

1 **Cranial biomechanics, bite force, and function of the endocranial sinuses in *Diprotodon***  
2 ***optatum*, the largest known marsupial**

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## 22 **Abstract**

23 The giant extinct marsupial *Diprotodon optatum* has unusual skull morphology for an animal  
24 of its size, consisting of very thin bone and large cranial sinuses that occupy most of the  
25 internal cranial space. The function of these sinuses is unknown as there are no living  
26 marsupial analogues. The finite element method was applied to identify areas of high and low  
27 stress and estimate the bite force of *Diprotodon* to develop hypotheses on the function of the  
28 extensive cranial sinuses. Detailed three-dimensional models of the cranium, mandible and  
29 jaw adductor muscles were produced. In addition, manipulations to the *Diprotodon* cranial  
30 model were performed to investigate changes in skull and sinus structure including a model  
31 with no sinuses (sinuses ‘filled’ with bone) and a model with a midsagittal crest. Results  
32 indicate that the cranial sinuses in *Diprotodon* significantly lighten the skull while still  
33 providing structural support, a high bite force and low stress, indicating the cranium may  
34 have been able to withstand higher loads than those generated during feeding. Data from this  
35 study supports the hypothesis that pneumatisation is driven by biomechanical loads and  
36 occurs in areas of low stress. The presence of sinuses is likely to be a by-product of the  
37 separation of the outer surface of the skull from the braincase due to the demands of soft  
38 tissue including the brain and the large jaw adductor musculature, especially the temporalis.  
39 In very large species, such as *Diprotodon*, this separation is more pronounced, resulting in  
40 extensive cranial sinuses due to a relatively small brain compared to the size of the skull.

41

42 **Key Words:** Finite element analysis; Marsupialia; morphology; bite force; Sinus;  
43 pneumatisation

44

## 45 **Introduction**

46 The extinct *Diprotodon optatum* is the largest marsupial that ever lived, weighing an  
47 estimated 2 to 3 metric tons as adults (Wroe et al., 2004). Like many other Australian  
48 megafauna species, *Diprotodon* became extinct during the late Pleistocene, about 45,000  
49 years ago. As a generalist browser-grazer, *Diprotodon* would have thrived feeding on grasses,  
50 herbs and small shrubs, and was well adapted to exploit different habitats (Webb, 2009;  
51 Gröcke, 1997).

52         Despite its large size, the cranium of *Diprotodon* is remarkably lightweight, and is  
53 composed of thin cranial bone pneumatized by extensive cranial sinuses. Cranial sinuses are  
54 air-filled, mucosal lined chambers resulting from bone remodelling in areas where  
55 biomechanical demands are low and structurally unnecessary bone is resorbed. The size and  
56 complexity of cranial sinuses in vertebrates varies with different groups (Badlangana et al.,  
57 2011; Farke, 2010; Siliceo et al., 2011; Curtis et al., 2015; Sharp, in press). In very large  
58 mammals like *Diprotodon*, the braincase is often separated from the outside surface of the  
59 skull by frontal sinuses, epitympanic sinuses, squamosal sinuses and parietal sinuses. In most  
60 cases, large sinuses are crisscrossed by many thin-walled trabeculae, which form a  
61 convoluted network of air cavities (Badlangana et al., 2011; Farke, 2010; Sharp, in press). It  
62 is unclear whether these struts provide support as the outer bone that forms the dorsal surface  
63 of the skull separates from the braincase, or if they are simply a by-product of rapid  
64 pneumatisation (Farke, 2008; Tanner et al., 2008; Zollikofer & Weissmann, 2008)

65         In *Diprotodon*, the cranial sinuses including the frontal, parietal and squamosal  
66 sinuses have expanded to surround the middle ear cavity and braincase in all but the ventral  
67 surface (Sharp, 2014). Large sinuses have also been recorded in other large extinct  
68 diprotodontian marsupials (Murray, 1992; Black et al., 2010; Sharp, in press). In juveniles,

69 the outer surface of the skull and the inner surface of the braincase are separated by a thick  
70 layer of cancellous bone called the diploe. During ontogeny, the two surfaces separate and air  
71 cavities form as the diploe expands, increasing the size of the cavities as the separation  
72 continues. In a recent study comparing the variation in volume of the cranial sinuses and  
73 brain cavity in extinct and extant vombatiform marsupials, Sharp (in press) concluded that the  
74 cranial sinuses expand to accommodate the temporalis muscle because the relatively small  
75 brain in these species does not allow sufficient surface area for their attachment. It was  
76 identified that as skull size gets larger, the sinuses display positive allometric growth, and the  
77 brain negative allometric growth, so that in very large animals the sinuses are relatively larger  
78 and the brain is relatively smaller than in smaller animals. The cranial sinuses in smaller  
79 extant species including koalas (*Phascolarctos cinereus*) and wombats (*Vombatus* and  
80 *Lasiiorhinus*) are restricted to the frontal bone and do not expand into the parietals.  
81 Conversely, in all extinct species analysed, varying in size from *Propalorchestes*  
82 (approximately 40 kg; Sharp, in press) to *Diprotodon optatum* (approximately 2-3 tons; Wroe  
83 et al. (2004)), the cranial sinuses expand into the parietal and occipital bones. This supports  
84 the hypothesis of Moss & Young (1960) who suggested that the demands of soft tissue,  
85 including the area for attachment of the masticatory musculature and the size of the brain,  
86 may be the main driver of sinus expansion.

87 Many functional hypotheses have been put forward to explain the presence of cranial  
88 sinuses (Keir, 2009; Márquez, 2008; Witmer, 1997; Farke, 2010; Moss & Young, 1960).  
89 However, it is likely there is no single function in all taxa. As previously noted, the most  
90 likely explanation is that sinuses form where bone is not structurally necessary, resulting in a  
91 lighter skull than if the same space was filled with cancellous bone. However, derived  
92 functions for pneumatized regions have also been hypothesized in special cases including  
93 assisting in thermoregulation of the brain in the giraffe (Mitchell & Skinner, 2003, 2004;

94 Ganey et al., 1990; Dyce et al., 2002), providing shock absorption during head-butting or  
95 neck-sparring (Badlangana et al., 2011; Davis et al., 1996; Schaffer & Reed, 1972), serving  
96 as a resonance chamber for the production of low frequency sounds in giraffe and cassowary  
97 (von Muggenthaler et al., 1999; Leakey & Walker, 1997; Naish & Perron, 2014) and  
98 dissipation of stress over the skull during mastication in bone-cracking hyenas, extinct  
99 borophagine canids and bamboo-eating pandas (Tanner et al., 2008; Buckland-Wright, 1978,  
100 1971; Joeckel, 1998).

