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1 **TITLE**

2 Supraorbital morphology and social dynamics in human evolution

3

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5

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18 signaling; Paleoanthropology.

19

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24 **TEXT**

25 Uniquely, with respect to Middle Pleistocene hominins, anatomically modern humans do not  
26 possess marked browridges, and have a more vertical forehead<sup>1</sup> with mobile eyebrows that  
27 play a key role in social signalling and communication<sup>2-3</sup>. The presence and variability of  
28 browridges in archaic *Homo* and their absence in ourselves have led to debate concerning  
29 their morphogenesis and function, with two main hypotheses being put forward; that  
30 browridge morphology is the result of the spatial relationship between the orbits and the  
31 braincase<sup>4</sup>, and that browridge morphology is significantly impacted by biting mechanics<sup>5</sup>.  
32 Here we virtually manipulate browridge morphology of an archaic hominin (Kabwe 1),  
33 showing that it is much larger than the minimum required to fulfil spatial demands and that  
34 browridge size has little impact on mechanical performance during biting. Since browridge  
35 morphology in this fossil is not driven by spatial and mechanical requirements alone, the role  
36 of the supraorbital region in social communication is a potentially significant factor. We  
37 propose that conversion of the large browridges of our immediate ancestors to a more vertical  
38 frontal in modern humans allowed highly mobile eyebrows to display subtle affiliative  
39 emotions<sup>6</sup>.

40

41 Why anatomically modern humans lack, and our Middle Pleistocene ancestors possessed, a  
42 pronounced supraorbital ridge is an unresolved debate, with the focus on structural and  
43 mechanical rather than social signalling roles. The spatial hypothesis considers browridges to  
44 be “*only a reflection of the spatial relationship between two functionally unrelated cephalic*  
45 *components, the orbit and the brain case*”<sup>4</sup> (p. 281). Additionally, brain and basicranial  
46 morphology<sup>7-9</sup> and the orientation of the face relative to the cranial vault influences  
47 browridge morphology<sup>10</sup>. Browridges also scale allometrically, with individuals of bigger  
48 species growing proportionally bigger ones<sup>11,12</sup>. However, basicranial morphology, facial  
49 hafting<sup>13</sup> and facial size differ little between Kabwe 1 (*Homo heidelbergensis*, dated from 125  
50 - 300 kya b.p.<sup>14</sup>) and Neanderthals and so do not explain why the comparably large faces of  
51 near relatives such as Neanderthals do not manifest equally massive browridges. On the other  
52 hand the differences between these archaic members of our genus and modern humans in  
53 brow morphology may well relate to gracilisation, our reduced facial size and its allometric  
54 consequences.

55 Importantly, the cranial gracilization that humans underwent has also been associated with  
56 prosociality<sup>15-16</sup>. Selection for increased sociality and tolerance has been argued to be  
57 associated with evolutionary changes in cranial form (reduction of browridge and upper facial  
58 size) via changes in hormonal reactivity that have pleiotropic effects in skeletal form,  
59 physiology and behavior, termed ‘self-domestication’<sup>15-16</sup> (*sensu* Hare and colleagues<sup>17</sup>). This  
60 hypothesis finds support from several studies of non-human mammals (dogs vs. wolves,  
61 selected vs non-selected foxes, bonobos vs. chimpanzees) that were able to demonstrate that  
62 domestication and increased social tolerance trigger a set of changes that include  
63 physiological, morphological and behavioral variables (for a review see<sup>16</sup>).

64 This association between cranial gracilization, prosociality and self domestication has also  
65 been hypothesized for bonobos, who, relative to chimpanzees, present a gracile cranium<sup>18</sup>

66 with smaller browridges<sup>19</sup>, prosocial behaviour and are hypothesized as self-domesticated<sup>16-</sup>  
67 <sup>17</sup>. This thus suggests a selective trade off between expressing dynamic affiliative signals and  
68 permanent competitive signals which affects the shape and size of the cranium in general and  
69 the browridge in particular. More affiliative based social relationships in bonobos, with  
70 frequent consolation<sup>20</sup>, are associated with both a reduced browridge and greater attention to  
71 the eye area in social communication<sup>21</sup> than in common chimpanzees. Despite this  
72 association it should be noted that bonobos are significantly smaller than chimpanzees<sup>18</sup> and  
73 that, as predicted by the allometric hypothesis<sup>11</sup>, browridges are expected to be proportionally  
74 smaller.

75 For modern humans, gracilisation and reduction of the facial skeleton results in significant  
76 changes to the supraorbital region, rendering the contour between the orbits and forehead  
77 more vertical and smooth. For the frontalis belly of occipito-frontalis there are particular  
78 consequences. We note that its vector of action changes to be more vertical and for the  
79 eyebrows this means they have the potential to move vertically over a relatively larger area,  
80 and of being more readily observed and more mobile (Supplementary figure 1).

81 Alternatively the mechanical hypothesis explains larger brows in terms of resistance to  
82 masticatory loadings. While not necessarily opposed to the spatial hypothesis, it posits that  
83 mechanical loadings experienced by the skull during biting and food pre-processing<sup>5,22-25</sup>  
84 impact decisively on the morphology of the browridges<sup>5</sup>. Studies focusing on fossil  
85 hominins<sup>26</sup>, extant humans<sup>5,27-28</sup> and other extant non-human primates<sup>29-31</sup> support this  
86 hypothesis, while it has been challenged by studies of non-human primates that failed to  
87 record elevated strains in the browridge during masticatory system loading<sup>29-31</sup>.

88 In addition to the above, other hypotheses have been proposed to explain large browridges.  
89 These include protection from blows to the head<sup>32-33</sup>, protection of the eyes in aquatic

90 environments<sup>34</sup>, provision of sunshade (Barton, 1895 in <sup>35</sup>), and prevention of hair from  
91 obscuring vision<sup>36</sup>, but have not been strongly supported by evidence and so are not widely  
92 held as feasible. Another factor that could explain the morphology of the browridge of  
93 Kabwe 1 is its massive frontal sinus. However the sinus appears to have no critical  
94 mechanical function during biting<sup>37-38</sup> and grows and develops secondarily to the browridge<sup>1</sup>.

95 Thus, after several decades of research, conflicting views still exist with regard to the  
96 mechanisms that give rise to large or small browridges and their function. Hypotheses that  
97 link the development of modern human browridge morphology to changes in sociality have  
98 tended to be set aside in favour of mechanical and spatial ones, aiming to explain large  
99 browridges rather than the causes and consequences of small ones.

100 While there is strong support for a spatial explanation of larger brow ridges in archaic vs  
101 modern humans, in that facial reduction reduces the need for large brows to accommodate the  
102 orbito frontal junction, this does not explain why the browridge of Kabwe 1 is much larger  
103 than that of Neanderthals despite generally similar facial size. It may be for mechanical  
104 reasons as noted above or it may be larger for other reasons such as social communication.

105 If it can be shown that the browridges of Kabwe 1 are much larger than is demanded by  
106 spatial requirements and have no mechanical function, then explanations of the very large  
107 browridge of Kabwe 1 in terms of social communication become more tenable and the  
108 consequences of interactions of small brows in modern humans with sociality, display and  
109 social communication become a focus of interest.

110 One of the reasons that spatial and mechanical explanations of large brows in archaic humans  
111 have not been falsified is because of the impossibility of carrying out in vivo experimental  
112 manipulations. However, recent advances in virtual functional simulation offer a way  
113 forward<sup>39-41</sup>. Through virtual modeling and manipulation of the Kabwe 1 cranium we show

114 that the browridge is much larger than the minimum size required to accommodate the  
115 disjunction between orbits and frontal bone. Thus, spatial requirements not fully explain the  
116 browridge of this specimen.

117 Next, improved craniofacial resistance to masticatory loads, as a consequence of the larger-  
118 than-needed browridge, is assessed through Finite Element Analysis (FEA). This allows us to  
119 virtually manipulate the morphology of the browridge while simulating masticatory system  
120 loadings to assess the impact of variations in form on functional performance. Thus, the skull  
121 of Kabwe 1 was virtually reconstructed to restore its original morphology<sup>42</sup> and two  
122 additional versions of the model were created in which the form of the browridge was  
123 progressively reduced to the minimum required to bridge the gap between the face and  
124 neurocranium (simulating the spatial hypothesis<sup>4</sup>). FE models were then created and loaded  
125 to simulate biting to assess the impact of different browridge morphologies on the  
126 biomechanical performance of the facial skeleton of Kabwe 1. This specimen was used in this  
127 study because it presents an extremely well developed, indeed iconic, browridge.

