

1 **Title: An assessment of the role of the falx cerebri and tentorium cerebelli in the**  
2 **cranium of the cat (*Felis silvestris catus*)**

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27 **Abstract:** The falx cerebri and the tentorium cerebelli are two projections of the dura  
28 mater in the cranial cavity which ossify to varying degrees in some mammalian species.  
29 The idea that the ossification of these structures may be necessary to support the loads  
30 arising during feeding has been proposed and dismissed in the past, but never tested  
31 quantitatively. To address this, a biomechanical model of a domestic cat (*Felis silvestris*  
32 *catus*) skull was created and the material properties of the falx and tentorium were  
33 varied for a series of loading regimes incorporating the main masticatory and neck  
34 muscles during biting. Under these loading conditions, ossification of the falx cerebri  
35 does not have a significant impact on the stress in the cranial bones. In the case of the  
36 tentorium, however, a localised increase in stress was observed in the parietal and  
37 temporal bones, including the tympanic bulla, when a non-ossified tentorium was  
38 modelled. These effects were consistent across the different analyses, irrespective of  
39 loading regime. The results suggest that ossification of the tentorium cerebelli may play  
40 a minor role during feeding activities by decreasing the stress in the back of the skull.

41

42 **Keywords:** Finite element analysis, biomechanics, Carnivora, dura mater, falx cerebri,  
43 tentorium cerebelli

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45 **Competing interests:** We have no competing interests.

46

47 **Authors' Contributions:** MJF, SEE and FG conceived the research programme and  
48 secured the funding. VSL designed the study (with MJF and SEE) and created the  
49 models, undertook the analyses and drafted the paper. HD and VSL undertook  
50 supporting experimental work, including specimen dissection (with SEE and AS). PJW  
51 and FG assisted in the FE modelling and analysis and interpretation of the results. All  
52 authors read and corrected earlier versions of the manuscript and approved the final  
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54

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60

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63

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## 84 **Introduction**

85 The dura mater is a fibrous membrane that covers the brain and spinal cord. It further  
86 extends into the cranial cavity in the shape of four folds or projections, two of which are  
87 the falx cerebri and the tentorium cerebelli. The falx cerebri divides the two cerebral  
88 hemispheres, while the tentorium separates the cerebral lobes from the underlying  
89 cerebellum (figure 1). Both the falx and tentorium are commonly found across a variety  
90 of mammal species, albeit not necessarily with the same degree of development [1].  
91 Moreover, some species exhibit an ossified falx or an ossified tentorium; occasionally  
92 both. Ossification can also be a prenatal or a postnatal process, and these differences in  
93 developmental patterns led Nojima [2] to discriminate between the prenatal carnivore  
94 type (e.g. Marsupialia, Sirenia, Carnivora) and the postnatal dolphin type (some Cetacea  
95 and Primates). The degree of tentorial ossification also varies across species. In  
96 carnivorans, the level of ossification ranges from none in the striped skunk (*Mephitis*  
97 *mephitis*), to partial (Canidae), or complete, as in members of the Felidae [3].

98 The functional role of the ossification of these structures remains unclear.  
99 Nojima [3] dismissed the idea that an ossified tentorium aids in the protection of the  
100 carnivoran brain during locomotion and feeding. This argument is largely based on  
101 evidence that other animal groups which perform similar activities, such as most  
102 herbivores and rodents, do not exhibit ossification. However, this is founded on casual  
103 observation, and to date no specific analysis has been performed to support or reject it.  
104 In this study, we examine quantitatively the biomechanical role that the falx and the  
105 tentorium play in the mammalian skull, and any particular effects for Carnivora that the  
106 ossification may offer under different biting regimes. In order to achieve this, we  
107 developed a detailed finite element (FE) model of a domestic cat (*Felis silvestris catus*)  
108 skull which included the falx and tentorium.

109 *Felis silvestris* is a polytypic species that includes various different subspecies  
110 which can produce viable offspring when crossed, *Felis silvestris catus*, the domestic  
111 cat, being one of them [4]. The use of this particular species has two main advantages: it  
112 is widely available for study and, being a felid, it has a fully ossified tentorium, in  
113 contrast to other carnivorans. Over the last 20 million years, felids have maintained a  
114 similar body plan [5], a factor that has made this group especially popular for allometric  
115 studies [6]. Following this general trend, the ossified tentorium of the domestic cat's

116 skull is also very similar to those of other felids. Moreover, it has been observed that in  
117 newborn cats the tentorium is in an almost complete stage of ossification [3].