101 In the case of *Diprotodon*, the convex frontoparietal region of the cranium and the  
102 associated large sinuses may be a more optimal way to increase the attachment area of the  
103 temporalis muscle than would a plate-like sagittal crest for an animals of such size with a  
104 proportionally small braincase (Sharp, 2014; Sharp, in press). A plate-like sagittal crest is a  
105 common feature among mammals for attachment of the temporalis muscle. Sagittal crests are  
106 common in felids, canids, primates and some marsupial taxa, including the extant koala;  
107 however, sagittal crests are not present in any large extinct marsupial megafauna and the  
108 reason is unknown. Compared to a solid plate-like sagittal crest, expended sinuses may  
109 provide a broader area for attachment of the temporalis muscle while keeping the skull  
110 lightweight.

111 The invasion of large sinuses from the frontal into the parietal bones in some hyaenids  
112 and borophagine canids (an extinct subfamily of bone-crushing dogs) may function to  
113 dissipate stress away from the facial region during bone-cracking (Tanner et al., 2008;  
114 Werdelin, 1989; Joeckel, 1998; Tseng, 2009). The presence of sinuses increases structural  
115 support and resists bending stresses imposed by the temporalis muscle when compared to a  
116 solid, plate-like sagittal crest. This function appears to be enhanced when the frontal bone is  
117 domed, as in *Diprotodon*. The braincase in *Diprotodon* is too small to allow for sufficient  
118 attachment of the temporalis muscle, so expansion of the sinuses may be in response to the

119 growth of these muscles during development, and the presence of sinuses may result in a  
120 more mechanically efficient skull. Alternatively, the shape and size of sinuses may reflect the  
121 loads placed on the skull, including loads imposed during mastication.

122 The extraordinary preservation of near-complete skulls of *Diprotodon* found at  
123 Bacchus Marsh in Victoria, Australia, has provided an opportunity to investigate their  
124 morphology and function. In the present study, finite element (FE) analysis was applied to  
125 explore the function of the extensive cranial sinuses in *Diprotodon*. The FE method is a  
126 computational tool used to predict the distribution of stress and strain for complex structures  
127 in response to applied loads, taking into account the elasticity and geometry of the structure  
128 (Richmond et al., 2005; Rayfield, 2007; Bright, 2014). To apply the method to a complex  
129 structure like a skull, the structure is simplified into a finite number of elements of simple  
130 geometry, typically triangles or squares for 2D models and cubes or tetrahedra for 3D  
131 models. An advantage of the FE method is that it is non-invasive and can be applied to fossil  
132 taxa. Furthermore, the geometry of digital models can be manipulated to test functional  
133 implications of different morphology.

134 Three main hypotheses for the function of the sinuses in *Diprotodon* were tested  
135 during loads generated by the masticatory muscles. The first is that the sinuses serve to  
136 lighten the skull; second, that they primarily function to dissipate stress; and finally that they  
137 are a by-product of rapid pneumatisation to provide a greater surface area for the attachment  
138 of the temporalis muscle. Three different FE models were constructed to explore the  
139 mechanical and functional effect of morphological change: (1) a skull model with normal  
140 sinus morphology maintained; (2) a hypothetical model with the cranial sinuses completely  
141 filled with bone ('filled-sinus' model) to test if this region experiences low stress and strain  
142 and if sinuses form where bone is not structurally necessary; and (3) a model with the sinuses  
143 removed and a solid plate-like sagittal crest added ('crest' model) to test if a pneumatised

144 domed frontalparietal region is more mechanically efficient. If the ‘filled-sinus’ model  
145 experiences low or no stress over the frontoparietal region, but stress in other regions is  
146 similar to the normal model, this would indicate that sinuses develop where bone is not  
147 mechanically necessary, and that the external morphology of the skull is more important for  
148 skull function than the presence of sinuses. This would support both hypotheses that the  
149 sinuses lighten the skull while providing sufficient surface area for the attachment of the  
150 temporals muscle. If the distribution of stress is more even in the normal model compared to  
151 both the filled and sagittal crest model, this would suggest that the presence of sinuses allows  
152 the skull to dissipate stress more evenly then when the space is filled with bone. If a stress  
153 dissipating effect is identified, this function may have evolved to accommodate high bite  
154 forces, which will also be estimated.

155

## 156 **Material and methods**

### 157 *Data collection*

158 A near complete cranium of *Diprotodon optatum* (NMV P31299), recovered from  
159 Pleistocene sediments at Bacchus Marsh in southern Victoria, Australia, was scanned by  
160 computed tomography (CT) using a Siemens Sensation 64 scanner (Siemens Medical  
161 Solutions) at St. Vincent’s Public Hospital, Melbourne. Voxels were 0.586 x 0.586 mm and  
162 slice thickness and interslice distance was 0.6 mm and 0.3 mm, respectively, to produce 978  
163 CT slices in the transverse plane. Two near-complete dentaries (NMV P151802 and NMV  
164 157382), also recovered from Bacchus Marsh, were CT scanned using the same facilities and  
165 parameters to produce one composite lower jaw for reconstruction of the masticatory  
166 muscles. The dentaries were similar in size so minimal scaling or manipulation was  
167 necessary.

168

169 *Model construction*

170 The CT data were imported into the image processing software program Mimics 13.1  
171 (Materialise), where manual editing of the CT slices took place to isolate the craniodental  
172 morphology from the inorganic matrix that remained inside some of the sinus cavities, and to  
173 generate STL surface files of the cranium and dentaries. The 3D surface files were then  
174 imported into Geomagic Studio (Geomagic, Inc.) to improve the quality of the surface mesh,  
175 and repair breaks and missing regions of the cranium, including the zygomatic arches. These  
176 missing regions were reconstructed using the mirroring tool of more complete areas, as well  
177 as reference from the morphology of the surrounding bone and other skull specimens with  
178 these regions preserved (notably NMV P150021). The model was then imported into  
179 Hypermesh (Altair Engineering Inc.), where a further series of steps were taken to ensure the  
180 quality of the surface mesh, including testing the aspect ratio of the triangles, the dihedral  
181 angle and the tetrahedral quality, before converting it to a solid 3D FE mesh composed of 4-  
182 noded tetrahedral elements (tet4; mean edge length of 1.805 mm) resulting in a model with  
183 5,277,638 elements. The element size was chosen so that thin bones in the skull had two or  
184 more elements thickness to accurately predict the displacement of nodes within the model  
185 due to the applied loads. Quadratic 10-noded tetrahedral elements (tet10) could have  
186 achieved the same outcome due to the placement of an extra node along each element edge;  
187 however, the computational time was increased significantly using tet10 elements, and  
188 previous studies have demonstrated that models with a high number of tet4 elements produce  
189 more stable measurements compared to tet10 models (Bright & Rayfield, 2011; Tseng &  
190 Flynn, 2015b; Dumont et al., 2005). A lower jaw model was also constructed following the  
191 same method by combining the CT scans from two, near complete mandibles from the same



192 fossil site (NMV P151802 and NMV 157382). The mandible was used to align the muscle  
193 force vectors but was excluded from the FE analysis.

