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1 **TITLE**

2 Supraorbital morphology and social dynamics in human evolution

3

4 Ricardo Miguel Godinho (corresponding author)*^{a, b}, Penny Spikins^c, Paul O'Higgins^a

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6 a) Department of Archaeology and Hull York Medical School, the University of York,
7 York, YO10 5DD, UK.

8 b) Interdisciplinary Center for Archaeology and Evolution of Human Behaviour
9 (ICArHEB), Faculdade das Ciências Humanas e Sociais, Universidade do Algarve,
10 Campus Gambelas, 8005-139, Faro, Portugal

11 c) Department of Archaeology, the University of York, York, YO10 5DD, UK.

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18 signaling; Paleoanthropology.

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20 ¹ Corresponding author; ricardomiguelgodinho@gmail.com

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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 forehead¹ with mobile eyebrows that
27 play a key role in social signalling and communication²⁻³. 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 braincase⁴, and that browridge morphology is significantly impacted by biting mechanics⁵.
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 emotions⁶.

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*”⁴ (p. 281). Additionally, brain and basicranial
46 morphology⁷⁻⁹ and the orientation of the face relative to the cranial vault influences
47 browridge morphology¹⁰. Browridges also scale allometrically, with individuals of bigger
48 species growing proportionally bigger ones^{11, 12}. However, basicranial morphology, facial
49 hafting¹³ and facial size differ little between Kabwe 1 (*Homo heidelbergensis*, dated from 125
50 - 300 kya b.p.¹⁴) 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 prosociality¹⁵⁻¹⁶. 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’¹⁵⁻¹⁶ (*sensu* Hare and colleagues¹⁷). 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 see¹⁶).

64 This association between cranial gracilization, prosociality and self domestication has also
65 been hypothesized for bonobos, who, relative to chimpanzees, present a gracile cranium¹⁸

66 with smaller browridges¹⁹, prosocial behaviour and are hypothesized as self-domesticated¹⁶⁻
67 ¹⁷. 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 consolation²⁰, are associated with both a reduced browridge and greater attention to
71 the eye area in social communication²¹ than in common chimpanzees. Despite this
72 association it should be noted that bonobos are significantly smaller than chimpanzees¹⁸ and
73 that, as predicted by the allometric hypothesis¹¹, 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^{5,22-25}
84 impact decisively on the morphology of the browridges⁵. Studies focusing on fossil
85 hominins²⁶, extant humans^{5,27-28} and other extant non-human primates²⁹⁻³¹ 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 loading²⁹⁻³¹.

88 In addition to the above, other hypotheses have been proposed to explain large browridges.
89 These include protection from blows to the head³²⁻³³, protection of the eyes in aquatic

90 environments³⁴, provision of sunshade (Barton, 1895 in ³⁵), and prevention of hair from
91 obscuring vision³⁶, 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 biting³⁷⁻³⁸ and grows and develops secondarily to the browridge¹.

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 forward³⁹⁻⁴¹. Through virtual modeling and manipulation of the Kabwe 1 cranium we show

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

Next, improved craniofacial resistance to masticatory loads, as a consequence of the larger-than-needed browridge, is assessed through Finite Element Analysis (FEA). This allows us to virtually manipulate the morphology of the browridge while simulating masticatory system loadings to assess the impact of variations in form on functional performance. Thus, the skull of Kabwe 1 was virtually reconstructed to restore its original morphology⁴² and two additional versions of the model were created in which the form of the browridge was progressively reduced to the minimum required to bridge the gap between the face and neurocranium (simulating the spatial hypothesis⁴). FE models were then created and loaded to simulate biting to assess the impact of different browridge morphologies on the biomechanical performance of the facial skeleton of Kabwe 1. This specimen was used in this study because it presents an extremely well developed, indeed iconic, browridge.

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

RESULTS

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

relationship between the orbits and frontal^{4,7} partly explains the large browridge of Kabwe, it appears to greatly exceed what would be required to simply bridge the gap (spatial model).