118

## 119 **Materials and methods**

120 The head of an adult *Felis silvestris catus* specimen, obtained from a deceased animal  
121 donated to the Liverpool Institute of Veterinary Science for teaching and research, was  
122 scanned in an X-Tek HMX 160 microCT ( $\mu$ -CT) system at the University of Hull, UK  
123 (scan resolution 61.7  $\mu$ m in all three axes). The sex of the specimen is unknown, as the  
124 body was not used in this study. The stack of .TIFF images obtained from  $\mu$ -CT  
125 scanning was then imported into Avizo (Version 9.0.1, Visualization Science Group)  
126 where segmentation of the different structures was achieved using a semi-automatic  
127 method, combining algorithms with further manual refinements. The skull was intact,  
128 apart from the cusp of the left canine tooth which was reconstructed digitally, while the  
129 first left premolar was also absent (no action was taken in this case, as it did not play  
130 any relevant role in the analyses). The mandible was also segmented in order to  
131 reconstruct jaw-closing muscle orientations. The nasal turbinates were represented  
132 independently and identified as a different structure, as was the nasal septum. Where  
133 possible, the delicate structures that compose the cribriform plate and the  
134 ethmoturbinates were maintained. The trabecular bone was visible in the CT scans and  
135 individual trabeculae were segmented. Voids in the trabecular bone and the empty  
136 spaces between the nasal turbinates were filled with a general filling material to  
137 simulate the presence of generic soft tissues, which also prevented errors during the FE  
138 solution arising from disconnected fragments of trabeculae. The cranial cavity was also  
139 filled with another material to reconstruct the gross volume of the brain and to allow  
140 modelling of the dura mater covering its surface at a later stage. However, as no other  
141 intermediate layers were modelled, this endocast should be regarded as a simplification  
142 of the brain, since it was connected directly to the bone in the model, and therefore the  
143 endocast surface strains are likely to be oversensitive to changes in bone strain. This  
144 prevents a more detailed analysis of the effects that the ossified structures might pose on  
145 this particular structure. The periodontal ligament (PDL) was included by covering the  
146 tooth roots and their proximal surfaces with a 3-4 voxel-wide layer of tissue (0.19-0.27  
147 mm [7]). Although the ossified tentorium forms a continuum with the parietal bone, it  
148 was carefully segmented as an independent structure (from where it attaches to the

149 internal parietal wall) in order to allow testing with different material properties during  
150 the analyses.

151 The falx cerebri was partially visible in the CT scans, being partly ossified in its  
152 posterior region, allowing it to be reconstructed. Although the ossification was  
153 unexpected in this species, it may not be such a rare occurrence, since a second  
154 dissected specimen (also donated to the Liverpool Veterinary School for teaching and  
155 research) exhibited what seemed to be similar patches of ossification (figure 2)  
156 (although we did not carry out further analyses to confirm their precise composition).

157 After segmentation, a finite element mesh was created, resulting in a model with  
158 nearly 5.9 million high order (quadratic) tetrahedral elements. Avizo landmark tools  
159 were used to define the origin and insertion areas of the muscles, with the data required  
160 for this step gathered during the dissection of two specimen heads. The left side of the  
161 modelled specimen was dissected together with the second head. Dissection data was  
162 also supported with information gathered from Hartstone-Rose *et al.* [8], Laison *et al.*  
163 [9], and Turnbull [10]. The mass of each individual muscle was measured to allow  
164 calculation of its physiological cross-sectional area (PCSA). The relative sizes of the  
165 muscles of the two specimens and those values reported in the literature were  
166 consistent, although interestingly the whole muscle mass of the second specimen was  
167 2.5 times greater, thus potentially 36% larger in each direction. (Note the pterygoid  
168 group was damaged in the second specimen, hence its weight was approximated by  
169 multiplying the value of the scanned specimen by the scaling factor of 2.5 (see  
170 Supporting Information, Table 1).

171 The muscles were placed in a 10% formaldehyde solution and stored in a fridge  
172 for one month, at which time the muscles were digested in a 30% nitric acid solution for  
173 72 hours in order to separate the individual muscle fibres. The acid was then substituted  
174 with a 50% aqueous glycerol solution to stop the digestion process. Ten to fifteen  
175 random fibres for each muscle were isolated, photographed and subsequently measured  
176 with the software ImageJ [11] to estimate mean fibre length. The PCSA was calculated  
177 using the following formula [12]:

$$178 \quad PCSA = \frac{\text{muscle mass (g)}}{\text{density (g/cm}^3\text{)} \times \text{fibre length (cm)}}$$