194 In addition to the original model, two modified models were produced: a ‘filled-sinus’  
195 model and a ‘crest’ model (Figure 1). The original surface model was imported to Avizo  
196 (Visage Imaging, Inc.) as a stereolithography (STL) file and converted to a series of 2D slices  
197 using the ‘ScanConvertSurface’ module. The ‘filled-sinus’ model was constructed by  
198 converting the sinus area from ‘air’ to ‘bone’, essentially filling in the space with elements  
199 that were later assigned the material properties of bone, see below (Figure 2B). The ‘crest’  
200 model was produced by filling the sinuses and modifying the external geometry of the skull  
201 by flattening the frontoparietal region and adding a midsagittal crest (Figure 2C). The  
202 construction of this model was guided by observations of koala skulls, a smaller but related  
203 species to *D. optatum* with a sagittal crest, and placental herbivores such as the Brazilian tapir  
204 (*Tapirus terrestris*) that have a high, broad and solid sagittal crest. Based on these  
205 observations, the height of the midsagittal crest was maintained at the same height as the  
206 dorsal surface of the original skull and the frontoparietal region was flattened as much as  
207 possible without modifying the location or shape of the orbits, braincase, or occipital crest.  
208 Surface models were then produced and converted to 3D FE meshes composed of 4-noded  
209 tetrahedral elements (‘filled-sinus’ model = 5,963,413 elements; ‘crest’ model = 4,998,012  
210 elements). The average element size was kept the same between all models to eliminate  
211 errors in model output and to allow differences between difference morphologies to be  
212 evaluated.

213 Each FE mesh was then imported to Abaqus CAE v6.12 where material properties  
214 and boundary conditions were applied. There are no data available summarising the material  
215 properties of bone in marsupial skulls, and material properties are often altered during  
216 diagenesis of fossils (Snively & Theodor, 2011; Tseng & Wang, 2010; Tseng, 2009; Oldfield

217 et al., 2012; Rayfield, 2007). Therefore, each model was assigned homogeneous and isotropic  
218 average values of Young's modulus ( $E = 20$  GPa) and Poisson's ratio ( $\nu = 0.3$ ) for  
219 mammalian bone (Tseng et al., 2011; Erickson et al., 2002; Dumont et al., 2005; Tseng &  
220 Wang, 2010; Figueirido et al., 2014; Tseng & Flynn, 2015a). This may produce stiffer  
221 models with higher bite forces than models with multiple material properties incorporating  
222 cancellous bone in areas where the skull is thick. However, this methodology was considered  
223 suitable for the present study, which compares relative stress and strain values due to broad  
224 changes in morphology. It has also been shown that using multiple material properties has  
225 little effect on large-scale patterns of stress and strain compared to variation in model shape,  
226 so it was assumed that interpretations of the results from this study would not differ  
227 substantially from those if heterogeneous material properties were used (Strait et al., 2005;  
228 Walmsley et al., 2013).

229 Each model was constrained by a single node at both temporomandibular joints (TMJ)  
230 to simulate the jaw hinge during biting. The left TMJ was fully constrained against  
231 displacement in all axes, and the right TMJ was constrained to allow lateral displacement of  
232 the skull, so as not to over constrain the model. Over constraining the model may produce  
233 unrealistic stresses and strains due to the Poisson's effect (compression in one direction  
234 causing expansion in the other two directions) (Dumont et al., 2005). Relaxed constrained  
235 such as those used in this study have been shown to produce more accurate results than  
236 models constrained in all axes at both TMJs (Tseng & Flynn, 2015b). To simulate biting at  
237 various positions a single node was constrained at the bite points in the direction  
238 perpendicular to the occlusal plane. Biting scenarios were modelled to simulate bilateral  
239 biting at each molar and at the incisors with the muscles on both sides of the skull fully  
240 activated to estimate maximum possible bite force. The incisors in *Diprotodon* continuously  
241 grown throughout the animals' life so would require considerable use to keep them

242 functional. Therefore, biting at the incisors may have an important functional role that  
243 contributes to skull morphology. The molars, however, do not continuously grow and will  
244 primarily be used to mechanically process large quantities of vegetation before being  
245 swallowed.

246         Muscle forces were applied to the FE models by distributing the load for each muscle  
247 over the entire surface of its origin by estimating the attachment area from muscle scars  
248 present on the fossilized bone and through comparisons with extant marsupials. Muscle  
249 orientations were determined by creating a vector between the origin and the corresponding  
250 insertion on the mandible. The jaw adductor musculature was considered to involve three  
251 main components; the temporalis, masseter and pterygoid muscles. Each muscle group was  
252 modelled with two or three subdivisions based on published studies of marsupial jaw muscles  
253 (Turnbull, 1970; Tomo et al., 2007; Warburton, 2009; Crompton et al., 2008; Murray, 1998;  
254 Sharp & Trusler, 2015; Sharp, 2014). The muscles included are *masseter superficialis*,  
255 *masseter profundus*, *zygomaticomandibularis*, *temporalis superficialis*, *temporalis profundus*,  
256 *pterygoideus medialis* and *pterygoideus lateralis*. These muscles were digitally reconstructed  
257 in 3D in Avizo following a similar method used by Lautenschlager (2013) and Curtis et al.  
258 (2009) and described for *Diprotodon* in Sharp (2014). The muscle forces (Table 1) were  
259 estimated by measuring the cross-sectional area of the reconstructed muscles and multiplying  
260 by a constant value of intrinsic muscle stress,  $0.3 \text{ N mm}^{-2}$  (Weijs & Hillen, 1985; van  
261 Spronsen et al., 1989; Thomason, 1991; McHenry et al., 2007; Wroe et al., 2005; Cox et al.,  
262 2012; Strait et al., 2005; Rayfield, 2007).

263

264 *Analysing Model Performance*

265 The resultant force, or bite force, at each bite point was recorded from Abaqus for each of the  
266 models and the mechanical efficiency, or mechanical advantage, was compared by  
267 calculating the ratio of the bite reaction force to the applied muscle force (Dumont et al.,  
268 2009). This measure provides a scale independent estimate of the efficiency of the jaw lever  
269 system that is defined by the fulcrum (TMJ), the effort (muscle force) and the resistance (bite  
270 point) as a third-class lever.