Further, when models with reduced browridges are compared with that with the original browridge there are no marked intra-bite differences among models in strain magnitudes and orientations (Figures 1 and 2), whereas inter-bite comparisons show clear differences in strain magnitudes and orientations (Figure 3). Visual examination of strains experienced by the cranium indicates a slight increase in the strain magnitudes experienced by the lateral margins of the ridges and over the frontal bone with decreasing browridge size. This increase in strain magnitudes is most marked over the post-orbital sulcus of the model with the smallest browridge (Figure 2). It is unknown if these would be sufficient for biomechanical bone adaptation to occur, as predicted by the mechanostat model⁴³. Thus it is possible that, to some extent, the growth and development of the browridge may be mechanically driven. However, the increases in strain magnitudes resulting from progressive reduction of the browridge are slight and thus unlikely to fully explain the massive browridge of Kabwe 1.

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

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 spatial⁴ and mechanical^{5,22-25} 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 Johnson⁴⁴ 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 display⁴⁵⁻⁴⁶. Growth and
170 development of the swellings in *Mandrillus leucophaeus* has been related to androgen
171 production⁴⁷. In humans the browridge is a sexually dimorphic anatomical trait⁴⁸ that has
172 been identified as relevant in the perception of an individual by others⁴⁹⁻⁵⁰ and its growth and
173 development have also been related to androgen production, along with general facial sexual
174 dimorphism⁵¹. 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 hominins³², it is more frequent in men than in women⁵² 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 aggression¹⁴.

182 Facial reduction in *H. sapiens*, which has been related to changes in brain and basicranial
183 morphology⁷⁻⁹, and food pre-processing and biting mechanics^{5,22-25}, 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 colleagues⁵³, 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 context⁵⁴⁻⁵⁵
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 1/6th of
202 a second, found cross culturally as a sign of contact readiness and recognition⁵⁶. A slow
203 eyebrow raise is in contrast a sign of surprise and in particular social indignation⁵⁷. The facial
204 expression of sympathy, shown by pulling eyebrows up at the middle⁵⁸ has the advantage of
205 removing need for the direct contact which is used to express sympathy in chimpanzees⁵⁹.
206 Subtle dynamic movements of eyebrows are also a key component of identifying
207 trustworthiness⁶⁰ 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

relationships, for example individuals who receive a cosmetic procedure (botox) that reduces muscle activity in the forehead and so affects eyebrow movement are less able to empathise with and identify other's emotions⁶¹.

When compared to our species, our nearest living relatives, chimpanzees, show minimal differences in underlying facial musculature⁶², however differences in facial morphology, pigmentation and other superficial characteristics impact upon the range and subtlety of their emotional expressions^{53,63}. As in humans, chimpanzees express emotions through the stretching of skin across prominent browridges but lack subtleties in eyebrow movement and signalling that modern humans display. This is apparent through the inability of chimpanzees to move the inner and outer brows independently (activated by the medial and lateral parts of the frontalis muscle, respectively) and to present the 'brow lower' action (activated by the corrugator, depressor supercilli and procerus muscles, and significant in identifying sadness and anger in humans)^{53,63}. The absence of these movements has been associated with the presence of a large browridge, which precludes marked saliency of these movements and thus of signalling function to conspecifics⁵³. Similarly, other non-human primates, such as macaques⁶⁴, gibbons⁶⁵ and orangutans⁶⁶, are also unable to move their inner and outer brows independently and display brow-lowering (excluding orangutans, which are able to perform the latter). Moreover, human eyebrows overlie a vertically flatter brow and hairless forehead, hence increasing eyebrow visibility and signalling⁶³.

The relative selective trade-offs between a pronounced browridge (a permanent social signal) and capacities to dynamically express affiliative pro-social emotions through highly mobile eyebrows are complex. Moreover competitive and collaborative strategies typically exist together, and vary dynamically through time and space⁶⁷. Even in modern hunter-gatherers more competitive and collaborative individuals tend to spatially locate together⁶⁸. We should 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 example⁶⁹.