179 The muscle density was estimated as 1.0564 g/cm<sup>3</sup>, a value taken from Murphy  
180 and Beardsley [12] for the cat soleus, which has also been used in studies of cat neck  
181 muscles [13] and felid masticatory analysis [8]. Different values have been reported for  
182 the intrinsic muscle tension (strength) produced by mammalian skeletal muscle, which  
183 typically ranges from 10 N/cm<sup>2</sup> to 50 N/cm<sup>2</sup>. An intermediate value of 30 N/cm<sup>2</sup> was  
184 chosen from a feline bite force estimation study by Hartstone-Rose *et al.* [8]. Muscle  
185 force was calculated for the scanned specimen using the following formula:

$$186 \quad \text{Muscle force} = \text{PCSA (cm}^2\text{)} \times \text{tension per unit CSA (N/cm}^2\text{)}$$

187 Detailed PCSA values and muscle forces for the specimens are available as part  
188 of the Supporting Information (Tables 2 and 3).

189 For the muscle insertion positions the mandible was positioned at a gape angle  
190 of approximately 0 degrees, i.e. complete occlusion. Because the specimen's head was  
191 not completely symmetric, landmarks were manually placed on both sides of the skulls,  
192 left and right side (instead of mirroring them) in order to maximise accuracy. A variable  
193 number of landmarks, between two and sixteen, were used for each muscle depending  
194 on its size. After calculating the x, y, z components of each force, a bespoke routine  
195 coded in R (Version 3.3.3 [14]) was employed to format the spatial information into  
196 ANSYS commands (Mechanical APDL, 14.5.7, ANSYS Inc., Canonsburg, PA, USA).

197 The dura mater was simulated in ANSYS by selecting all the surface elements of  
198 the brain endocast material and creating a covering layer of thin shell elements (ANSYS  
199 SHELL181). Shell elements are a simple but effective way to model very thin structures  
200 such as the dura, and the ability to modify section data was also useful for assigning  
201 different thicknesses to the structure during sensitivity tests. Although the dura actually  
202 extends over the brain and around the spinal cord, only the part that enclosed the brain  
203 was considered in this model, hence the dura was discontinued after reaching the  
204 infratentorial region.

205 Muscle wrapping was considered necessary for the superficial temporalis, given  
206 the origin area of the muscle and the curvature of the parietal and the temporal bones in  
207 the cat cranium. For this, we created a semi-automatic procedure in ANSYS to handle a  
208 muscle lying over a curvilinear surface. The process involves the creation of a series of  
209 paths, each consisting of a line of short "hairs", using truss-type elements (ANSYS  
210 LINK180) positioned perpendicular to the bone surface (supporting information, figure

211 1). Landmarks for each individual hair were defined manually in Avizo and later  
212 imported into ANSYS. The node at the outer end of each hair was then connected to its  
213 neighbours with further link elements, thereby creating muscle strands wrapping around  
214 the cranium. The total force specified for the superficial temporalis muscle was then  
215 divided by the number of strands, and the resulting force was applied to the most  
216 inferior node of each strand.

217 The action of the neck muscles was also included in the model in order to  
218 simulate pull back and lateral pull. Neck muscle data were not available for the  
219 specimens considered in this study, hence the information was extracted from Reighard  
220 and Jennings [15], Wickland *et al.* [13] and Sebastiani and Fishbeck [16] (see  
221 Supporting Information, Table 4). The *rectus capitis* group, which is composed of three  
222 individual muscles (*major*, *medius* and *minor*) was considered as a single unit for the  
223 analyses, while the *obliquus capitis caudalis*, with its origin on the atlas vertebra (C1),  
224 was not modelled. The number of landmarks per muscle, used to define the number of  
225 strands, was based on the size of the neck origin areas. As the original vertebrae and  
226 scapula were not present in the specimen, two octagons with different sizes were  
227 modelled and imported into Avizo to provide a surface for easier placement of the  
228 insertion landmarks. A small octagon was positioned at the axis vertebra (C2) and a  
229 larger one at the scapula, closely following the bone's orientation (Supporting  
230 Information, Figures 2 and 3). The purpose of the octagonal shape was only to provide  
231 topological information (vertex and sides) to place the landmarks more easily. The neck  
232 muscle origin and insertion landmarks were then imported into ANSYS and muscle  
233 strands defined as flexible link elements with equivalent soft tissue material properties.