271 Contour plots of von Mises (VM) stress, and maximum and median VM stresses,  
272 were extracted from Abaqus as an indicator of the strength of the structure. Structures with  
273 lower values of stress are less likely to fail under a given load and are considered stronger. In  
274 addition, models were also analysed by sampling stress values along the dorsal cranium.  
275 Seven landmarks were sampled along the midsagittal axis from the tip of the nasals to the  
276 occipital crest: 1) rostral-most contact between the nasal bones; 2) between the infraorbital  
277 foramina; 3) between the rostral-most point of the orbits; 4) between the post-orbital  
278 processes; 5) between the post-orbital constriction of the parietal bones; 6) half-way along the  
279 length of the braincase; and 7) at the caudal end of the sagittal crest. At each location, ten  
280 nodes were selected and the average VM stress was calculated. Total internal strain energy, a  
281 measure of energy efficiency or the stiffness of a structure, was also recorded for each model  
282 simulation. Structures with higher strain energy are more compliant and will deform more  
283 easily, store more energy and transmit less energy to the bite point (Dumont et al., 2009).  
284 Thus, stiffer models will be more efficient than compliant models.

285

## 286 **Results**

287 *Bite force and mechanical efficiency*

288 The bite force at the incisors, premolars and each molar along the tooth row was estimated  
289 and compared for each model (Table 2). The maximum bite force estimated for the original  
290 skull model of *Diprotodon* is 2374 N at the incisors and between 4118 and 11134 N at the  
291 cheek teeth from the premolar to the fourth molar. For all models, bite force and mechanical  
292 efficiency increased as the bite point moved from the incisors to the fourth molar. The normal  
293 model had slightly higher bite force at every bite location (approximately 10% and 5% higher  
294 than the ‘filled-sinus’ model and ‘crest’ model respectively), indicating that the internal  
295 structure of the sinuses may affect the biting performance of the skull. This difference may  
296 fall within the margin of error between the models; however, the error was minimised by  
297 keeping the element size the same between the models, and by applying homogenous  
298 material properties, limiting error that may be due to distribution of material properties within  
299 the models.

300

### 301 *Stress distribution and strain energy*

302 The area of highest stress for all models was the zygomatic arch. During incisor biting, the  
303 premaxilla also experienced high stress. The pattern of stress distribution in each model for  
304 incisor biting and first and fourth molar biting are displayed in figure 3. Despite the change in  
305 sinus structure between the models, the stress distribution stays relatively similar across the  
306 zygomatic arch, the palate, and the rostrum for all bite locations. The only major difference is  
307 stress over the frontal and parietal regions where the sinuses develop. Stress is more evenly  
308 spread across the dorsal surface of the normal skull. The ‘crest’ model shows a higher  
309 concentration of stress anterior to the frontoparietal region compared with the normal model,  
310 similar to observations in previous studies on other taxa (Tseng, 2009; Tanner et al., 2008). In  
311 the model with the sinuses filled with bone, almost zero stress is experienced over the

312 frontoparietal region. Stress within the skull is also low (Figure 4). In the normal model, low  
313 stress is experienced around the external bone of the frontoparietal sinuses and the structural  
314 struts within it, while in the ‘filled-sinus’ model, stress in this region is essentially zero.  
315 Stress distribution along the midsagittal plane is shown with landmarks from the tip of the  
316 nasals to the occipital crest in figure 5. Stress is highest in the normal model at all points  
317 along the midsagittal axis except point 2 where the ‘crest’ model is higher. The highest stress  
318 in the ‘filled-sinus’ and ‘crest’ models is located at point 2 in the nasal region. For the normal  
319 model, the highest stress is shifted posteriorly to point 4, located on the frontal. Also in figure  
320 5 is a dorsal view with the skull roof cut-away showing the stress inside the sinuses. The  
321 ‘filled-sinus’ and ‘crest’ models have almost zero stress in this region.

322         Quantitative differences between the three models are displayed in figure 6 for biting  
323 at each molar and the incisors. The ‘filled-sinus’ model has the lowest median VM stress and  
324 strain at all bite points. Strain energy, an indicator of the stiffness of the model, is highest in  
325 the normal skull model, meaning it deforms more easily. This is expected, because thinner  
326 bone allows more deformation than thick solid bone.

327

## 328 **Discussion**

### 329 *Bite force*

330 The exceptionally high bite forces at the molar tooth row suggest that *Diprotodon* was able to  
331 consume a variety of food, including tough, fibrous grasses which require more work or  
332 energy to fracture the plant material (Sanson, 2006). Isotope analysis of fossil teeth revealed  
333 that *Diprotodon* consumed both C3 and C4 plants (Gröcke, 1997), allowing this species to  
334 thrive feeding on grasses, herbs and small shrubs, and exploit different habitats. However, the

335 low levels of stress across the cranium indicate that the skull could withstand greater forces  
336 than those generated by the jaw muscles during feeding. It has been suggested that high bite  
337 forces at the incisors allowed the largest fossil rodent *Josephoartigasia monesi* to use their  
338 incisors to dig for food or defend against predators (Cox et al., 2015). Since sexual  
339 dimorphism has been suggested as an explanation for a high degree of size variation in  
340 *Diprotodon* specimens, it is possible that *Diprotodon* used its massive incisors in male-male  
341 competition. This may be testable using FEA by applying large forces to the incisors to  
342 determine the loads that *Diprotodon* could withstand.

343 We cannot directly compare the bite force of *Diprotodon* to other large herbivores,  
344 such as elephants or rhinoceros, because bite force has not been recorded for these species, *in*  
345 *vivo* or *in vitro*. However, bite force has been estimated in some large herbivorous taxa  
346 including rodents and the giant panda (Cox et al., 2015; Christiansen & Wroe, 2007;  
347 Figueirido et al., 2014). The herbivorous giant panda (*Ailuropoda melanoleuca*) has an  
348 estimated maximum bite force of 1816 N at the carnassial (Christiansen & Wroe, 2007) and  
349 1710 N at the second molar (Figueirido et al., 2014). In rodents, the largest fossil rodent  
350 (*Josephoartigasis monesi*, approximately 1000 kg) has an estimated bite force of 4165 N at  
351 the third molar (Cox et al., 2015). The bite forces estimated in *Diprotodon* are higher than  
352 those estimated in these species (4118 to 11134 N), possibly because *Diprotodon* is larger  
353 and has a relatively larger temporalis muscle. However, it must be noted that the methods  
354 used between these studies and the way the finite element models were constructed and  
355 loaded are different and, therefore, confidence in these comparisons is limited. It is also  
356 possible that this study overestimates the bite forces for *Diprotodon* due to the model being  
357 assigned homogenous material properties or modelled with single node constraints that could  
358 make the model stiffer than in real life. In addition, these bite forces are considered the

359 maximum possible bite forces and probably do not represent the bite forces during normal  
360 mastication.

