>Feeding: form, function and evolution in tetrapod vertebrates</i> (ed. Schwenk K), pp. 337–358, San Diego: Academic Press.
439 440	D'Amore DC (2009) A functional explanation for denticulation in theropod dinosaur teeth. <i>Anat Rec</i> , 292 , 1297–1314.
441 442 443	D'Amore DC, Moreno K, McHenry CR, Wroe S (2011) The effects of biting and pulling on the forces generated during feeding in the Komodo dragon (<i>Varanus komodoensis</i>). <i>PLOS ONE</i> , 6 , e26226.
444 445	Dumont E, Grosse I, Slater G (2009) Requirements for comparing the performance of finite element models of biological structures. <i>J Theor Biol</i> , 256 , 96–103.
446 447 448	Erickson G, Gignac P, Steppan S, et al. (2012) Insights into the ecology and evolutionary success of crocodilians revealed through bite-force and tooth-pressure experimentation. <i>PLOS ONE</i> , 7 , e31781.
449 450	Farmer CG, Sanders K (2010) Unidirectional airflow in the lungs of alligators. <i>Science</i> , 327 , 338–340.
451 452 453	Figueirido B, Lautenschlager S, Pérez-Ramos A, Valkenburgh B (2018) Distinct predatory behaviors in scimitar- and dirk-toothed sabertooth cats. <i>Curr Bio</i> , 28 , 3260–3266.
454 455	Gignac P, O'Brien H (2016) Suchian feeding success at the interface of ontogeny and macroevolution. <i>Integr Comp Biol</i> , 56 , 449–458.
456 457	Gignac P, Erickson G (2017) The Biomechanics behind Extreme Osteophagy in <i>Tyrannosaurus rex. Sci Rep</i> , 7 , 2012.

458 459	Godoy PL (2020) Crocodylomorph cranial shape evolution and its relationship with body size and ecology. <i>J Evol Biol</i> , 33, 4–21.
460 461 462	Godoy PL, Montefeltro FC, Norell MA, Langer MC (2014) An additional baurusuchid from the cretaceous of Brazil with evidence of interspecific predation among crocodyliformes. <i>PLOS ONE</i> , 9 , e97138.
463 464 465	Godoy PL, Bronzati M, Eltink E, et al. (2016) Postcranial anatomy of <i>Pissarrachampsa sera</i> (Crocodyliformes, Baurusuchidae) from the Late Cretaceous of Brazil: insights on lifestyle and phylogenetic significance. <i>PeerJ</i> , 4 , e2075.
466 467	Godoy PL, Benson RBJ, Bronzati M, Butler R (2019) The multi-peak adaptive landscape of crocodylomorph body size evolution. <i>BMC Evol Biol</i> , 19 , 167.
468 469 470	 Godoy PL, Ferreira G, Montefeltro FC, Vila Nova BC, Butler RJ, LangerMC (2018) Evidence for heterochrony in the cranial evolution of fossil crocodyliforms. <i>Palaeontology</i>, 61, 543–558.
471 472	Guillette Jr LJ, Edwards TM, Moore BC (2007) Alligators, contaminants and steroid hormones. <i>Environ Sci</i> , 14 , 331–347.
473 474 475	 Holliday C, Witmer LW (2009) The epipterygoid of crocodyliforms and its significance for the evolution of the orbitotemporal region of eusuchians. <i>J Vert Paleontol</i>, 29, 715–733.
476 477 478	Holliday C, Tsai H, Skiljan R, George I, Pathan S (2013) A 3D interactive model and atlas of the jaw musculature of <i>Alligator mississippiensis</i> . <i>PLOS ONE</i> , 8 , e62806.
479 480	Lautenschlager S (2015). Estimating cranial musculoskeletal constraints in theropod dinosaurs. <i>R Soc Open Sci</i> , 2 , 150495
481 482	Lloyd GT, Davis KE, Pisani D, et al. (2008). Dinosaurs and the Cretaceous terrestrial revolution. <i>Proc R Soc B</i> , 275 , 2483–2490.
483 484 485	Mannion P, Benson R, Carrano M, Tennant J, Judd J, Butler R (2015). Climate constrains the evolutionary history and biodiversity of crocodylians. <i>Nat</i> <i>Commun</i> , 6, 8438.
486 487 488 489	 Marsola, J. C. A., Batezelli, A., Montefeltro, F. C., Grellet-Tinner, G. & Langer, M. C. (2016). Palaeoenvironmental characterization of a crocodilian nesting site from the Late Cretaceous of Brazil and the evolution of crocodyliform nesting strategies. <i>Palaeogeogr Palaeoclimatol Palaeoecol</i>, 457, 221–232.
490 491	Melstrom KM, Irmis RB (2019) Repeated evolution of herbivorous crocodyliforms during the Age of Dinosaurs. <i>Curr Bio</i> , 29 , 2389–2395.
492 493	Montefeltro FC (2019). The osteoderms of baurusuchid crocodyliforms (Mesoeucrocodylia, Notosuchia). <i>J Vert Paleontol</i> . e1594242.
494 495 496	Montefeltro FC, Larsson HCE, Langer MC (2011) A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the late cretaceous of Brazil and the phylogeny of Baurusuchidae. <i>PLOS ONE</i> , 6 , e21916.