234

### 235 **Material properties**

236 The model was assigned bone material properties taken from the cortical bone of  
237 domestic dogs (Young Modulus, i.e.  $E = 13.7$  GPa;  $\nu = 0.30$ ), following Slater and Van  
238 Valkenburgh [6] in which these values were applied to various felid species. To the best  
239 of our knowledge, there are no material property data for the cat's dura in the literature,  
240 but human values are well known and were selected as a reasonable approximation ( $E =$   
241  $31.5$  MPa;  $\nu = 0.45$  (after Kleiven and Holst [17])). The same applies to the PDL ( $E = 50$   
242 MPa;  $\nu = 0.49$ ) which was taken from Rees and Jacobsen [18]. A 0.5 MPa value was

243 assigned to the remaining generic soft tissues [19], including the brain endocast, link  
244 elements and filling materials ( $\nu = 0.45$ ).

245 All material properties assigned to the different tissues were assumed to be  
246 isotropic, homogeneous, and linear elastic, as it has been demonstrated that models  
247 using these properties still produce reasonable estimates of the stress and strain  
248 distributions [20-22]. Also, as this study focuses on a comparison of two versions of the  
249 same model by varying the material properties of the structures of interest, minor  
250 inaccuracies in the material properties will not be critical as long as these remain  
251 constant in both versions. Nevertheless, because specific material property data for *Felis*  
252 *silvestris catus* were not available, sensitivity tests were undertaken for the soft tissues,  
253 to assess their impact on the results (see Table 1). All these tests were performed for a  
254 bilateral canine bite. A dura mater thickness of 0.55 mm was taken from Cotton *et al.*  
255 [23] for humans, but further sensitivity tests with constant thickness values of 0.2 mm  
256 and 1.5 mm were also undertaken. The dura mater analyses were also carried out with  
257 values of 3 MPa and 300 MPa, and for the generic facial soft tissue various values (5  
258 MPa, 50 MPa and 500 MPa) were tested independently. Sensitivity tests were also  
259 carried out to assess the importance of wrapping the superficial temporalis.

260

## 261 **Boundary conditions**

262 The skull was subjected to bilateral and unilateral canine and carnassial bites with  
263 different falx and tentorium material properties simulating either soft dural or hard  
264 osseous tissues in various combinations (see Supporting Information, Table 5). For the  
265 bilateral canine analyses, one node was constrained dorso-ventrally at the tip of each  
266 canine, with one node at the left glenoid fossa constrained in all degrees of freedom and  
267 the opposite node on the right side constrained in two directions (anterior-posteriorly  
268 and dorso-ventrally). These minimal constraints reduce the risk of artefacts from over-  
269 constraining the model [24, 25]. For the unilateral canine analyses, only the node at the  
270 tip of the left canine was constrained. For the carnassial analyses the same configuration  
271 at the glenoid fossae was maintained, but the anterior constraints were located at the  
272 notch between the paracone and the metacone of each carnassial (left carnassial in the  
273 case of the unilateral biting).

274           Additionally, two extrinsic loading regimes were applied to the model, one to  
275 simulate a pullback movement, the other a lateral pull. Similar types of analyses have  
276 been performed in previous studies of felids [6, 26], but using different approaches.  
277 Here, the extrinsic loading conditions were applied in combination with biting by  
278 applying the muscle forces *and* reaction forces at the glenoid fossae and the canines for  
279 bilateral biting as predicted by the previous analyses. (In theory, these forces place the  
280 loaded skull in perfect equilibrium, however due to unavoidable rounding errors in the  
281 software, there will inevitably be some, albeit negligible, out-of-balance force). In  
282 addition, while the bite force loading was maintained, further loads were superimposed  
283 to simulate the pullback or lateral pull action, thereby replicating the loading of the skull  
284 *in vivo*. Two constraint conditions were applied; one with, and one without the neck.  
285 For the first model, without the neck, three locations on the posterior cranium were  
286 minimally constrained; two at the occipital condyles and the third located between  
287 them, over the foramen magnum. One node was constrained in all degrees of freedom,  
288 the second in only two directions (anterior-posteriorly and dorso-ventrally), while the  
289 third (over the foramen magnum) was constrained anterior-posteriorly only. In the  
290 second variation, when the neck was modelled, all nodes corresponding to the muscle  
291 insertion points were constrained in all degrees of freedom. For the pullback simulation,  
292 once a bite force loading and the constraint option had been specified, an arbitrary  
293 pullback force of 25 N was applied to the upper posterior area of each canine, directed  
294 in a posterior-anterior direction, and subjecting the skull to tensional forces. For the  
295 lateral pull, the same force was applied to the left lateral surface of the canines. Thus,  
296 the two loading analyses were carried out with and without the neck structure, and the  
297 differences compared.