128 Our findings show that the browridges of Kabwe 1 are larger than is needed to fulfill spatial  
129 requirements in accommodating the orbitofrontal junction and that they have no marked role  
130 in resisting masticatory loading. As such, sociality and social communication must be  
131 considered in relation to both the larger than needed browridges of Kabwe 1 and the reduced  
132 browridges and more vertical forehead of modern humans.

133

## 134 **RESULTS**

135 The browridge can be much reduced in size, but not eliminated, without creating any  
136 significant disjunction between orbits and the frontal bone. Thus, while the spatial

137 relationship between the orbits and frontal<sup>4,7</sup> partly explains the large browridge of Kabwe, it  
138 appears to greatly exceed what would be required to simply bridge the gap (spatial model).

139 Further, when models with reduced browridges are compared with that with the original  
140 browridge there are no marked intra-bite differences among models in strain magnitudes and  
141 orientations (Figures 1 and 2), whereas inter-bite comparisons show clear differences in strain  
142 magnitudes and orientations (Figure 3). Visual examination of strains experienced by the  
143 cranium indicates a slight increase in the strain magnitudes experienced by the lateral  
144 margins of the ridges and over the frontal bone with decreasing browridge size. This increase  
145 in strain magnitudes is most marked over the post-orbital sulcus of the model with the  
146 smallest browridge (Figure 2). It is unknown if these would be sufficient for biomechanical  
147 bone adaptation to occur, as predicted by the mechanostat model<sup>43</sup>. Thus it is possible that, to  
148 some extent, the growth and development of the browridge may be mechanically driven.  
149 However, the increases in strain magnitudes resulting from progressive reduction of the  
150 browridge are slight and thus unlikely to fully explain the massive browridge of Kabwe 1.

151 When considering strains experienced by the face under the same bite, only very small  
152 differences were found between models (Figure 4). The geometric morphometric analysis of  
153 changes in size and shape shows that loaded models cluster tightly by bite rather than by  
154 browridge morphology (Figure 5). Thus the vectors of deformation (changes in size and  
155 shape) connecting the unloaded and loaded models reflect almost identical modes and  
156 magnitudes of deformation in the same bite, irrespective of browridge morphology.

157

158 **DISCUSSION**



159 These results demonstrate that the browridge is significantly larger than is required to bridge  
160 the gap between orbits and the frontal. Further, changing the morphology of the browridge  
161 does not impact in any substantial way on the mode or magnitude of deformation experienced  
162 by the face during biting. As such we falsify spatial<sup>4</sup> and mechanical<sup>5,22-25</sup> hypotheses as  
163 complete explanations of the large browridge of this fossil. Rather, the findings suggest that  
164 the browridge in Kabwe 1 likely has other causes.

165 Relevant in this regard is the work of Hylander and Johnson<sup>44</sup> who have demonstrated that  
166 facial bony structures, such as the paranasal swellings in *Mandrillus sphinx*, form due to  
167 factors that are neither spatial nor mechanical. Rather they reflect social behaviour and  
168 structure; these structures underlie the vibrant soft tissue colourings of the muzzle of male  
169 mandrills, which bear an important function in social signalling and display<sup>45-46</sup>. Growth and  
170 development of the swellings in *Mandrillus leucophaeus* has been related to androgen  
171 production<sup>47</sup>. In humans the browridge is a sexually dimorphic anatomical trait<sup>48</sup> that has  
172 been identified as relevant in the perception of an individual by others<sup>49-50</sup> and its growth and  
173 development have also been related to androgen production, along with general facial sexual  
174 dimorphism<sup>51</sup>. In this regard we note that the vermiculate bone found over the browridge of  
175 Kabwe 1 presents macroscopic similarities to the bone found in the paranasal swellings of  
176 *Mandrillus*. Although vermiculate bone is less frequent in modern humans than other middle  
177 and late Pleistocene hominins<sup>32</sup>, it is more frequent in men than in women<sup>52</sup> and hence its  
178 formation is likely related to hormonal factors. It is, therefore, plausible that the morphology  
179 of the browridge of Kabwe 1 might also be related to factors such as sexually dimorphic  
180 display and social signalling. Like antlers, they are fixed, and have been hypothesized to  
181 signal dominance or aggression<sup>14</sup>.

182 Facial reduction in *H. sapiens*, which has been related to changes in brain and basicranial  
183 morphology<sup>7-9</sup>, and food pre-processing and biting mechanics<sup>5,22-25</sup>, is accompanied by

184 gracilisation of the brows, and the development of a more vertical frontal. The upper facial  
185 morphological changes found in *H. sapiens* position the frontal bone more vertically,  
186 inevitably altering the mechanical functioning of the frontalis belly of the occipito-frontalis  
187 muscle, causing contraction to raise the supraorbital skin whereas previously it would have  
188 pulled it more posteriorly over the browridge and the low, more horizontal forehead  
189 (Supplementary figure 1). Having lost a large low browridge, our ancestors gained the  
190 possibility of greater range, subtlety and visibility, of movement of the skin overlying the  
191 frontal, particularly affecting movements of the eyebrow. This suggestion is consistent with  
192 the work of Parr and colleagues<sup>53</sup>, who suggest that the absence of specific movements of the  
193 brows in chimpanzees when compared to humans may relate to the presence of large  
194 browridges (see below). Effectively these anatomical changes enhance the capacity of the  
195 frontalis muscle to move eyebrows over the frontal, a key component of social signalling and  
196 non-verbal communication in our highly socially complex species.

197 Our mobile hairy eyebrows are crucial in subtle signalling behaviours. The eye region is  
198 known to develop increasing social significance in a human evolutionary context<sup>54-55</sup>  
199 however the mobility of eyebrows specifically has received little attention. Mobile eyebrows,  
200 without the constraints of a pronounced browridge, allow subtle affiliative emotions to be  
201 expressed (Supplementary table 3), such as the rapid ‘eyebrow flash’, lasting around 1/6<sup>th</sup> of  
202 a second, found cross culturally as a sign of contact readiness and recognition<sup>56</sup>. A slow  
203 eyebrow raise is in contrast a sign of surprise and in particular social indignation<sup>57</sup>. The facial  
204 expression of sympathy, shown by pulling eyebrows up at the middle<sup>58</sup> has the advantage of  
205 removing need for the direct contact which is used to express sympathy in chimpanzees<sup>59</sup>.  
206 Subtle dynamic movements of eyebrows are also a key component of identifying  
207 trustworthiness<sup>60</sup> as well as identifying subtle indications of deception. Any constraints on  
208 muscle movements in the supraorbital region affect emotional expressions and in turn social

209 relationships, for example individuals who receive a cosmetic procedure (botox) that reduces  
210 muscle activity in the forehead and so affects eyebrow movement are less able to empathise  
211 with and identify other's emotions<sup>61</sup>.

212 When compared to our species, our nearest living relatives, chimpanzees, show minimal  
213 differences in underlying facial musculature<sup>62</sup>, however differences in facial morphology,  
214 pigmentation and other superficial characteristics impact upon the range and subtlety of their  
215 emotional expressions<sup>53,63</sup>. As in humans, chimpanzees express emotions through the  
216 stretching of skin across prominent browridges but lack subtleties in eyebrow movement and  
217 signalling that modern humans display. This is apparent through the inability of chimpanzees  
218 to move the inner and outer brows independently (activated by the medial and lateral parts of  
219 the frontalis muscle, respectively) and to present the 'brow lower' action (activated by the  
220 corrugator, depressor supercilli and procerus muscles, and significant in identifying sadness  
221 and anger in humans)<sup>53,63</sup>. The absence of these movements has been associated with the  
222 presence of a large browridge, which precludes marked saliency of these movements and thus  
223 of signalling function to conspecifics<sup>53</sup>. Similarly, other non-human primates, such as  
224 macaques<sup>64</sup>, gibbons<sup>65</sup> and orangutans<sup>66</sup>, are also unable to move their inner and outer brows  
225 independently and display brow-lowering (excluding orangutans, which are able to perform  
226 the latter). Moreover, human eyebrows overlie a vertically flatter brow and hairless forehead,  
227 hence increasing eyebrow visibility and signalling<sup>63</sup>.