361

### 362 *Sinus function*

363 The normal model had the highest overall stress and strain of the three morphologies tested.  
364 The thin bone that forms the external surface of the sinuses and the struts within, undergo  
365 more deformation than the ‘filled-sinus’ and ‘crest’ models with solid bone in the frontal and  
366 parietal regions. The ‘filled-sinus’ model had the lowest overall stress and strain, indicating it  
367 is both strong and resistant to deformation. This is not unexpected since thick bone will not  
368 deform as readily as thin bone. The pattern of stress distribution showed very little stress over  
369 the frontal and parietal region where the sinuses develop. This is consistent with the  
370 hypothesis that sinuses form where there is low, or no biomechanical stress. As described  
371 previously, sinuses develop through a process called pneumatisation. Bone remodelling in  
372 response to biomechanical demands results in the removal of structurally unnecessary bone,  
373 and the deposition of bone to reinforce areas that experience higher levels of stress (Moss &  
374 Young, 1960; Witmer, 1997; Farke, 2008, 2010). The frontoparietal region in *Diprotodon*  
375 experiences very low stress and, therefore, thick bone in this area is unnecessary for structural  
376 support.

377         The presence of sinuses may be a by-product of the separation of the outer surface of  
378 the skull from the braincase, providing a larger area for the temporalis muscles that is not  
379 offered by a the relatively small brain in *Diprotodon* (Sharp, in press). This was first outlined  
380 by Moss & Young (1960) in their explanation of neurocranial growth, emphasising the  
381 response of different functional components (an outer table, a diploe, and an inner table) to  
382 the demands of soft tissue they support and protect. *Diprotodon* and many other marsupials



383 have proportionally larger temporalis muscles compared to placental herbivores such as  
384 ungulates (Turnbull, 1970; Sharp, 2014). The relative size of the jaw muscle complex is an  
385 important factor in cranial morphology, and assuming that very large marsupials like  
386 *Diprotodon* retained the jaw muscle proportions of ancestral marsupials, the bony  
387 architecture must also be retained despite a small braincase. Expansion of the sinuses  
388 provides the necessary surface area for the attachment of large temporalis muscles, while  
389 potentially increasing mechanical efficiency and lightening the skull.

390 The sinus volume of the *Diprotodon* specimen is 2675 cm<sup>3</sup>, accounting for  
391 approximately 25% of the total cranial volume (Sharp, in press). Assuming bone density is  
392 approximately 1.5 g cm<sup>-3</sup> (Hall, 2005), the ‘filled-sinus’ model would be 4.0 kg heavier than  
393 the real skull, or approximately 30% heavier when just considering the bone mass of the  
394 head. However, if the sinus region was filled with bone it would most likely be cancellous  
395 bone which is considerably less dense than compact bone. So, while the sinuses increase the  
396 amount of stress and deformation of the skull, this amount is very low and may be  
397 inconsequential compared to the benefit of a lighter skull.

398 There is some evidence to support the hypothesis that the cranial sinuses function to  
399 evenly dissipate stress from the bite point, posteriorly over the cranium away from the nasal  
400 region. In figure 5, the highest stress in the ‘filled-sinus’ and ‘crest’ models is located at the  
401 nasal bone (point 2), while in the normal model, the highest stress is shifted posteriorly to the  
402 frontoparietal region (point 4). In hyenas, the pattern of stress distribution follows an arch  
403 along the vaulted forehead, and the frontoparietal sinuses help to resist loads by dissipating  
404 stress over the skull surface (Tanner et al., 2008). This adaptation is thought to have evolved  
405 to provide a stronger structure for bone-cracking and prevent weak points occurring in the  
406 facial region that are prone to failure under very high bite forces. As an herbivore, bone-  
407 cracking is not required by *Diprotodon*, but as discussed earlier the bite force is still very

408 high, and the cranium may be able to withstand greater forces than those generated during  
409 feeding. Therefore, the skull appears to be “over-engineered” for biting at both the incisors  
410 and molars during loads generated by the masticatory muscles. Furthermore, as a very large  
411 mammal, *Diprotodon* would have consumed large quantities of food requiring long  
412 processing times and a high frequency of mastication cycles. The adaptation to dissipate  
413 stress more evenly over the skull could help to reduce the likelihood of fatigue failure caused  
414 by repetitive stress on the craniodental system, as has been suggested for the red panda  
415 (*Ailurus fulgens*) (Figueirido et al., 2014). The stress dissipating effect that the sinuses appear  
416 to provide may limit areas of high stress, decreasing the chances of failure over time.

417         The role of the trabeculae, or struts, within the sinuses was not tested in the present  
418 study. Previous research has demonstrated that the trabeculae may not have a function other  
419 than being a by-product of sinus formation (Farke, 2008). Some bovids have very few struts  
420 (e.g. *Alcelaphus* and *Damaliscus*), while others have elaborate strutting (e.g. *Ovis canadensis*  
421 and *Syncerus caffer*) (Farke, 2007; Farke, 2010). However, the morphology, or complexity of  
422 the struts was not correlated with behaviours such as head-butting. Instead, the complexity of  
423 sinuses was more strongly correlated with phylogeny. The configuration of trabeculae within  
424 the sinuses of *Diprotodon* is very simple; however, despite this simplicity they are unlikely to  
425 reduce the structural integrity of the skull, as indicated by the low stress observed in this  
426 study. The struts are more likely to correspond with cranial sutures. There is some evidence  
427 that the sinuses in other taxa do not cross sutural boundaries, and that the size and  
428 morphology of sinuses are restricted, or influenced, by sutures (Farke, 2007; Farke, 2010). In  
429 *Diprotodon*, the midsagittal strut, separating the frontal sinuses into left and right portions,  
430 corresponds to the interfrontal suture. A strut perpendicular to this, dividing the sinuses into  
431 anterior and posterior portions, is located at the frontoparietal suture. The frontal sinuses  
432 themselves have no further struts. The only other recorded species with such limited strutting

433 in the frontal sinus is the Hartebeest (*Alcelaphus buselaphus*) (Farke, 2007; 2010), so it is  
434 unclear what determines the complexity of the trabecula network.

435 In future, biomechanical performance tests could also be applied to other extinct  
436 marsupial megafauna, including *Zygomaturus*, and to extant megafauna such as elephants and  
437 giraffes to examine the structure and function of sinuses in other species. Furthermore, the  
438 mechanisms that might control the formation and morphology of the trabecula network  
439 within the sinuses could be investigated through ontogenetic studies. It would be of  
440 considerable interest to determine whether the strut patterns are based on phylogeny,  
441 behavioural functions, biomechanical stress distribution, ontogenetic development, or  
442 through a combination of these. Another possible step would be a comparative analysis of  
443 large herbivores to investigate the hypothesis that herbivore skulls are overbuilt to reduce the  
444 risk of fatigue failure.