298           The total maximum bite force predicted by the model, measured at the tip of the  
299 canines for a bilateral bite, was 101.1 N, while the unilateral carnassial bite force was  
300 predicted to be 175.8 N. By using a modified version of the dry skull method [27],  
301 Sakamoto *et al.* [28] estimated a canine bite force of 177 N based on the skull width of  
302 fourteen specimens of *Felis silvestris catus* (median skull width, 62 mm; the skull width  
303 of our model is 75 mm, measured across the zygomatic arches, following Sakamoto and  
304 Ruta [29]). In contrast, using the same dry skull method, Christiansen and Wroe [30]  
305 (skull width not provided) reported a lower value of 73.3 N.

306 Performance of the skulls was evaluated by considering the von Mises stress  
307 value as this measure has been employed previously to assess skull behaviour  
308 (including earlier research in felid cranial biomechanics, such as McHenry *et al.* [31],  
309 Wroe [26], and Slater and Van Valkenburgh [6]). Von Mises stress is also convenient  
310 because it is a scalar function combining the three principal stresses, is related to the  
311 von Mises failure criterion, and is useful for comparing the performance of complex 3D  
312 geometries.

313 Due to the large number of comparative analyses performed in this study,  
314 difference plots are used to present the results in an easy and concise manner, and in  
315 such a way that even small differences in stress values become immediately evident  
316 (Supporting Information, figure 4), as it has been done in previous research [7]. For the  
317 difference plots, the following convention is used for all the results: the minuend of the  
318 subtraction is always the model with the osseous material properties while the  
319 subtrahend is the model with the soft tissue material properties. Thus negative values  
320 (cold colours) represent areas in which stress is lower in the osseous model, and positive  
321 values (warm colours) are areas in which stress is higher in the osseous model, and  
322 areas with no significant stress differences are centred around green. More even stress  
323 distributions and lower stress values represent a structure more adapted to withstand  
324 stresses under a particular loading regime [6].

325

### 326 **Sensitivity tests**

327 The preliminary sensitivity tests demonstrated that neither the stress magnitude nor  
328 distribution were significantly affected by the variations considered. As a result detailed  
329 stress plots are not presented here, and the following summarizes the outcome of those  
330 investigations. Changes in dura mater thickness did not lead to any discernable  
331 differences in the stress pattern and magnitude in the bone. Similarly, no meaningful  
332 differences were noticed between dura mater elastic modulus values of 3 MPa and 30  
333 MPa, but there was a slight decrease in stress in the skull roof area for a value of 300  
334 MPa, as would be expected. The sensitivity tests also demonstrated that using the higher  
335 elastic modulus value for the (soft tissue) cavity filling materials resulted in lower  
336 stresses across the skull, but the changes were negligible between the range of 0.5 MPa  
337 and 50 MPa. Concerning the muscle wrapping, and ignoring the local artefacts caused

338 by the attachment of the muscle “hairs” of each wrapping strand, again almost  
339 imperceptible variations in stress distribution were observed through the model. During  
340 bilateral canine biting, changes in bite force between the models with and without  
341 muscle wrapping, as measured at the tip of both canines, were also negligible ( $< 1$  N).  
342 Increasing the number of muscle strands would have distributed the loading more  
343 evenly over the bone, but it seems highly unlikely that it would have changed the  
344 overall conclusion of this test, as the direction of the resultant force would not change.

345

## 346 **Results**

347 After the sensitivity tests, the model was subjected to a series of intrinsic and extrinsic  
348 loading regimes in which canine and carnassial biting were simulated. Considering the  
349 models with a soft falx and an ossified tentorium first (*i.e.* the natural condition in *Felis*  
350 *silvestris catus*), for the bilateral canine biting simulation stresses were equally high in  
351 the rostrum, the zygomatic arches and the palatine and presphenoid bones (Supporting  
352 Information, figure 5, left columns). In the rostrum, the nasal bones experience lower  
353 stresses than the surrounding bones, with the stress transmitted through the maxilla and  
354 into the frontal bone, until it reaches the approximate location of the coronal suture,  
355 where it dissipates. Regions of low or no stress can be identified within the parietal and  
356 interparietal bones, the tympanic bullae and the postorbital processes. In the carnassial  
357 bilateral biting simulation, stress in the rostrum and the palatine were greatly reduced  
358 but remained constant in the zygomatic arches and seemed to be slightly higher  
359 throughout the orbit and in certain areas of the zygomatic bone. With unilateral biting,  
360 either with canine or carnassial teeth, stresses were higher on the working side both in  
361 the rostrum and the cranial roof (Supporting Information, figure 5, right columns). It is  
362 also worth noting that the stress at the back of the skull remains essentially unchanged  
363 for all these loading regimes. In the case of the extrinsic loads with an ossified  
364 tentorium, the pullback loading regime seemed to most closely replicate the simple  
365 bilateral bite (Supporting Information, figure 6). For the lateral pull, higher stresses  
366 manifested in the skull roof of the side opposite to the applied force. The largest  
367 differences between the two sides seemed to be located in the frontal bone and  
368 postorbital processes. Slight variations of stress magnitude were detected with the  
369 inclusion of the neck muscles in the analyses for either case, but there were no  
370 meaningful differences in stress distribution.