238

239

240 **METHODS**

241 The Kabwe 1 cranium reconstruction⁷⁰ 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'Higgins⁷⁰. Thus, here we briefly report the reconstruction. Automated, semi-automated and
252 manual segmentation of the cranium was performed using Avizo[®] (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[®] (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

elsewhere in the cranium did not differ significantly between the models with hollow and filled frontal sinus³⁸. The morphology of the brow-ridge was manipulated, using Geomagic[®], by decreasing its size (model 2) and creating a post orbital sulcus in model 3 (Figure 1). Voxel based finite element models were then generated by direct conversion using the vox2vec software.

Constraints

Identical constraints were applied to all models using the FEA software tool, VoxFE⁷¹. The models were constrained at the temporo-mandibular joints (laterally, superoinferiorly and anteroposteriorly) and a third constraint was applied at the simulated bite point (superoinferiorly) in each of the biting simulations (left central incisor, left second pre-molar, left second molar).

Material properties

Following prior sensitivity studies that showed only local effects of differentiating the material properties of teeth and the surrounding bone these were assigned the same material properties in all the models used in this study. Further, sensitivity analyses that assessed the effect of model simplifications in a human cadaveric cranium⁷², a cranium of *Macaca fascicularis*⁷³ and a varanoid lizard mandible⁷⁴ show that infilling of trabecular bone stiffens the skull and so reduces strain magnitudes but that the distribution of regions of high and low strain and of global modes (rather than magnitudes) of deformation are not much affected. Allocating teeth the same material properties as bone has the effect of locally reducing strain gradients in the alveolar region, with little effect elsewhere. This is relevant to the present

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

Cortical bone, trabecular bone and the teeth were allocated isotropic properties, with a Young's modulus of 17 Gpa. and a Poisson's ratio of 0.3. The modulus of elasticity was derived from nanoindentation studies of cortical bone in a cadaveric *Homo sapiens* skull⁷². The resulting value of 17 Gpa is within the range of values found in previous studies⁷⁵⁻⁷⁶.

Muscle loads

Loads were applied to the model to represent the actions of six muscles active during biting: right and left temporalis, right and left masseter, right and left medial pterygoid. Absence of the mandible precludes direct estimation of the direction of muscle force vectors and estimation using bony proxies of anatomical cross sectional areas (and so maximum forces) of muscles that attach to the mandible (masseter and medial pterygoid). However, given that three versions of the same model with identical loads and constraints are to be compared, it matters little that applied muscle force vectors approximate rather than replicate physiological loadings. Significantly more important is that these forces are identical between models and so do not, in themselves, produce differences in strains (modes of deformation) between models. As such, the maximum estimated muscle forces estimated from a *Homo sapiens* cadaveric head were applied identically to each model⁷² (Supplementary table 1). The directions of muscle force vectors were estimated by scaling a *Homo neanderthalensis*

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

Model solution and analysis

The finite element models 1-3 were solved using VoxFE⁷¹. The resulting deformations of the finite element models were compared through (1) visual assessment of strain magnitudes and directions of maximum (ϵ_1) and minimum (ϵ_3) principal strains, (2) plotting of ϵ_1 and ϵ_3 at 30 nodes (points) located in the facial skeleton, common to all models (Supplementary figure 2), (3) an analysis of changes in size and shape between loaded and unloaded models of a configuration of 33 landmarks (points) from the whole cranium (Supplementary figure 3 and supplementary table 2). The size and shape analysis employs geometric morphometrics to compare changes in size and shape between the unloaded and loaded models. This consists of an initial registration step comprising scaling to unit size and then translation of landmark configurations to their centroids, with subsequent rotation to minimise the sum of squared distances between each scaled, translated configuration and the mean configuration. This is followed by rescaling of each configuration to its original centroid size and by a PCA of the resulting size and shape coordinates⁷⁷⁻⁷⁸. This analysis leads to a quantitative comparison of

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

Data availability statement

Data subject to third party restrictions.

The data that support the findings of this study are available from the authors but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of the Centre for Human Evolution Studies, The Natural History Museum, London.