445

## 446 **Conclusion**

447 This study is the first to examine the biomechanical performance of the skull and cranial  
448 sinuses of an extinct herbivorous species of marsupial megafauna and illustrates that the  
449 extensive cranial sinuses may benefit *Diprotodon* by providing adequate surface area for the  
450 attachment of the temporalis muscle while also increasing mechanical efficiency of biting,  
451 dissipating stress and lightening the skull. The presence of large sinuses is likely explained by  
452 the pneumatisation of the frontal and parietal bones due to low mechanical stress and the  
453 necessity for a large attachment area for the temporalis muscle that is not provided by the  
454 relatively small surface area of the braincase. The sinuses in *Diprotodon* also significantly  
455 lighten the skull while still providing structural support. The seemingly delicate-for-it's-size  
456 cranium of *Diprotodon* is actually a remarkably strong structure that improves transmission

457 of muscle force into bite force. By comparing the original skull morphology with  
458 hypothetical morphologies including the construction of a midsagittal crest, this study shows  
459 that the combination of the externally domed frontals and an associated sinus allows for  
460 similar increases in surface area like a sagittal crest would, but is much better at dissipating  
461 stress, as has been shown in other taxa (Tanner et al., 2008; Tseng, 2009; Joeckel, 1998). The  
462 loads simulated in this study were those produced by the jaw muscles; the temporalis,  
463 masseter and pterygoids. The resultant bite force was high, but stress was still low over the  
464 cranium, which might indicate the cranium could withstand higher loads not generated during  
465 feeding. Higher forces may have been produced by using the incisors during competition with  
466 rival individuals or defense against predators. Alternatively, the low and evenly distributed  
467 stress over the cranium may reduce the likelihood of fatigue failure from prolonged and  
468 repetitive masticatory cycles. Finally, this study also demonstrates the utility of the FE  
469 method. The ability to experiment with altered morphologies in a non-invasive way provides  
470 opportunities to address questions of form-function relationships in extinct species where  
471 specimens are fragile or rare.

472

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479 Massachusetts, Amherst. We would also like to thank the reviewers for their very helpful  
480 comments for improving this manuscript.

481

### 482 **Author contributions**

483 A.C.S. designed and carried out the study, analysed the results and contributed to the writing  
484 and editing of the manuscript. T.H.R. arranged access and CT scanning of the specimen and  
485 contributed to study design and editing of the manuscript.

486

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- 658
- 659

660 **Tables**

661 **Table 1.** Muscle cross-sectional areas (CSA) and forces applied to each side of the skull for  
 662 each finite element model. The muscle forces were estimated based on the cross-sectional  
 663 area of reconstructed muscles is described in Sharp (2014).

<b>Muscle</b>	<b>CSA (cm<sup>2</sup>)</b>	<b>Force (N)</b>
Deep temporalis	5096.39	1529
Superficial temporalis	1491.95	448
<b>Temporalis Total</b>	<b>6588.34</b>	<b>1977</b>
Zygomatmandibularis	5182.75	1555
Deep masseter	1593.21	478
Superficial masseter	4887.63	1466
<b>Masseter Total</b>	<b>11663.59</b>	<b>3499</b>
Medial pterygoid	4438.50	1331
Lateral pterygoid	729.42	219
<b>Pterygoid Total</b>	<b>5167.92</b>	<b>1550</b>
<b>Total</b>	<b>23419.85</b>	<b>7026</b>

664

665

666 **Table 2.** Predicted bite force for each model for each biting location

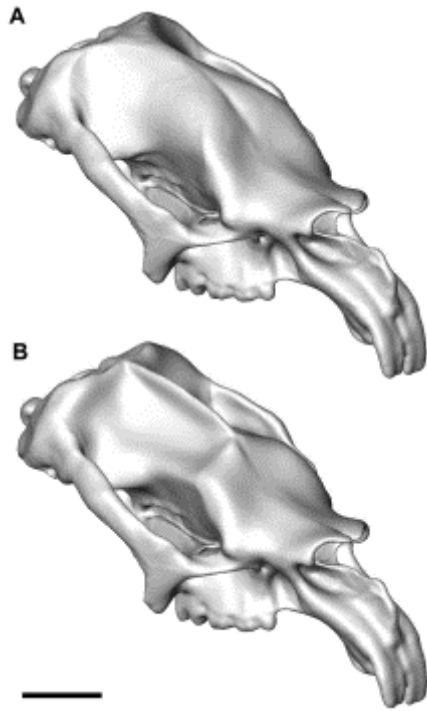
<b>Biting tooth</b>	<b>Bite force (N)</b>		
	Normal	Filled-sinus	Crest
I	2374	2091	2245
PM	4118	3688	3939
M1	4493	4033	4333
M2	5418	4855	5154
M3	6886	6352	6747
M4	11134	10257	11129