371           When models with ossified structures are compared to those with soft structures,  
372 differences in stress distribution and magnitude in cranial bone are also uncommon,  
373 regardless of the biting regime. Changes in the material properties of the falx cerebri do  
374 not lead to any discernible variations in the external skull stress patterns. However,  
375 difference plots demonstrate that the models with an ossified tentorium consistently  
376 exhibit lower stress values in the parietal and temporal bones, including the tympanic  
377 bulla (figures 3 and 4), with slight or minor differences depending on the particular  
378 regime. To provide further detail about the differences, 40 nodes at three sample  
379 locations of approximately 0.5 mm diameter were probed (Supporting Information,  
380 figure 7) for both ossified and non-ossified tentorium models during a bilateral canine  
381 biting regime. The highest stress decrease identified was 2.11 MPa at the inferior region  
382 of the temporal bone. Also, locally high stresses are observed in the interparietal and the  
383 sagittal crest for the lateral pull plus biting regime with no neck. These appear to be a  
384 consequence of the oversimplified constraints applied, causing the load path to be  
385 focussed through those regions, because the equivalent version with neck muscles does  
386 not display them, and therefore they probably don't have mechanical significance. It is  
387 worth noting that stresses in the rostrum and the anterior area of the skull roof remained  
388 unaltered for all cases tested.

389           Examination of the stresses in the tentorium both ossified and non-ossified  
390 versions (figure 5 and supplementary figure 8; note the different scales of the contour  
391 plots) shows that higher stresses are located anteriorly, with peak stress values in the  
392 area in contact with the parietal wall, and lower values in the borders of the tentorial  
393 notch. Apart from these differences in magnitude, the actual stress distribution remains  
394 unchanged for the different material properties and biting regimes. In the falx cerebri  
395 (figure 6), the stress is more unevenly distributed, but appears to be higher at the  
396 anterior third (especially in the soft falx cerebri) and the posterior end, particularly in  
397 the osseous falx for all regimes except the carnassial unilateral biting, and in the soft  
398 falx for both canine bites. The stresses in the osseous falx and tentorium are to various  
399 degrees of magnitude higher than those in the versions with soft tissue material  
400 properties, but in the extrinsic biting regimes (supplementary figure 9) the soft falx  
401 seems to experience higher stresses overall. Moreover, adding or removing the dura  
402 mater layer over the brain endocast surface does not seem to have any effects on the  
403 results. In general, the cranial vault of the cat skull does not experiences meaningful

404 amounts of tension or compression (Supporting Information, figure 10), but the area of  
405 the temporal bone where the tentorium is located is subjected to compressive stresses.  
406 Compression is also visible in the tentorium cerebelli wings and in the posterior end of  
407 the midline, at the attachment of the falx cerebri.

408

## 409 **Discussion and conclusions**

410 Our aim was to test whether the presence of the osseous falx or tentorium played a  
411 significant role in reducing stress in the cranial bones under different biting regimes in  
412 *Felis silvestris catus*. We observed that changing their material properties did lead to a  
413 considerable reduction of stress in the originally softer structures (figures 5 and 6 and  
414 supplementary figures 8 and 9) but we did not observe the same effect in the cranial  
415 bone when considering the model as a whole.

416 In the case of the falx cerebri, the alteration of its material properties did not lead  
417 to any changes in the von Mises stress pattern of the cranium. According to the CT  
418 scans, the patches of ossification in the falx of the original specimen are mainly located  
419 in the middle to posterior end regions of the structure (in the case of the non-scanned  
420 specimen, ossification nodules appear in the middle section; see figure 2). Thus there  
421 does not seem to be any correlation between their location and the predicted stress  
422 pattern from the FE analyses (figure 6, supplementary figure 9) and, in any case, it  
423 seems unlikely that these isolated nodules have any mechanical significance, since they  
424 appear disconnected from the cranial roof. For the tentorium cerebelli, the stress is  
425 concentrated at the end of both “wings” of the structure (figure 5, supplementary figure  
426 8).