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AUTHOR CONTRIBUTIONS

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

COMPETING INTERESTS

The authors have no competing financial interests.

FIGURE LEGENDS

Figure 1: Models 1 - 3. Model 1 represents the original reconstruction of Kabwe 1; model 2 represents the reconstruction of Kabwe 1 with a reduced browridge; model 3 represents the 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 (ϵ_1) are
594 represented in columns 3-5, and minimum principal strains (ϵ_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 ϵ_1 (rows 1, 3 and 5) and ϵ_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



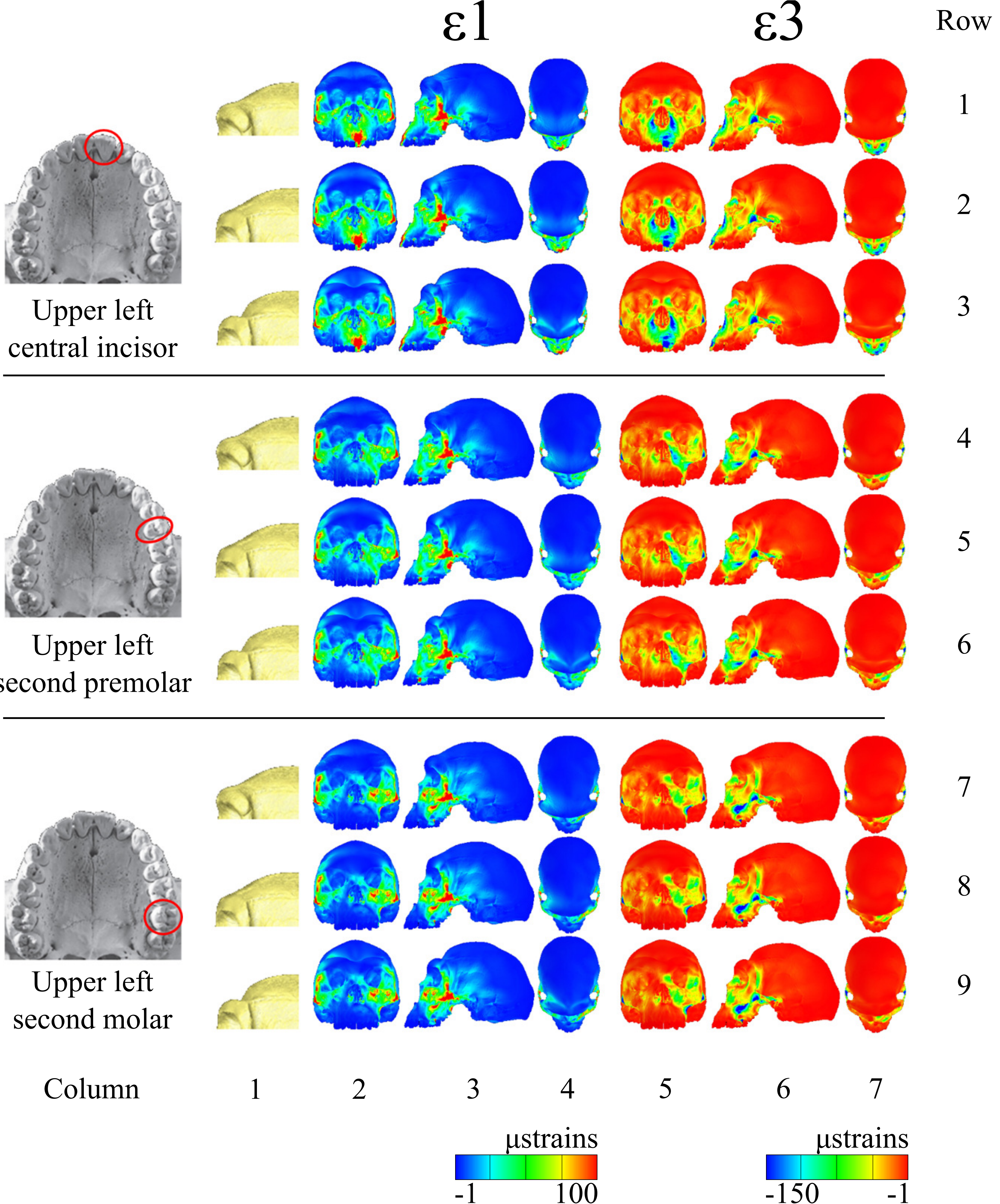
MODEL 2

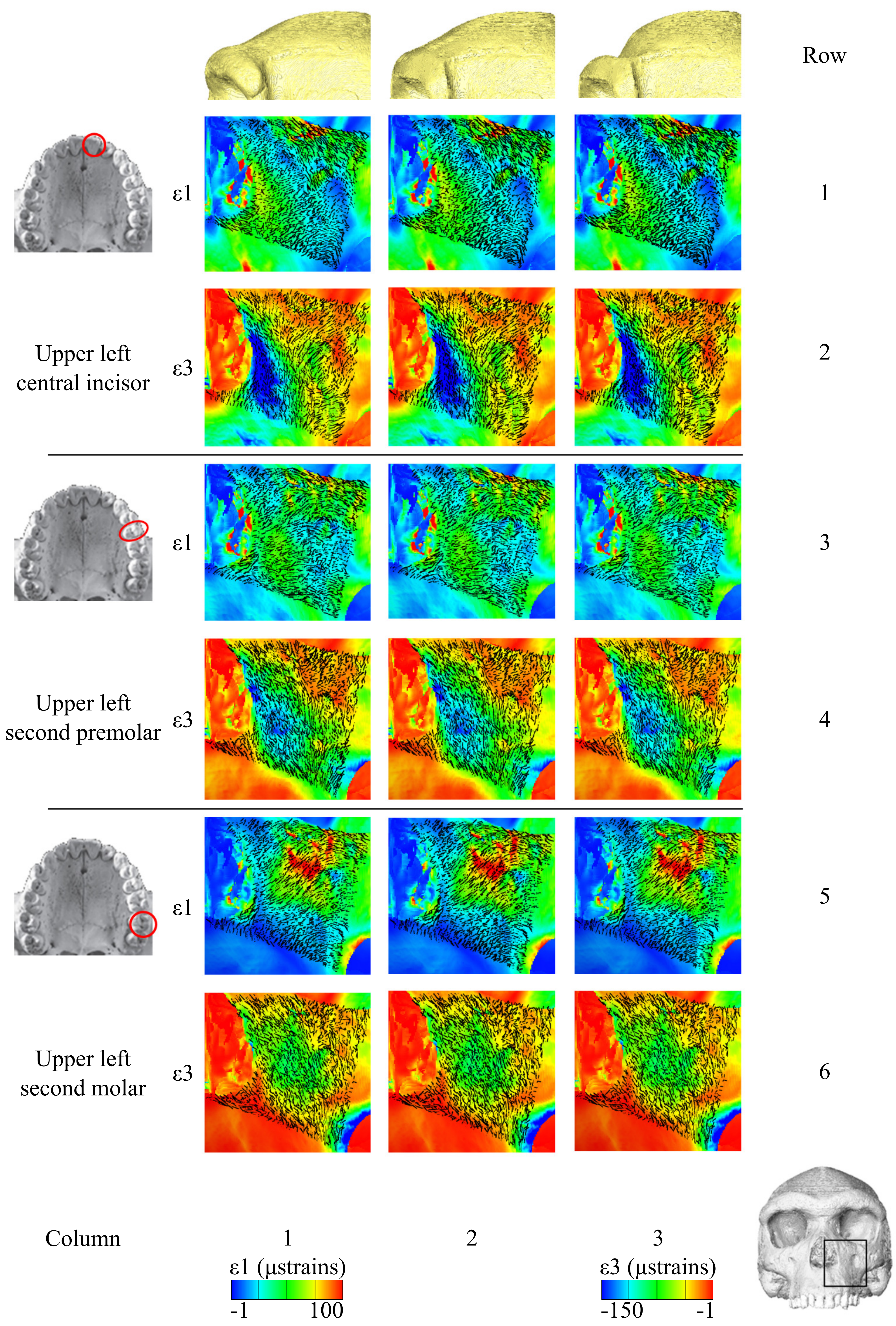


MODEL 3

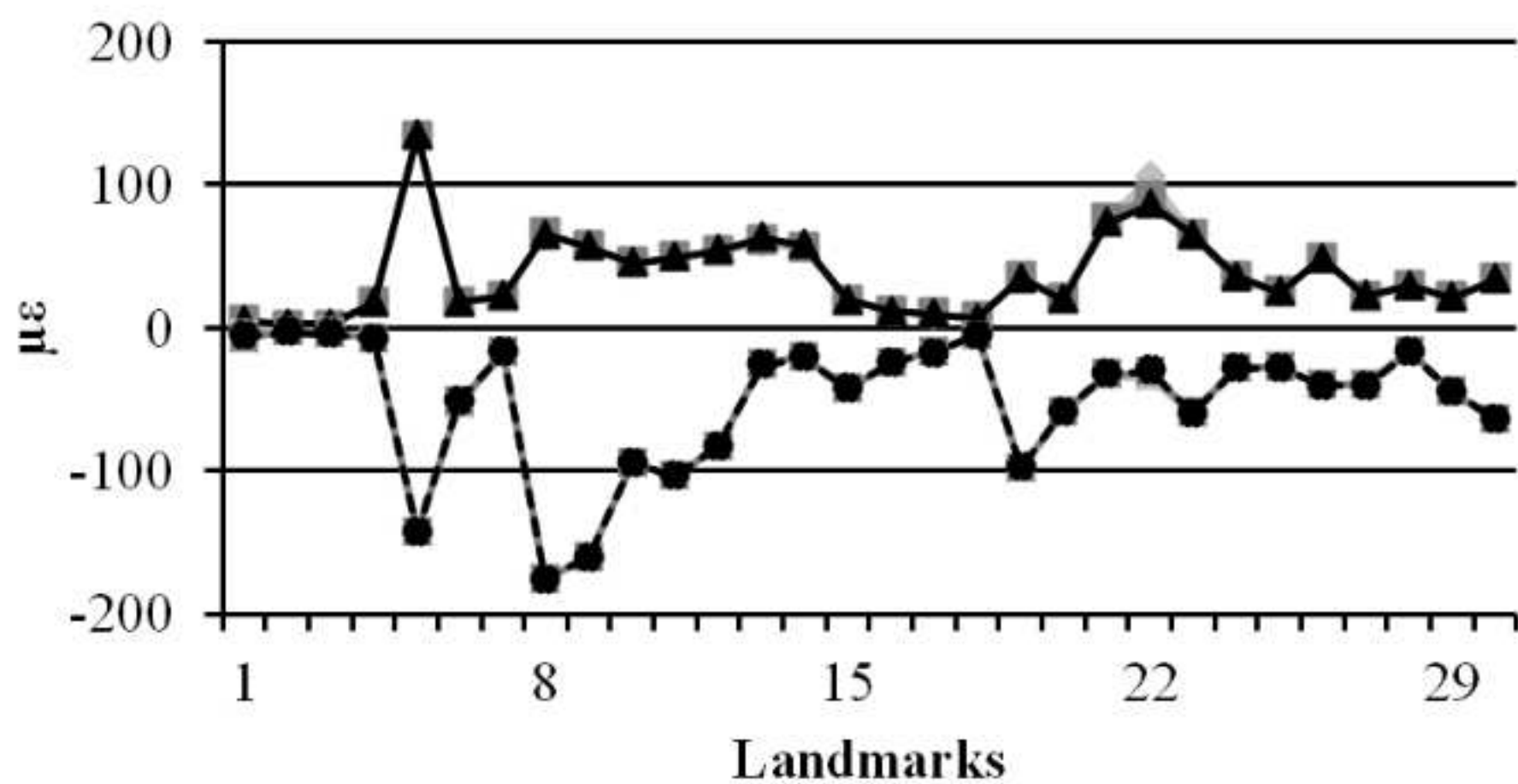


1 cm.