667

668

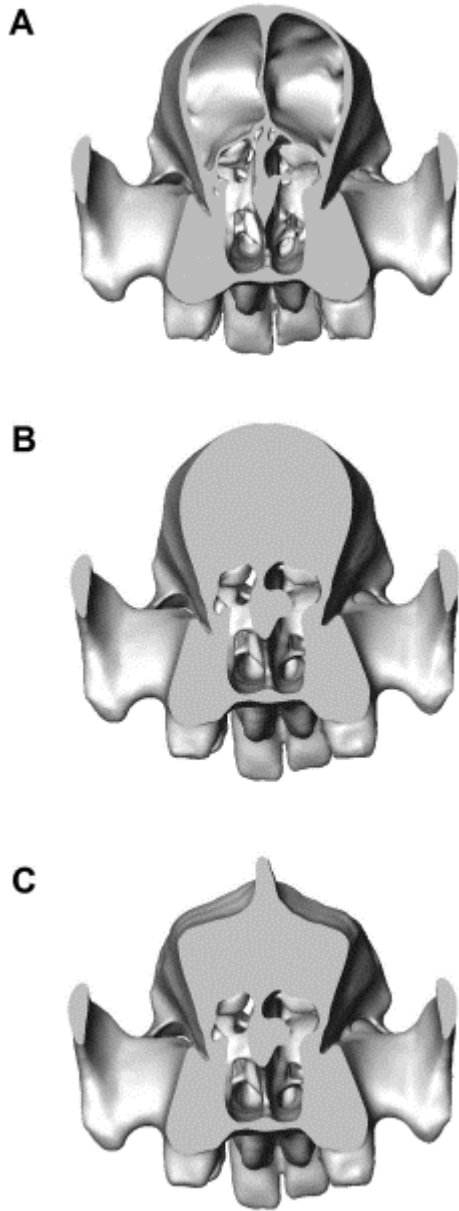
669

670 **Figures**



671

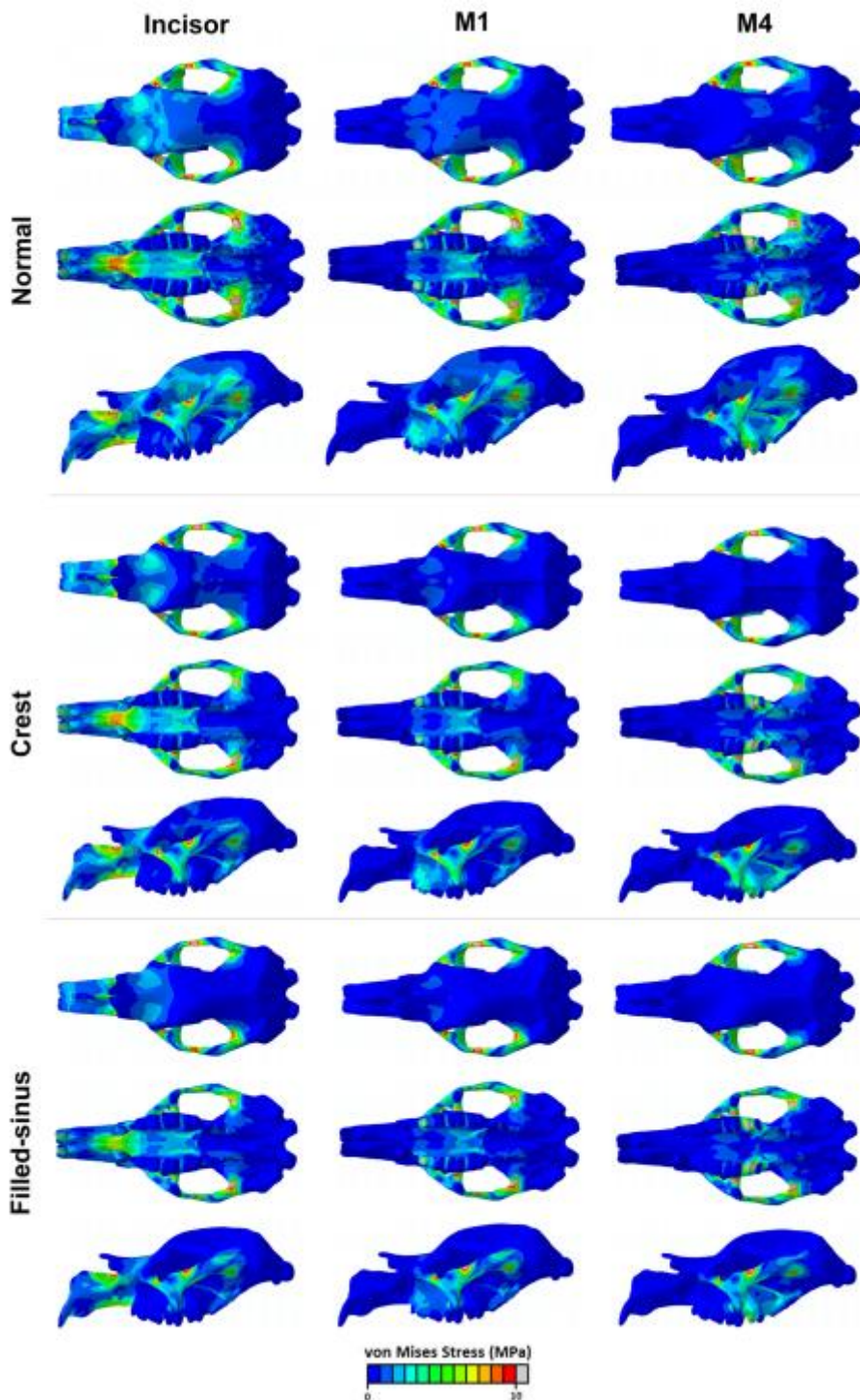
672 **Figure 1.** Skull surface models illustrating the different external morphologies of (A) the  
673 normal and 'filled-sinus' models and (B) the 'crest' model. Scale = 10 cm.



674

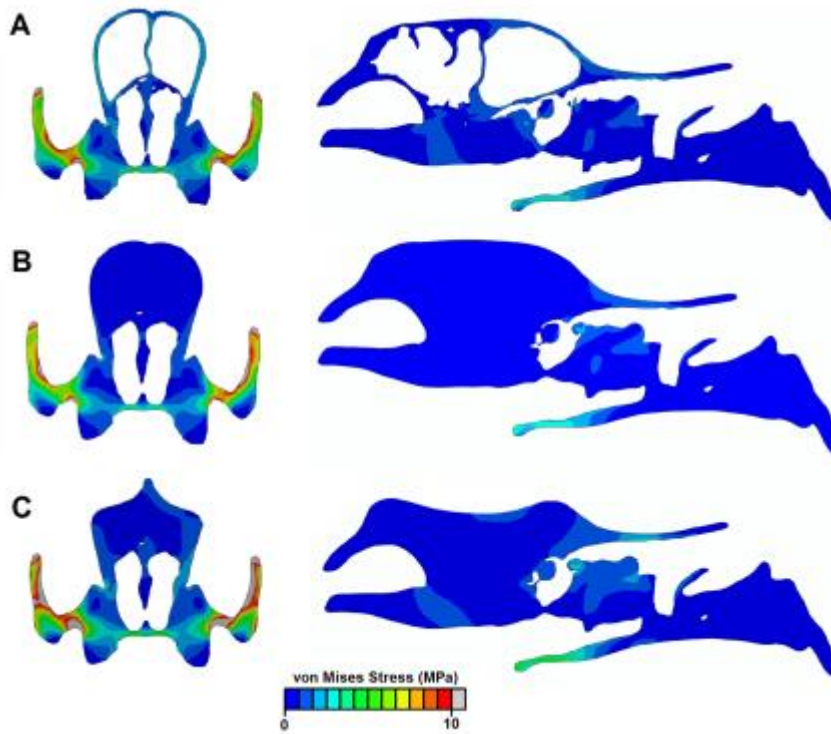
675 **Figure 2.** Frontal view cross-sections of the skull surface models illustrating the different  
676 morphologies of (A) the normal model, (B) 'filled-sinus' model and (C) 'crest' model. Scale  
677 = 10 cm.

678



679

680 **Figure 3.** Von Mises stress patterns for the normal model, the ‘crest’ model and the ‘filled-  
 681 sinus’ model when bilateral biting at the incisors, first molar (M1) and fourth molar (M4).  
 682 Each model is shown in dorsal (top), ventral (middle) and lateral (bottom) views. Cool  
 683 colours represent areas of low VM stress, and warm colours high stress.