427 Stress differences between models with ossified and non-ossified tentoria were  
428 limited to the back of the skull, and specifically to the bones adjacent to the tentorium  
429 (parietal and temporal, including the tympanic bulla), and perhaps indicates that the  
430 tentorium may play a minor role during feeding. The difference in stress magnitude is  
431 however small (see Supporting Information, figure 7) and therefore these results should  
432 be treated with caution. A more detailed model is necessary to assess the specific effects  
433 that this reduction in stress may pose on the brain. The area of interest at the back of the  
434 skull initially suggested a link between the neck muscles, as they are primarily attached  
435 to this region, but the extrinsic analyses that incorporated the neck did not reveal any

436 meaningful differences. A recent study by McIntosh and Cox [32] demonstrates that, for  
437 mole-rats, a progressive increase in gape leads to a decrease in stress in the anterior  
438 regions of the cranium and an increase posteriorly. Felids are known to exhibit high  
439 values of maximum gape ( $61.3^\circ$  in *Felis chaus* [33], a closely related species to *Felis*  
440 *silvestris catus*), and it is possible that analysis with higher gape angles may reveal a  
441 more significant role for an ossified tentorium.

442         The use of simple linear elastic properties for the falx and the tentorium is one of  
443 the limitations of the current analysis. In particular for this study, the non-ossified  
444 materials are assumed to resist loads in both tension and compression, whereas in reality  
445 they are tension-only materials. As a result, the model may overestimate their influence.  
446 However since the stiffness of these structures is orders of magnitude less than that of  
447 bone and their thicknesses are much smaller, their effect will be minimal, as  
448 demonstrated by the sensitivity studies. We believe therefore that this simplification  
449 does not alter the overall conclusions of the study.

450         Of the four different intrinsic biting regimes considered (Supporting  
451 Information, figure 5), the unilateral carnassial bite generates the highest peak stresses,  
452 being particularly high in the orbital region. From simple lever mechanics, it is evident  
453 that carnassial bites will generate higher forces than canine ones (for example, 118.1 N  
454 vs. 73.3 N, as calculated by Christiansen and Wroe [30]; 180.6 N vs. 101.1 N in our  
455 model for the bilateral carnassial bite). The results from this study show that the most  
456 efficient biting regime in *Felis silvestris catus* is the carnassial bilateral bite, as this is  
457 the one that generates the highest bite forces while experiencing the lowest overall  
458 stresses and the lowest peak stresses. In nature, biting and grasping are mostly carried  
459 out with the incisors and canines, while the carnassials are used for cutting and tearing  
460 food [34-36]. However, according to Orsini and Hennet [35], the upper jaw is larger  
461 than the lower in cats and therefore, for the teeth of both sides to be joined during  
462 mastication, the mandible has to be brought to one side, so it is highly doubtful that this  
463 type of carnassial bilateral bite will ever be used in nature. Force variation between  
464 bilateral and unilateral carnassial bites (180.6 N vs. 175.8 N) seems to be, in any case,  
465 negligible.

466         The skull shape of felids is rather conservative [37, 38]. Some researchers have  
467 developed FE models of extinct saber-toothed cats and other felids [6, 26, 31, 38] where  
468 biting regimes were based upon the cat's masticatory cycles and hunting behaviour.

469 These studies demonstrated that felid skulls exhibit similar stress patterns when biting,  
470 and that stress is largely confined to the rostrum, the mandible and the zygomatic arch  
471 region. Our results follow a similar trend and replicate the ones obtained by Slater and  
472 Van Valkenburgh [6] from the cranium of *Felis lybica*, a closely related species, and  
473 also largely agree with the classic experimental study of a *Felis silvestris catus* cranium  
474 performed by Buckland-Wright [34].

475 According to the literature, the most probable function for the tentorium  
476 cerebelli is to withstand the weight of the cerebral hemispheres [39, 40], given that it is  
477 present in birds and mammals, and that both groups are characterised by a more  
478 developed brain than other tetrapods. Even when closely comparing different mammal  
479 species (see Klintworth [1], Table 1), it seems reasonable to infer a relationship between  
480 tentorium development and encephalization quotient [41], using values of tentorial  
481 index as indicators (the tentorium is considered to be more developed as the length of  
482 the straight sinus increases). The lower values are consistently present in orders with  
483 low brain quotients, such as Rodentia, Lagomorpha and Chiroptera, and increase in  
484 Carnivora, Cetacea and Primates [42]. The function of the falx cerebri may be to  
485 constrain the brain and limit displacement and rotation inside the cranium [43, 44].  
486 However, the presence of a bony falx and tentorium defies a simple explanation. The  
487 degree of ossification varies among different species and groups and it can develop  
488 before or after birth [1, 3]. In carnivorans, an ossified tentorium cerebelli is present in  
489 almost all species, with the exception of *Mephitis mephitis*. It is more developed in  
490 Felidae, Viverridae and Hyaenidae, where the structure is fully ossified and crosses the  
491 petrosa, than in other groups such as Phocidae or Canidae, where ossification does not  
492 reach the base of the skull [3]. An ossified falx is present in all pinnipeds, but also in the  
493 genus *Ursus* [3]. Sometimes the condition manifests in species that normally exhibit a  
494 soft-tissue falx and tentorium: for example, partial falx ossification is relatively frequent  
495 in humans (around 10% of the adult population [45, 46]) and tentorium ossification,  
496 while rarer, also exists [45, 47].