228 The relative selective trade-offs between a pronounced browridge (a permanent social signal)  
229 and capacities to dynamically express affiliative pro-social emotions through highly mobile  
230 eyebrows are complex. Moreover competitive and collaborative strategies typically exist  
231 together, and vary dynamically through time and space<sup>67</sup>. Even in modern hunter-gatherers  
232 more competitive and collaborative individuals tend to spatially locate together<sup>68</sup>. We should  
233 thus expect a long period of differing facial forms, reflecting differing social strategies, both

234 within and between groups before the selective advantages of expressing complex pro-social  
235 emotions becomes stable. This pattern seems typical of archaic humans, with substantial  
236 variability in the definition of browridges amongst early modern humans at Jebel Irhoud for  
237 example<sup>69</sup>.

238

239

240 **METHODS**

241 The Kabwe 1 cranium reconstruction<sup>70</sup> was based on a CT scan provided by the Natural  
242 History Museum, London (courtesy of *Robert Kruszynski*). After reconstruction, two  
243 additional models were created in which the morphology of the browridge was the only  
244 anatomical region modified. The models were then directly converted into voxel based finite  
245 element models and used to simulate three different bites (left central incisor, left second  
246 premolar, left second molar) to assess the biomechanical performance of the facial skeleton  
247 during these bites.

248

249 Skull reconstruction and model creation

250 A complete description of the reconstruction of Kabwe 1 is presented by Godinho and  
251 O'Higgins<sup>70</sup>. Thus, here we briefly report the reconstruction. Automated, semi-automated and  
252 manual segmentation of the cranium was performed using Avizo<sup>®</sup> (version 7.0). Manual  
253 segmentation was required to remove sedimentary matrix present in the maxillary and  
254 sphenoidal sinuses. When possible, reconstruction of missing parts was performed by  
255 mirroring preserved contralateral elements and warping them to the existing structures. When  
256 small gaps were present, Geomagic<sup>®</sup> (Studio 2011) was used to fill them using the surface of  
257 surrounding structures as the reference for interpolation. Portions of a CT reconstruction of a  
258 cadaveric *Homo sapiens* skull were used to reconstruct part of the occipital and missing tooth  
259 crowns for which there were no antimeres preserved.

260 Once the reconstruction was complete (model 1), the frontal sinuses were infilled to allow  
261 later excavation of this region to produce variant morphologies. Analysis of the impact of  
262 infilling the sinus in model 1 showed that the surface strains over the brow-ridge and

263 elsewhere in the cranium did not differ significantly between the models with hollow and  
264 filled frontal sinus<sup>38</sup>. The morphology of the brow-ridge was manipulated, using Geomagic<sup>®</sup>,  
265 by decreasing its size (model 2) and creating a post orbital sulcus in model 3 (Figure 1).  
266 Voxel based finite element models were then generated by direct conversion using the  
267 vox2vec software.

268

## 269 Constraints

270 Identical constraints were applied to all models using the FEA software tool, VoxFE<sup>71</sup>. The  
271 models were constrained at the temporo-mandibular joints (laterally, superoinferiorly and  
272 anteroposteriorly) and a third constraint was applied at the simulated bite point  
273 (superoinferiorly) in each of the biting simulations (left central incisor, left second pre-molar,  
274 left second molar).

275

## 276 Material properties

277 Following prior sensitivity studies that showed only local effects of differentiating the  
278 material properties of teeth and the surrounding bone these were assigned the same material  
279 properties in all the models used in this study. Further, sensitivity analyses that assessed the  
280 effect of model simplifications in a human cadaveric cranium<sup>72</sup>, a cranium of *Macaca*  
281 *fascicularis*<sup>73</sup> and a varanoid lizard mandible<sup>74</sup> show that infilling of trabecular bone stiffens  
282 the skull and so reduces strain magnitudes but that the distribution of regions of high and low  
283 strain and of global modes (rather than magnitudes) of deformation are not much affected.  
284 Allocating teeth the same material properties as bone has the effect of locally reducing strain  
285 gradients in the alveolar region, with little effect elsewhere. This is relevant to the present

286 study because trabecular bone is neither well enough preserved nor imaged at sufficient  
287 resolution to accurately represent it in a finite element model and the dentition is incomplete  
288 and required reconstruction. As such, in all models, trabecular bone and teeth were not  
289 separately represented and were allocated the same material properties as cortical bone.  
290 Based on prior sensitivity analyses we expect this to have little impact on the mode of  
291 deformation of the loaded cranium, but to reduce the degree to which it deforms.

292 Cortical bone, trabecular bone and the teeth were allocated isotropic properties, with a  
293 Young's modulus of 17 Gpa. and a Poisson's ration of 0.3. The modulus of elasticity was  
294 derived from nanoindentation studies of cortical bone in a cadaveric *Homo sapiens* skull<sup>72</sup>.  
295 The resulting value of 17 Gpa is within the range of values found in previous studies<sup>75-76</sup>.

296

#### 297 Muscle loads

298 Loads were applied to the model to represent the actions of six muscles active during biting:  
299 right and left temporalis, right and left masseter, right and left medial pterygoid. Absence of  
300 the mandible precludes direct estimation of the direction of muscle force vectors and  
301 estimation using bony proxies of anatomical cross sectional areas (and so maximum forces)  
302 of muscles that attach to the mandible (masseter and medial pterygoid). However, given that  
303 three versions of the same model with identical loads and constraints are to be compared, it  
304 matters little that applied muscle force vectors approximate rather than replicate  
305 physiological loadings. Significantly more important is that these forces are identical between  
306 models and so do not, in themselves, produce differences in strains (modes of deformation)  
307 between models. As such, the maximum estimated muscle forces estimated from a *Homo*  
308 *sapiens* cadaveric head were applied identically to each model<sup>72</sup> (Supplementary table 1). The  
309 directions of muscle force vectors were estimated by scaling a *Homo neanderthalensis*

310 mandible (Tabun 1 specimen) to the Kabwe 1 skull. These directions were applied to all  
311 models and simulations. While this mandible is not from the same fossil it provides a  
312 reasonable estimate of muscle vectors. The impact of error in the estimation of the orientation  
313 of the muscle vectors was assessed in a sensitivity analysis in which muscle vectors were  
314 varied through 5° anteroposteriorly and mediolaterally. Results showed that regions of high  
315 and low strain varied very little in location (Supplementary figure 3) while the average  
316 magnitude of strains varied from ~2% in mediolateral manipulation to ~5% in anteroposterior  
317 changes (Supplementary table 4).

318

#### 319 Model solution and analysis

320 The finite element models 1-3 were solved using VoxFE<sup>71</sup>. The resulting deformations of the  
321 finite element models were compared through (1) visual assessment of strain magnitudes and  
322 directions of maximum ( $\epsilon_1$ ) and minimum ( $\epsilon_3$ ) principal strains, (2) plotting of  $\epsilon_1$  and  $\epsilon_3$  at  
323 30 nodes (points) located in the facial skeleton, common to all models (Supplementary figure  
324 2), (3) an analysis of changes in size and shape between loaded and unloaded models of a  
325 configuration of 33 landmarks (points) from the whole cranium (Supplementary figure 3 and  
326 supplementary table 2). The size and shape analysis employs geometric morphometrics to  
327 compare changes in size and shape between the unloaded and loaded models. This consists of  
328 an initial registration step comprising scaling to unit size and then translation of landmark  
329 configurations to their centroids, with subsequent rotation to minimise the sum of squared  
330 distances between each scaled, translated configuration and the mean configuration. This is  
331 followed by rescaling of each configuration to its original centroid size and by a PCA of the  
332 resulting size and shape coordinates<sup>77-78</sup>. This analysis leads to a quantitative comparison of



333 global model deformations (changes in size and shape) in terms of the directions (modes) and  
334 magnitudes (degree or extent) of deformation arising from loading.

335

336 Data availability statement

337 Data subject to third party restrictions.

338 The data that support the findings of this study are available from the authors but restrictions

339 apply to the availability of these data, which were used under license for the current study,

340 and so are not publicly available. Data are however available from the authors upon

341 reasonable request and with permission of the Centre for Human Evolution Studies, The

342 Natural History Museum, London.

343

344

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570

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579

580 **AUTHOR CONTRIBUTIONS**

581 RMG, PS and PO'H designed the experiment. RMG performed the simulations. RMG, PS  
582 and POH wrote the manuscript.

583

584 **COMPETING INTERESTS**

585 The authors have no competing financial interests.

586

587 **FIGURE LEGENDS**

588

589 Figure 1: Models 1 - 3. Model 1 represents the original reconstruction of Kabwe 1; model 2  
590 represents the reconstruction of Kabwe 1 with a reduced browridge; model 3 represents the  
591 reconstruction of Kabwe with a reduced browridge and a *post-orbital* sulcus.