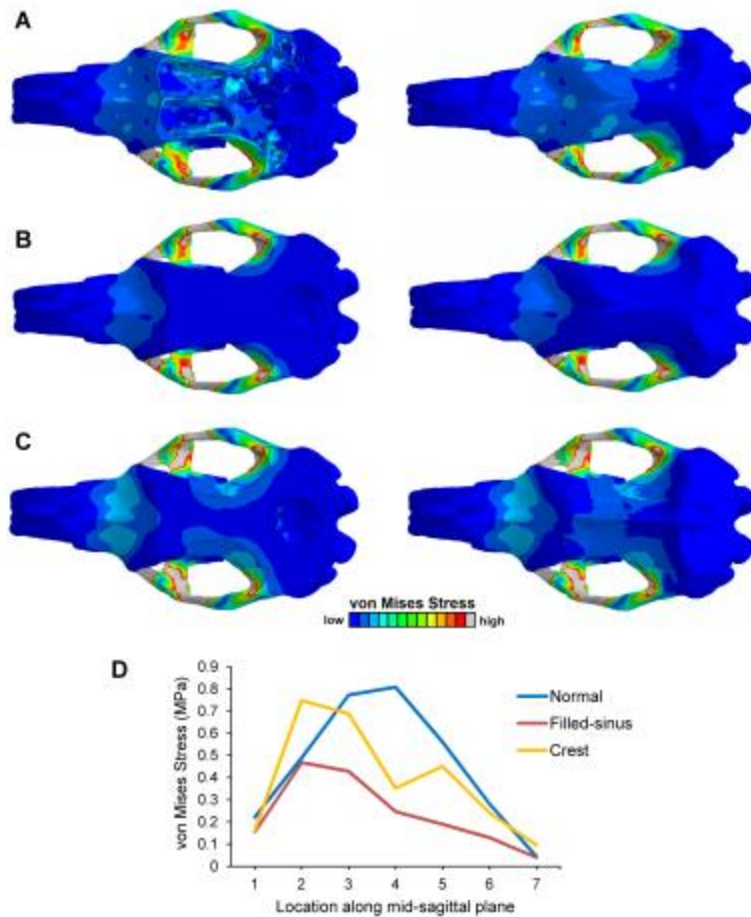


684

685 **Figure 4.** Von Mises stress patterns for the normal model (A), the ‘filled-sinus’ model (B)  
 686 and the ‘crest’ model (C) in transverse slices showing the frontal sinus (left) and sagittal  
 687 slices just offset from the midsagittal plane (right) when bilateral biting at the second molar.

688

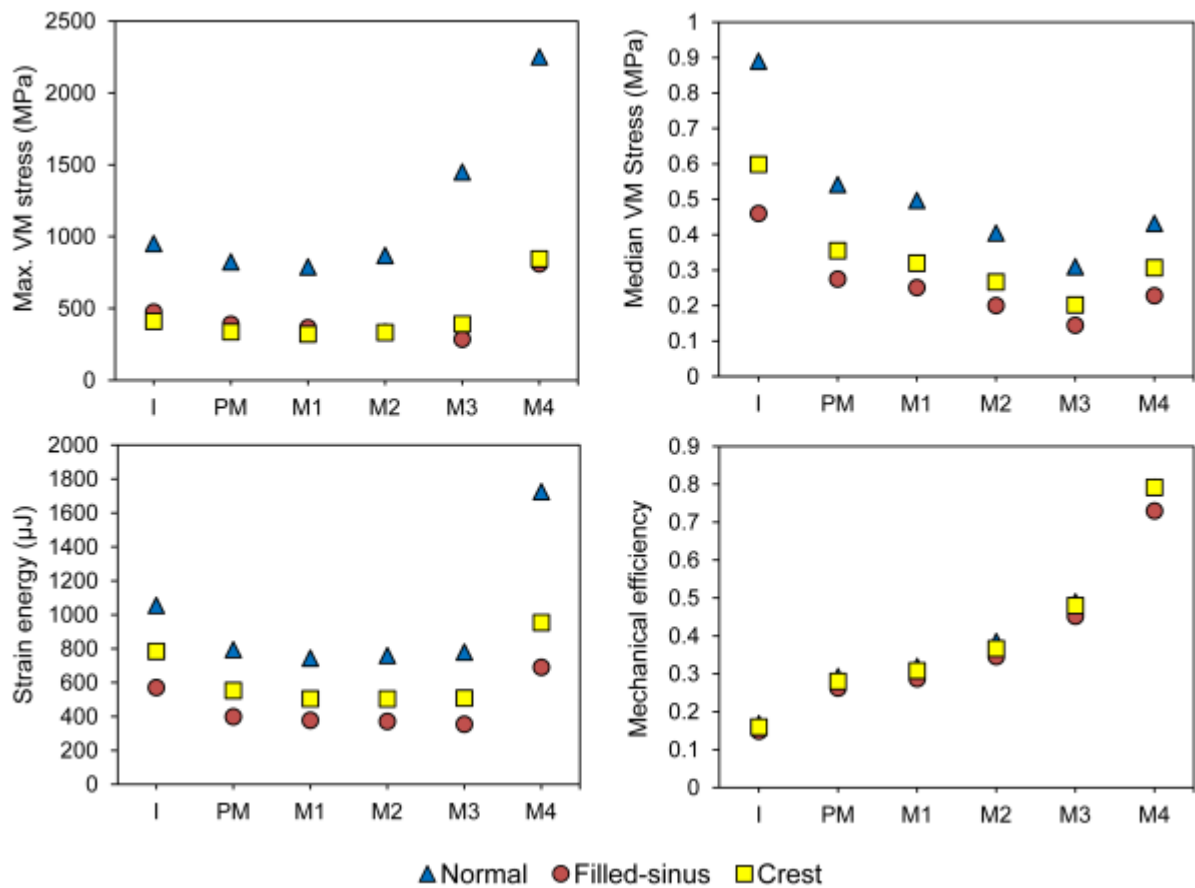




689

690 **Figure 5.** Von Mises stress patterns for the normal model (A), the ‘filled-sinus’ model (B)  
 691 and the ‘crest’ model (C) showing the dorsal surface (right) and with the dorsal skull roof cut  
 692 away to reveal the internal sinus morphology (left). The graph (D) displays von Mises stress  
 693 values at seven locations along the mid-sagittal axis for each of the models.

694



695

696 **Figure 6.** Biting performance during bilateral biting at each tooth in the normal cranial model  
 697 (blue triangle), ‘filled-sinus’ model (red circle) and ‘crest’ model (yellow square).  
 698 Abbreviations: I, incisor; PM, premolar; M1, first molar; M2, second molar; M3, third molar;  
 699 M4, fourth molar.

700