497 In the analyses presented, all intrinsic and extrinsic biting regimes consistently  
498 resulted in the same pattern of stress across the cranium, which suggests that the  
499 function of the dural ossifications is not related to the forces exerted by struggling prey  
500 or in the action of pulling or tearing a carcass. However, feral *Felis silvestris catus*  
501 mostly feed on small prey such as birds, mice and even some invertebrates [48],

502 therefore similar tests should be run on larger predatory felids before completely ruling  
503 out a protective role for the dural ossifications during prey handling and feeding. This is  
504 especially important given the fact that small felids have proportionally larger  
505 braincases [49] and that may have a meaningful effect on the results. A new model with  
506 a more detailed brain would also help to resolve whether the stress reductions observed  
507 in the back of the skull lead to a corresponding decrease in the stress in the brain.  
508 Equally, it is important to note that the skulls of carnivorans in general, and felids in  
509 particular, are subjected to forces other than those associated with feeding, such as the  
510 ones resulting from acceleration or deceleration. In the past, various functional  
511 hypotheses have been proposed for the ossified falx and tentorium in carnivorans,  
512 notably that they serve as an extra protection for the brain to avoid injuries during  
513 locomotion (particularly relevant in the case of felids) or during mastication [3].  
514 Nojima's argument to dismiss this is based on the fact that most carnivorans manifest  
515 ossification but most herbivores do not, despite displaying a wide range of different  
516 speeds and behaviours. This still remains a strong case, but perhaps future research  
517 should focus on these and other alternative loading situations in order to address the role  
518 of the osseous falx and tentorium.

519

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659

660

661 **Figures and Tables**

662

Sensitivity test	Values tested	Standard value used
Young's Modulus (MPa) of dura mater	3, 31.5, 300	31.5 MPa <sup>1</sup>
Thickness (mm) of dura mater	0.2, 0.55, 1.5	0.55 mm <sup>2</sup>
Young's modulus (MPa) of other soft tissues	0.5, 5, 50, 500	0.5 MPa <sup>3</sup>

663 **Table 1.** Sensitivity test values for the dura mater and other soft tissues (which also  
664 include the filling materials and the link elements).<sup>1</sup> Kleiven and Holst, 2002, <sup>2</sup> Cotton  
665 *et al.*, 2016, <sup>3</sup> Huempfer-Hierl *et al.*, 2015.

666

667 **Figure 1:** Left: The skull used for the *in silico* model after performing a virtual  
668 parasagittal cut in the braincase to reveal the falx cerebri and the tentorium cerebelli  
669 (displayed in blue and red, respectively). Top right: Falx cerebri in medial-lateral view.  
670 Bottom right: Tentorium cerebelli in dorsal view.

671

672 **Figure 2:** Left: parasagittal cut of the second specimen, with patches of ossification  
673 (highlighted in red) in the posterior falx. Right: Coronal view of a CT image slice which  
674 shows an oval shape following the midline.

675

676 **Figure 3:** Von Mises stress difference plots for the (intrinsic) biting analyses,  
677 comparing osseous and soft tentorium models. (See Supporting Information, figure 4,  
678 for an explanation of the differencing process).

679

680 **Figure 4:** Von Mises stress difference plots for extrinsic analyses (biting plus  
681 pulling/tearing loads) comparing osseous and soft tentorium models. (See Supporting  
682 Information, figure 4, for an explanation of the differencing process).

683

684 **Figure 5:** Von Mises stress plots for the tentorium cerebelli. Top row: Osseous and soft  
685 tentorium in dorsal view for all intrinsic regimes. Bottom row: Soft tentorium for the  
686 same loading regimes as the top row, but with adjusted contour levels to reveal the  
687 stress patterns.

688

689 **Figure 6:** Von Mises stress plots for the falx cerebri. Top row: osseous falx cerebri in  
690 medial-lateral view for all intrinsic regimes. Bottom row: soft falx cerebri for the same  
691 analyses, but with adjusted contour levels to reveal the stress patterns.