592

593 Figure 2: Strain contour plots of the biting simulations. Maximum principal strains ( $\epsilon_1$ ) are  
594 represented in columns 3-5, and minimum principal strains ( $\epsilon_3$ ) in columns 5-7. Model 1 is  
595 represented in rows 1, 4 and 7; model 2 in rows 2, 5 and 8; model 3 in rows 3, 6 and 9) under  
596 the different simulated bites.

597

598 Figure 3: Strain contour plots and strain directions of  $\epsilon_1$  (rows 1, 3 and 5) and  $\epsilon_3$  (rows 2, 4  
599 and 6) over the maxilla (see inset frontal view for location) in the different models (model 1  
600 in left column; model 2 in middle column; model 3 in right column) under the different bites  
601 simulated. The bottom left inset shows the anatomical region included in vector plots.

602

603 Figure 4: Plots of facial strains experienced by the models at 30 anatomical points.

604

605 Figure 5: Size and shape Principal Components Analysis (PCA) of the unloaded and loaded  
606 models in the three different simulated bites.

607

609

610

**MODEL 1**



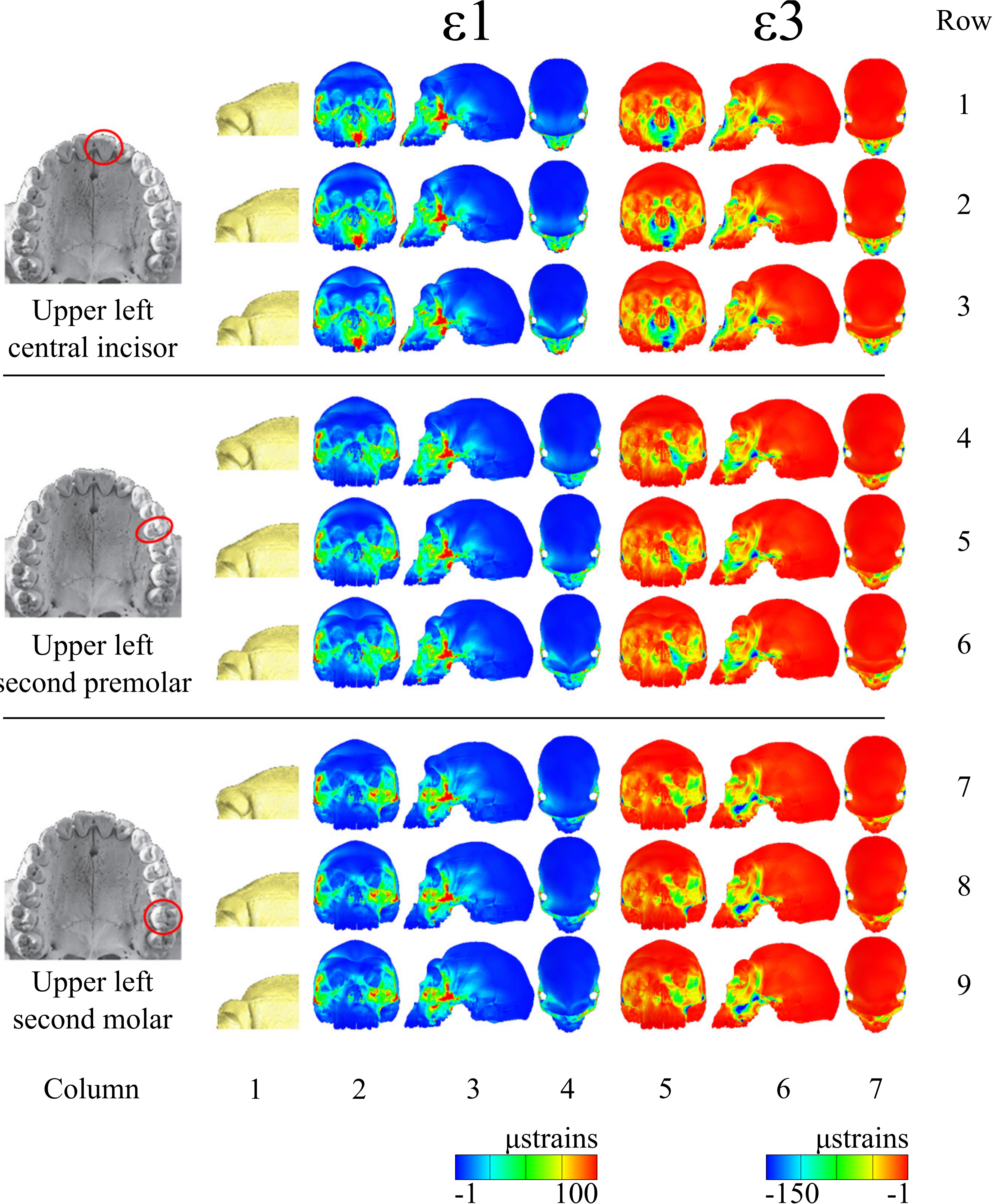
**MODEL 2**

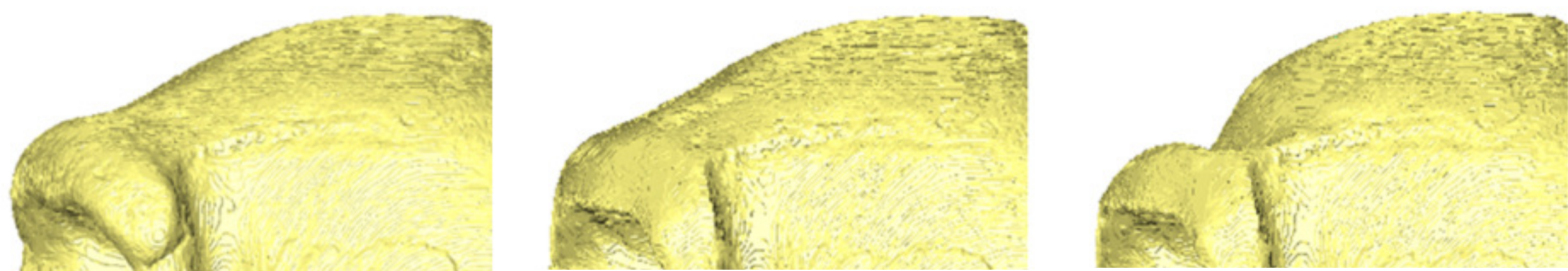


**MODEL 3**

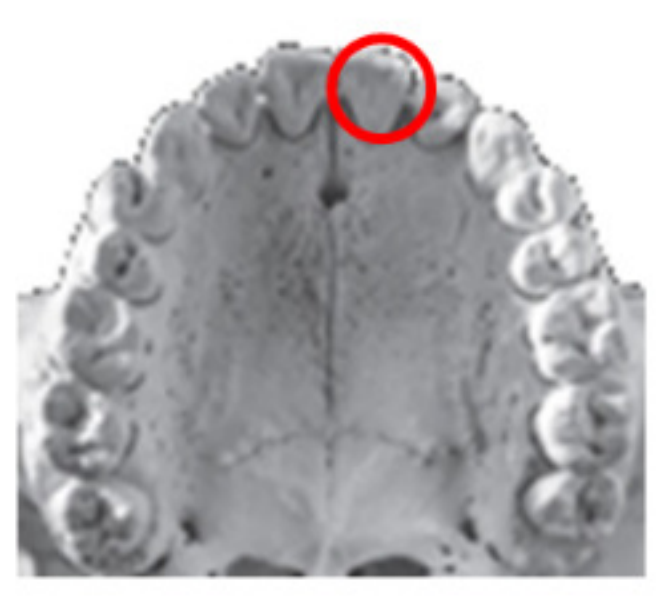


1 cm.