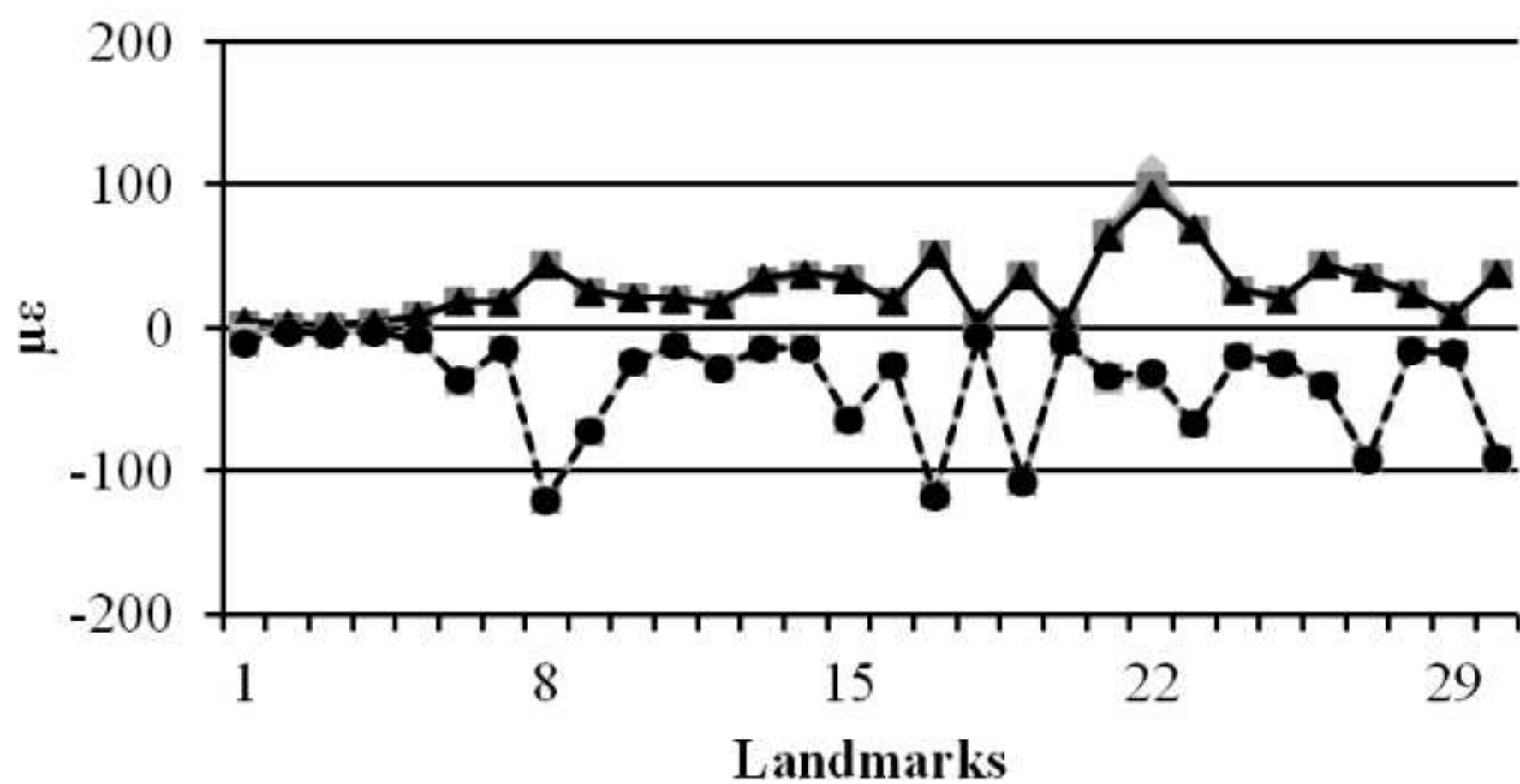




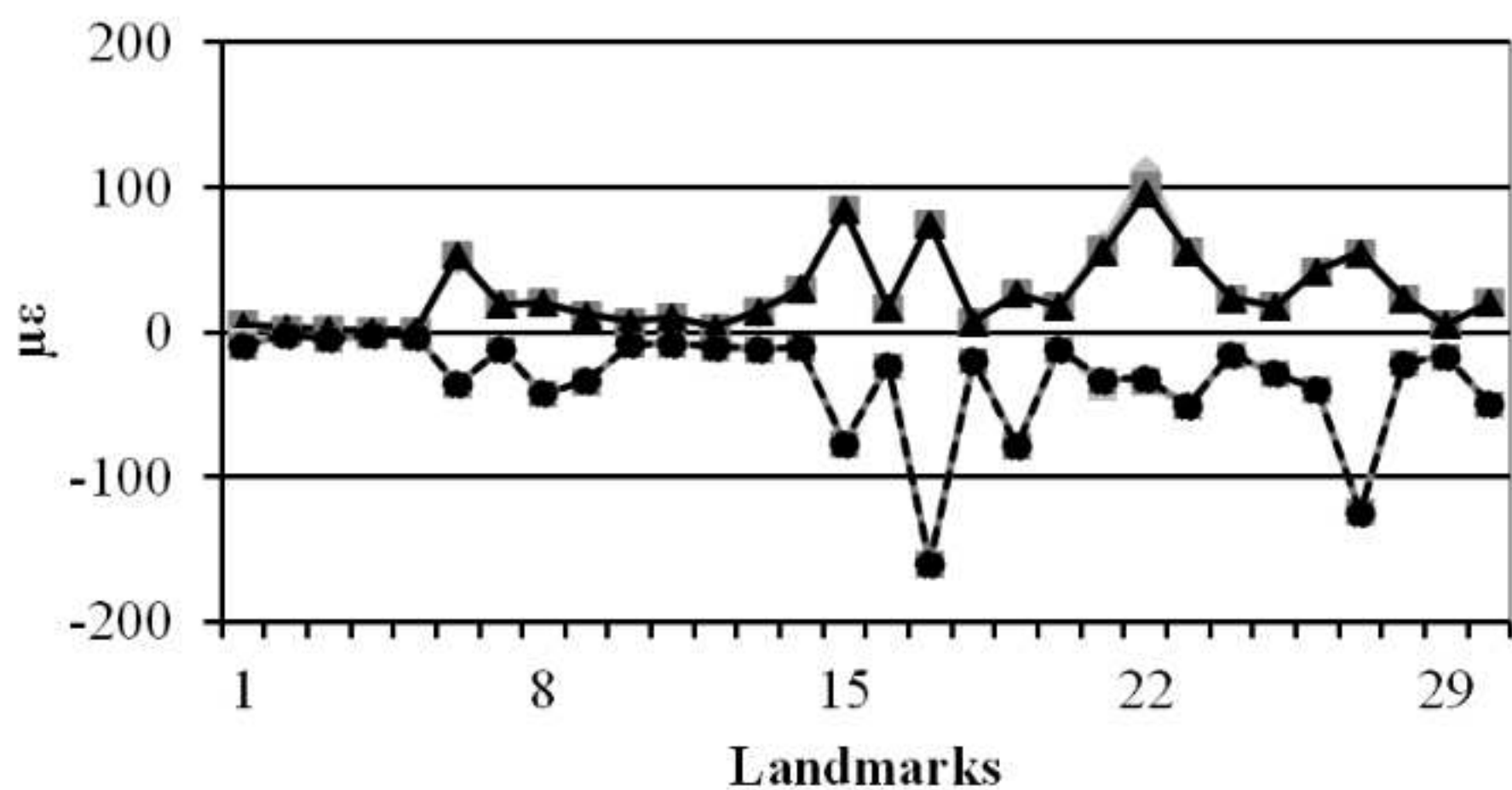
Upper left incisor 1 bite



Upper left premolar 2 bite



Upper left molar 2 bite



PC 1 (70.9%)

PC 2 (26.0%)