497 498 499 500 501	 Pol D, Leardi J (2015) Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. In: <i>Reptiles Extintos –</i> <i>Volumen en Homenaje a Zulma Gasparini</i> (ed. Fernández M, Herrera Y), pp. 172–186, Buenos Aires: Publicación Electrónica de la Asociación Paleontológica Argentina.
502 503 504	Porro L, Holliday C, Anapol F, Ontiveros L, Ontiveros L, Ross C (2011) Free body analysis, beam mechanics, and finite element modeling of the mandible of <i>Alligator mississippiensis</i> . <i>J of Morphol</i> , 272 , 910–937.
505 506	Rayfield E (2004) Cranial mechanics and feeding in <i>Tyrannosaurus rex</i> . <i>Proc R Soc B</i> , 271 , 1451–1459.
507 508	Rayfield E (2005) Aspects of comparative cranial mechanics in the theropod dinosaurs <i>Coelophysis, Allosaurus</i> and <i>Tyrannosaurus. Zool J Lin Soc</i> , 144 , 309–316.
509 510 511	Rayfield E (2011) Structural performance of tetanuran theropod skulls, with emphasis on the Megalosauridae, Spinosauridae and Carcharodontosauridae. <i>Spec Pap Palaeontol</i> , 86 , 241–253.
512 513	Rayfield E, Norman DB, Horner CC, et al. (2001) Cranial design and function in a large theropod dinosaur. <i>Nature</i> , 409 , 1033–1037.
514 515	Rayfield E, Milner A (2008) Establishing a framework for archosaur cranial mechanics. <i>Paleobiology</i> , 34 , 494–515.
516 517 518	Reed DA, Porro LB, Iriarte-Diaz J, et al. (2011) The impact of bone and suture material properties on mandibular function in <i>Alligator mississippiensis</i> : testing theoretical phenotypes with finite element analysis. <i>J Anato</i> , 218 , 59–74.
519 520 521	Riff D, Kellner A (2011) Baurusuchid crocodyliforms as theropod mimics: Clues from the skull and appendicular morphology of <i>Stratiotosuchus maxhechti</i> (Upper Cretaceous of Brazil). <i>Zool J Lin Soc</i> , 163(suppl_1) , S37–S56.
522 523	Sakamoto M (2010) Jaw biomechanics and the evolution of biting performance in theropod dinosaurs. <i>Proc R Soc B</i> , 277 , 3327–3333.
524 525	Sakamoto M, Ruta M, Venditti C (2019) Extreme and rapid bursts of functional adaptations shape bite force in amniotes. <i>Proc R Soc B</i> , 286 , 20181932.
526 527 528	Sellers K, Middleton K, Davis J, Holliday C (2017) Ontogeny of bite force in a validated biomechanical model of the American alligator. <i>J Exp Biol</i> , 220 , 2036–2046.
529 530 531	Torices A, Wilkinson R, Arbour VM, Ruiz-Omenaca JI, Currie PJ (2018) Puncture-and- pull biomechanics in the teeth of predatory coelurosaurian dinosaurs. <i>Curr Bio</i> , 28, 1467–1474.
532 533	Verdade LM (2000) Regression equations between body and head measurements in the broad-snouted caiman (<i>Caiman latirostris</i>). <i>Rev Bras Biol</i> , 60 , 469–482.
534 535	Wilberg EW (2017) Investigating patterns of crocodyliform cranial disparity through the Mesozoic and Cenozoic. <i>Zool J Lin Soc</i> , 181 , 189–208.

536	Wilberg EW, Turner AH, Brochu CA (2019) Evolutionary structure and timing of	
537	major habitat shifts in Crocodylomorpha. Sci Rep, 9, 1–10.	
538	Witmer L, Ridgely R (2008) The paranasal air sinuses of predatory and armored	
539	dinosaurs (Archosauria: Theropoda and ankylosauria) and their contribution to	
540	cephalic structure. Anat Rec, 291 , 1362–1388.	
541	Zanno L, Makovicky P (2013) Neovenatorid theropods are apex predators in the Late	
542	Cretaceous of North America. Nat Commun. 4. 2827.	

543

ion per perien ont

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

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

562

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 mucle-driven bite; JUMB.: jaw unilateral mucledriven bite; SBMB.: skull bilateral muscle-driven bite; SUMB.; skull unilateral muscledriven bite; UPMB.: unilateral premaxillary muscle-driven bite.

- **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

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 pullback; S.S.: canine skull shake.

582

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.:

586 skull unilateral muscle-driven bite.

587

588 Figure 6. Comparison of von Mises stress distribution for scaled models of different

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;

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.

597 TABLES

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

599

601 Table 2. Total force inferred from cranial and lower jaw attachments for each

602 **muscle modeled.**

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



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.

210x177mm (300 x 300 DPI)



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 mucle-driven bite; JUMB.: jaw unilateral mucle-driven bite; SBMB.: skull bilateral muscle-driven bite; SUMB.; skull unilateral muscle-driven bite; UPMB.: unilateral premaxillary muscle-driven bite.

204x133mm (300 x 300 DPI)



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.

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; MCB.: maxilla canine bilateral bending; MCB.: maxilla canine unilateral bending, MPB: maxilla posterior unilateral bending; PMB.: unilateral premaxillary bending.

237x54mm (300 x 300 DPI)