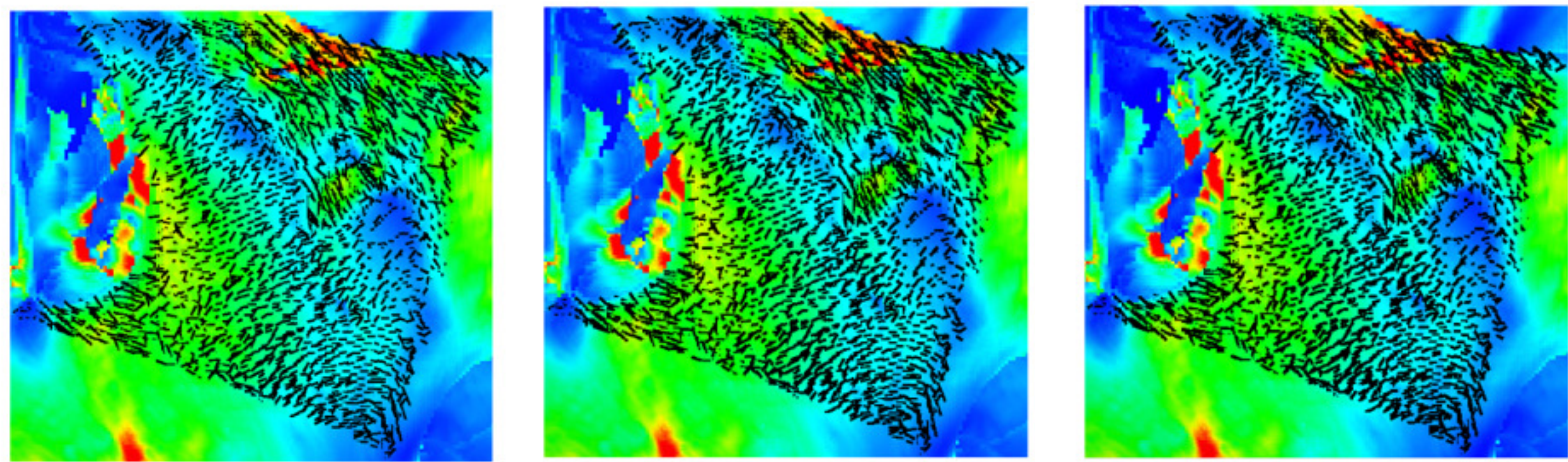




Row



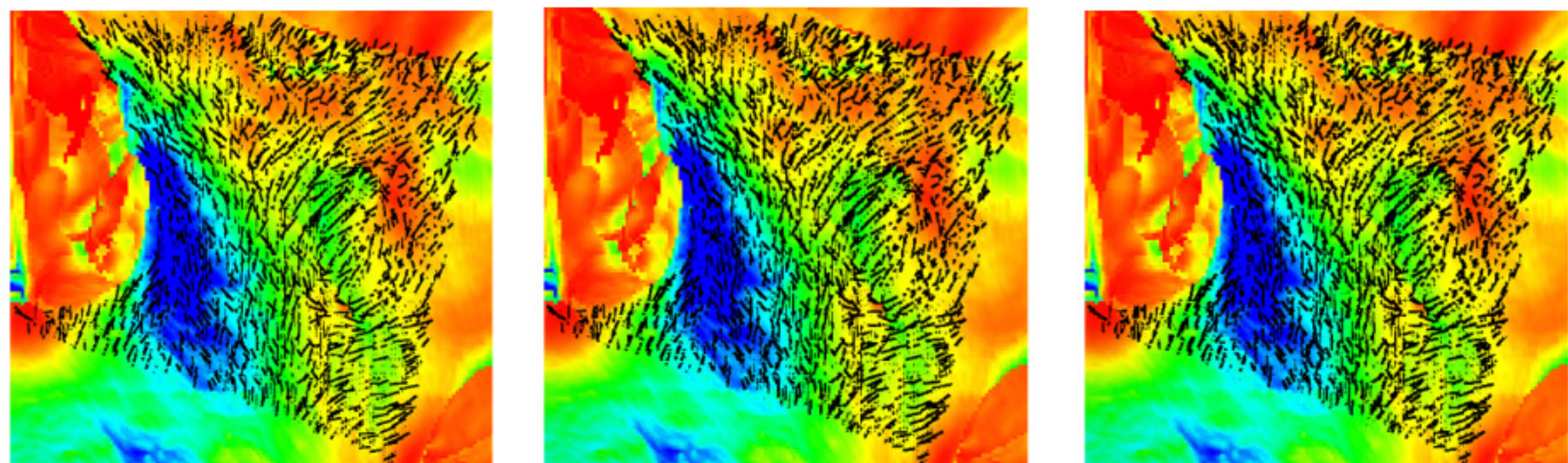
$\epsilon_1$



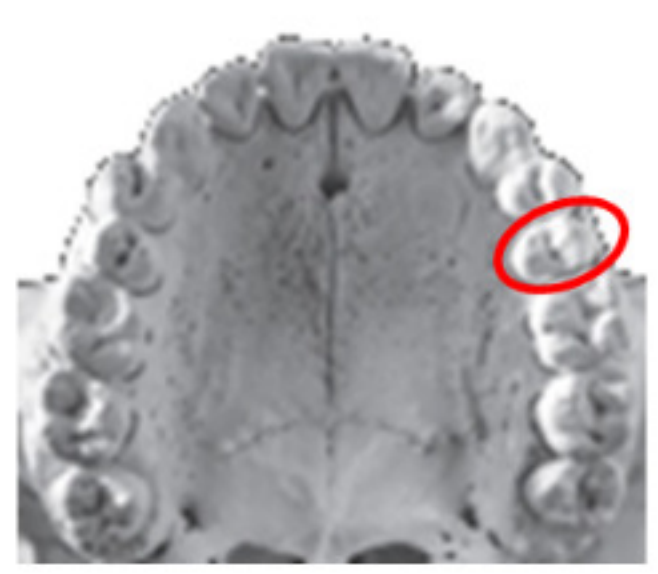
1

Upper left central incisor

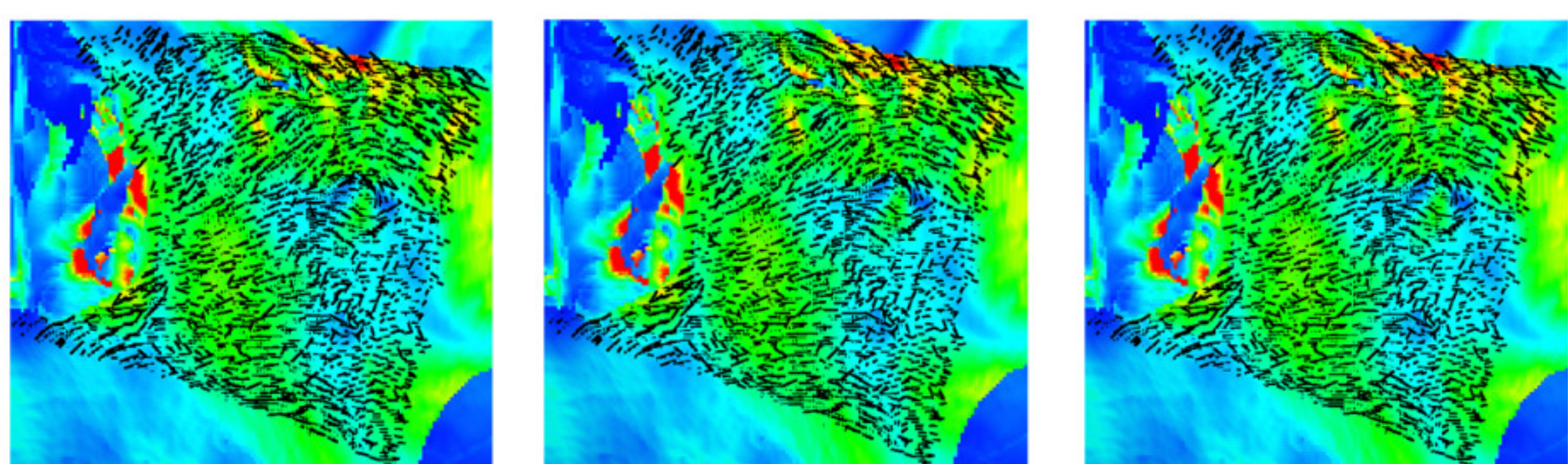
$\epsilon_3$



2



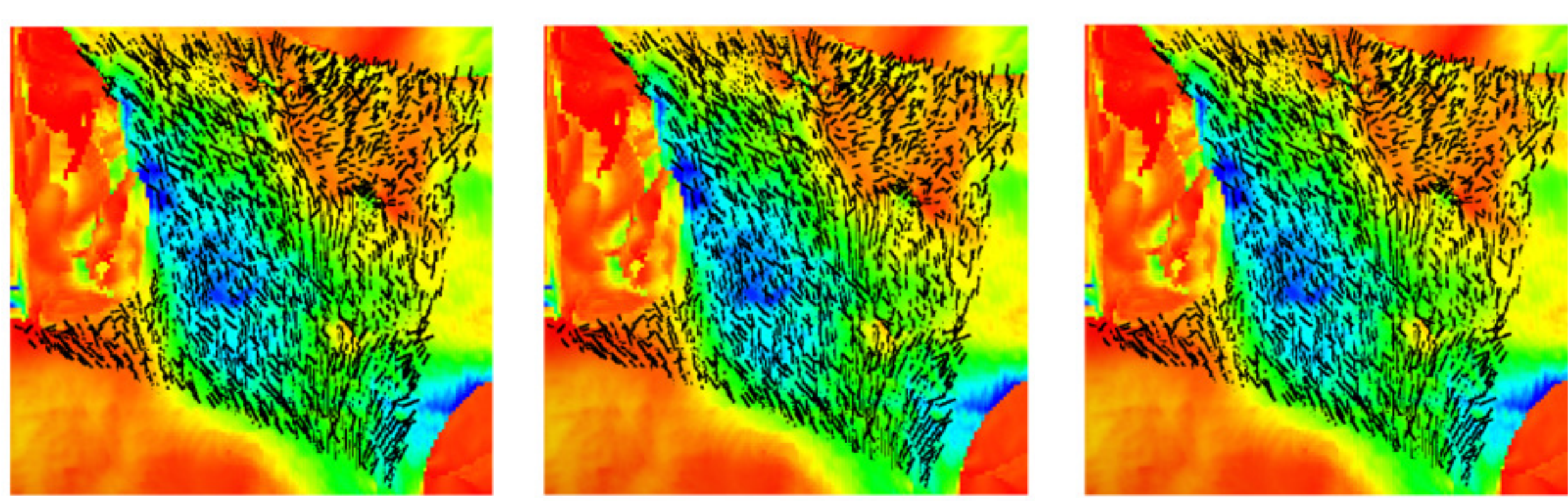
$\epsilon_1$



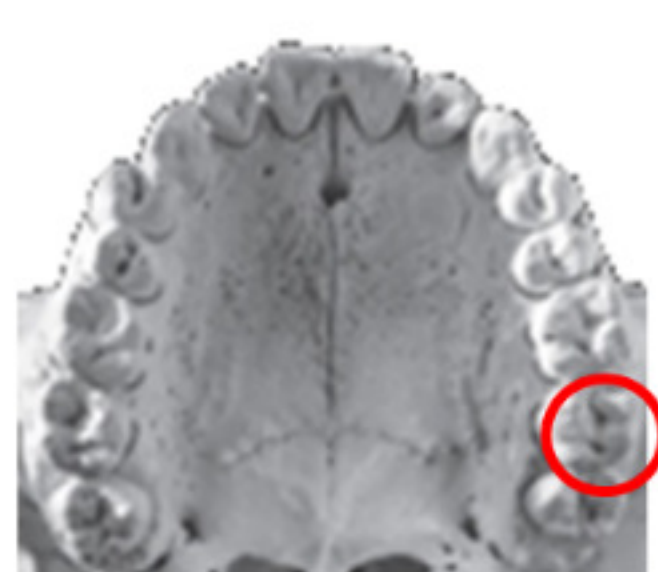
3

Upper left second premolar

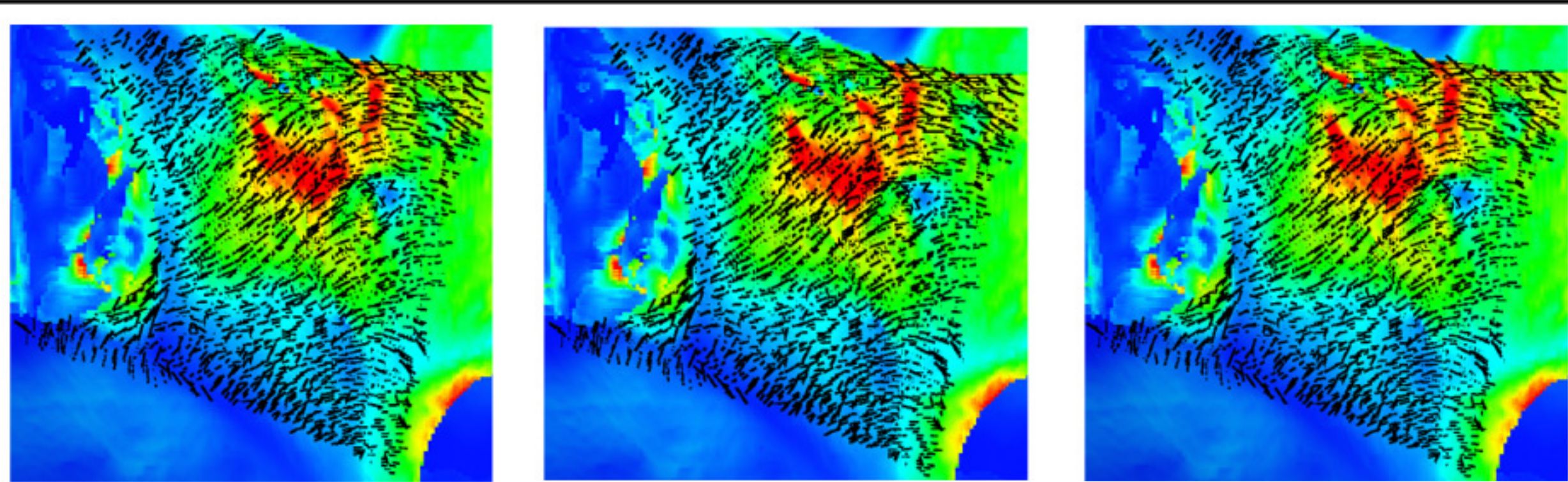
$\epsilon_3$



4



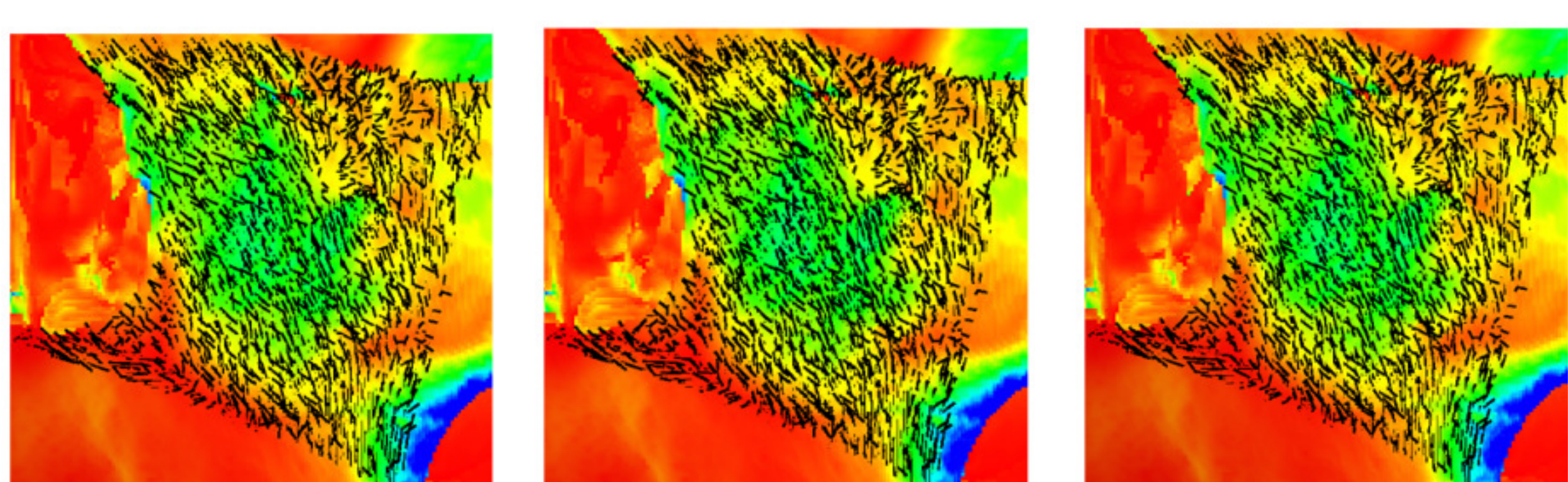
$\epsilon_1$



5

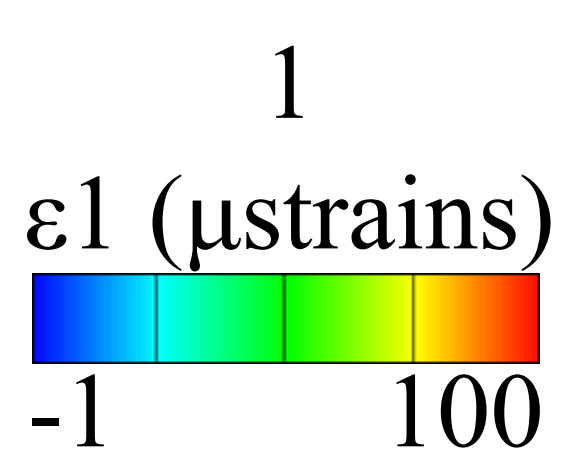
Upper left second molar

$\epsilon_3$

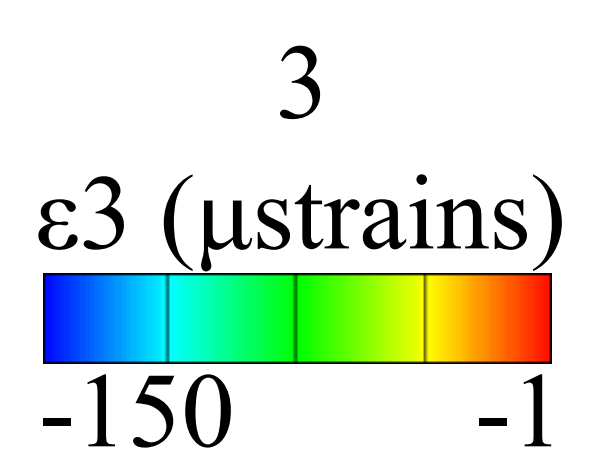


6

Column

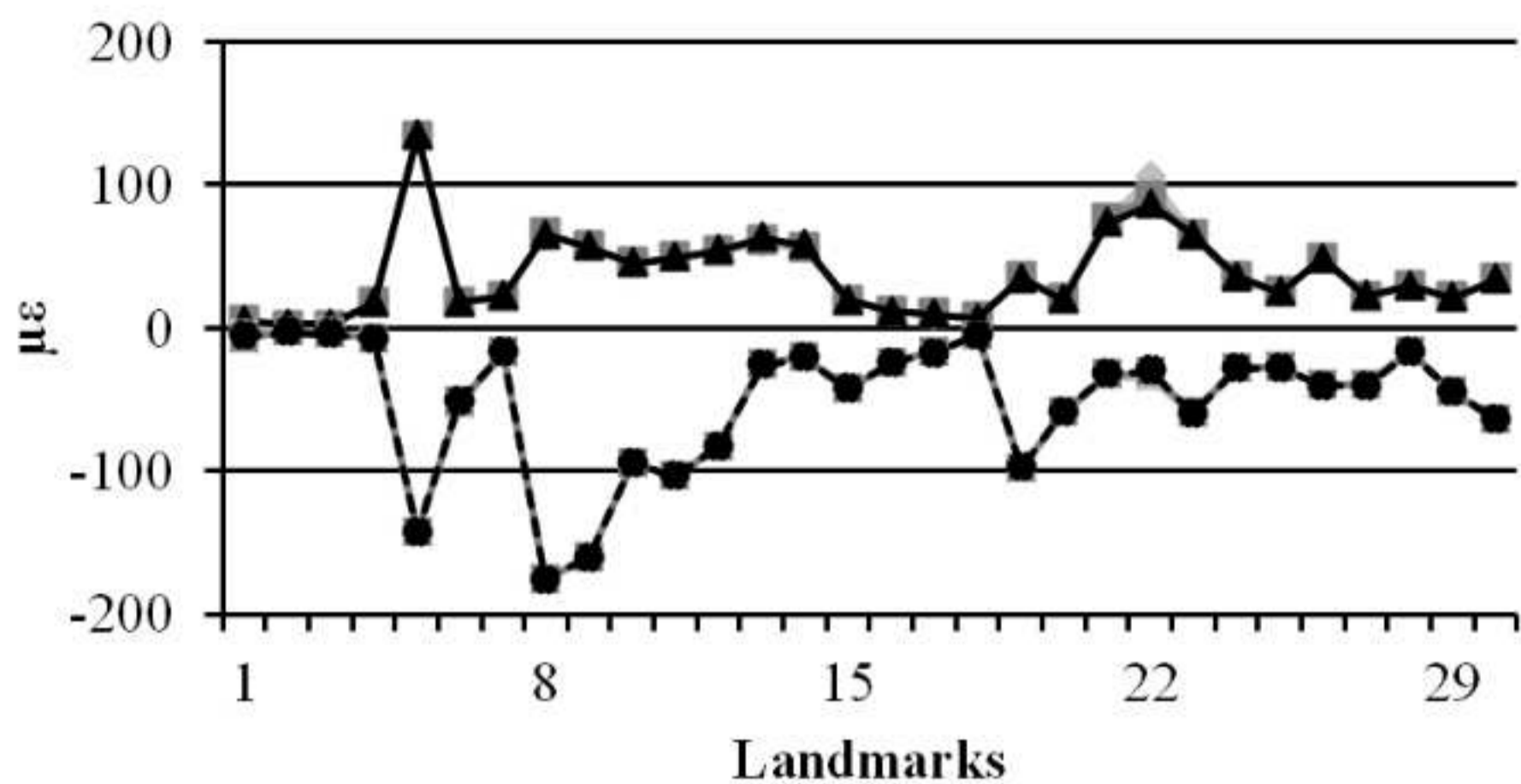


2

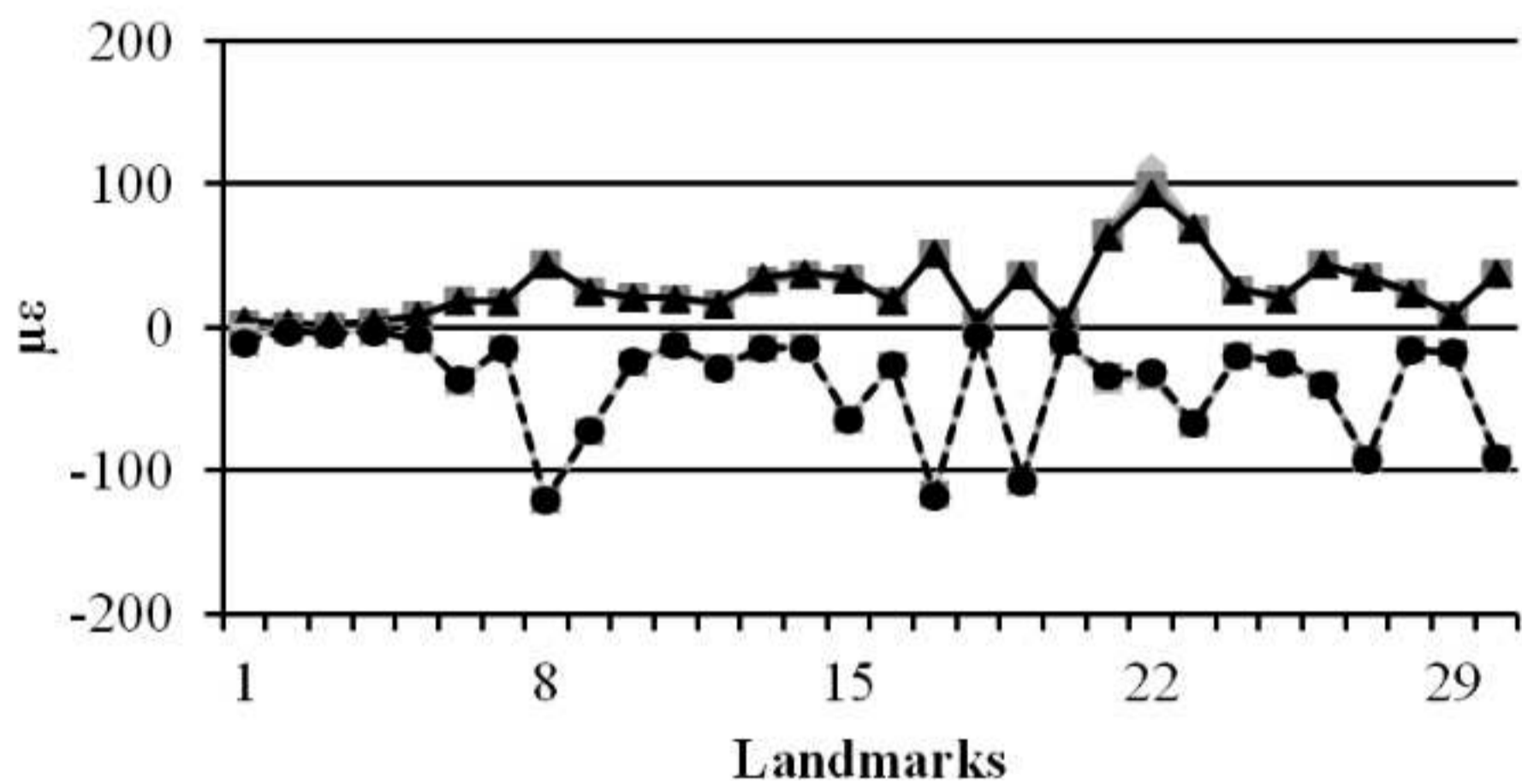




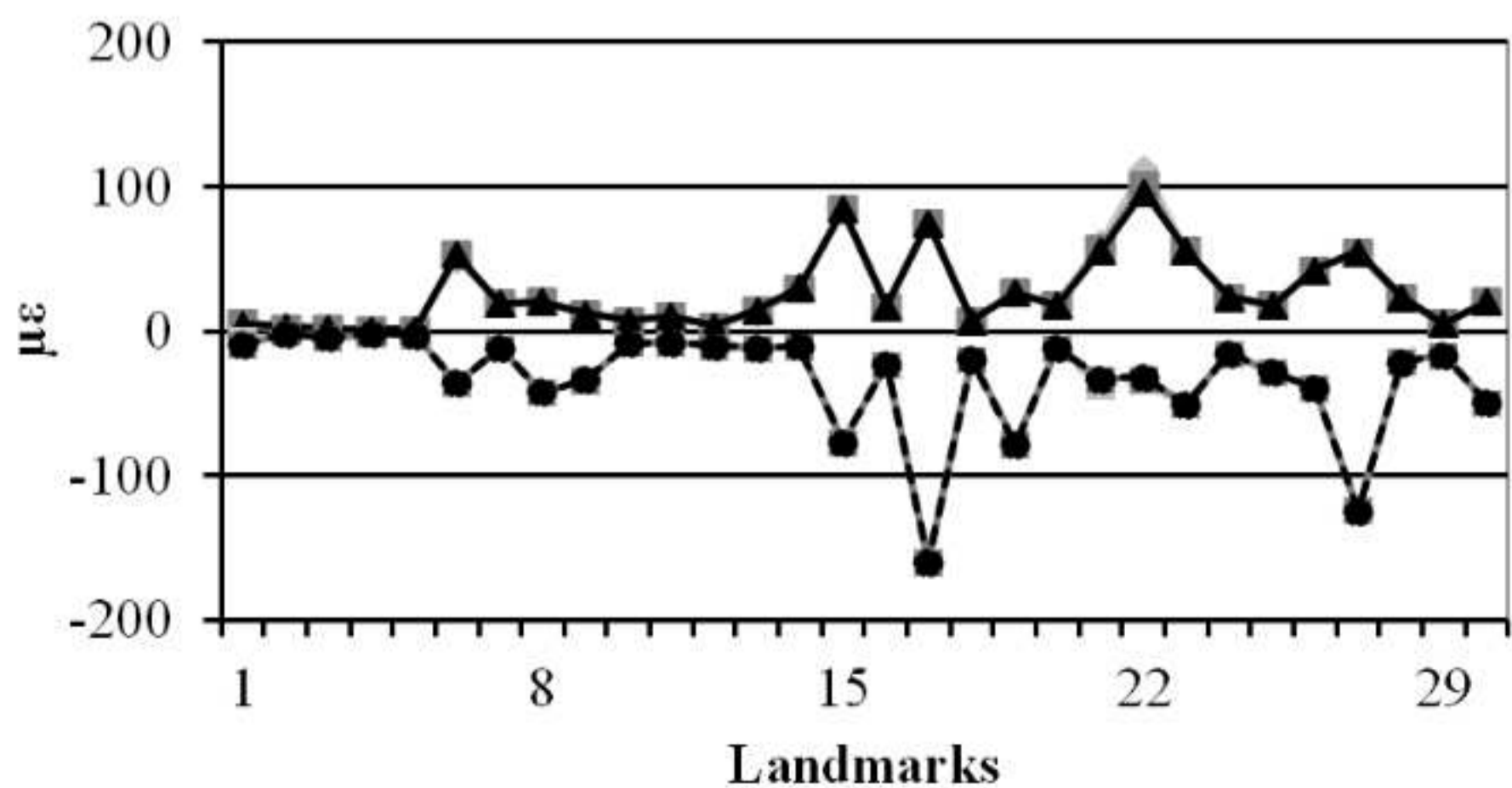
### Upper left incisor 1 bite



### Upper left premolar 2 bite

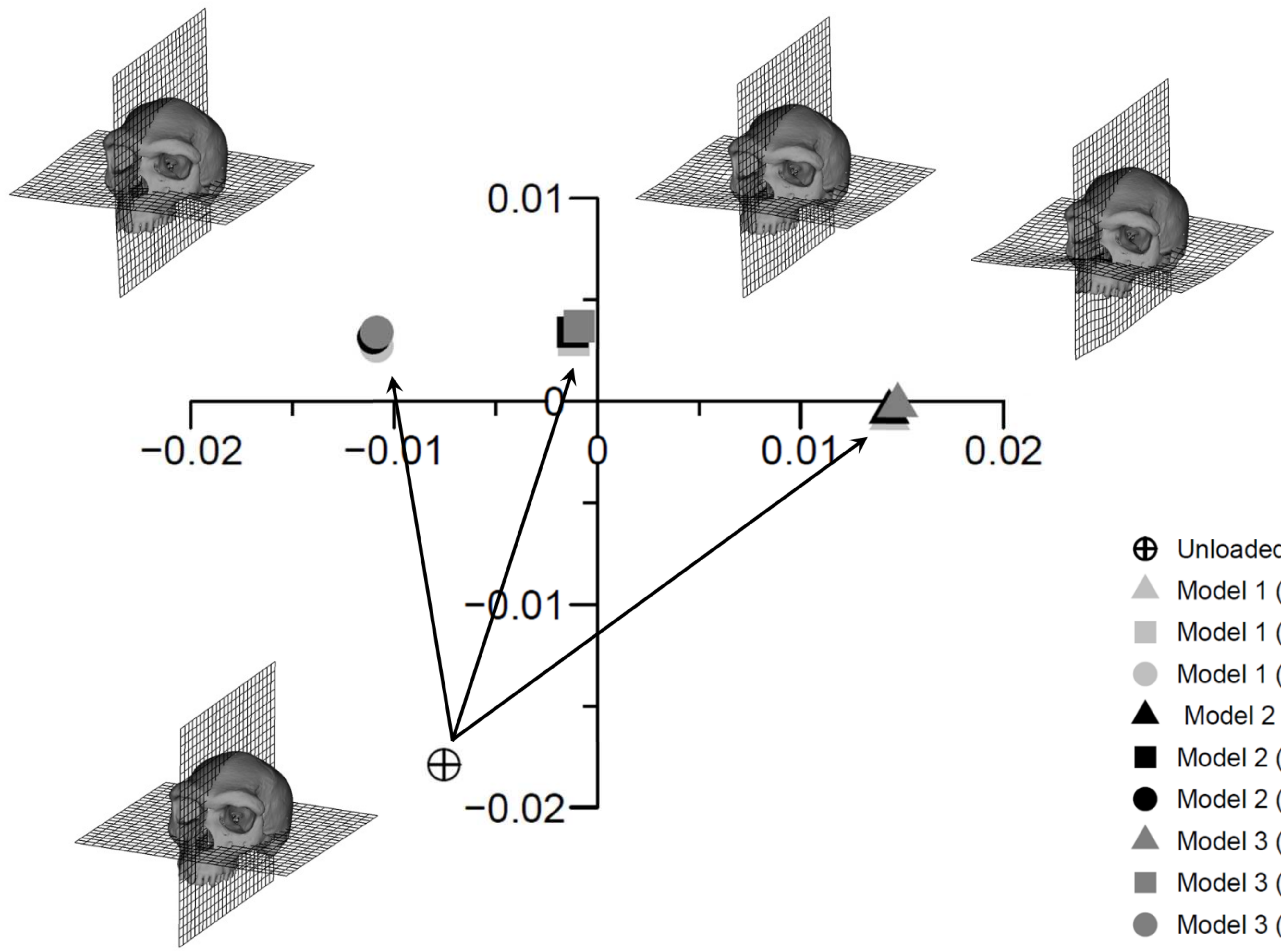


### Upper left molar 2 bite



PC 1 (70.9%)

PC 2 (26.0%)



- ⊕ Unloaded
- ▲ Model 1 (LI1)
- Model 1 (LPM2)
- Model 1 (LM2)
- ▲ Model 2 (LI1)
- Model 2 (LPM2)
- Model 2 (LM2)
- ▲ Model 3 (LI1)
- Model 3 (LPM2)
- Model 3 (LM2)