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TITLE

Supraorbital morphology and social dynamics in human evolution

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TEXT

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

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

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

This association between cranial gracilization, prosociality and self domestication has also been hypothesized for bonobos, who, relative to chimpanzees, present a gracile cranium[18] with smaller browridges[19], prosocial behaviour and are hypothesized as self-domesticated[16-17]. This thus suggests a selective trade off between expressing dynamic affiliative signals and permanent competitive signals which affects the shape and size of the cranium in general and the browridge in particular. More affiliative based social relationships in bonobos, with frequent consolation[20], are associated with both a reduced browridge and greater attention to the eye area in social communication[21] than in common chimpanzees. Despite this association it should be noted that bonobos are significantly smaller than chimpanzees[18] and that, as predicted by the allometric hypothesis[11], browridges are expected to be proportionally smaller.

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

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

In addition to the above, other hypotheses have been proposed to explain large browridges. These include protection from blows to the head[32-33], protection of the eyes in aquatic environments[34], provision of sunshade (Barton, 1895 in [35]), and prevention of hair from obscuring vision[36], but have not been strongly supported by evidence and so are not widely held as feasible. Another factor that could explain the morphology of the browridge of Kabwe 1 is its massive frontal sinus. However the sinus appears to have no critical mechanical function during biting[37-38] and grows and develops secondarily to the browridge[1].

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

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

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

One of the reasons that spatial and mechanical explanations of large brows in archaic humans have not been falsified is because of the impossibility of carrying out in vivo experimental manipulations. However, recent advances in virtual functional simulation offer a way forward[39-41]. 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 morphology[42] 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 hypothesis[4]). 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 model[43]. 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

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

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

Facial reduction in *H. sapiens*, which has been related to changes in brain and basicranial morphology[7-9], and food pre-processing and biting mechanics[5,22-25], is accompanied by gracilisation of the brows, and the development of a more vertical frontal. The upper facial morphological changes found in *H. sapiens* position the frontal bone more vertically, inevitably altering the mechanical functioning of the frontalis belly of the occipito-frontalis muscle, causing contraction to raise the supraorbital skin whereas previously it would have pulled it more posteriorly over the browridge and the low, more horizontal forehead (Supplementary figure 1). Having lost a large low browridge, our ancestors gained the possibility of greater range, subtlety and visibility, of movement of the skin overlying the frontal, particularly affecting movements of the eyebrow. This suggestion is consistent with the work of Parr and colleagues[53], who suggest that the absence of specific movements of the brows in chimpanzees when compared to humans may relate to the presence of large browridges (see below). Effectively these anatomical changes enhance the capacity of the frontalis muscle to move eyebrows over the frontal, a key component of social signalling and non-verbal communication in our highly socially complex species.

Our mobile hairy eyebrows are crucial in subtle signalling behaviours. The eye region is known to develop increasing social significance in a human evolutionary context[54-55] however the mobility of eyebrows specifically has received little attention. Mobile eyebrows, without the constraints of a pronounced browridge, allow subtle affiliative emotions to be expressed (Supplementary table 3), such as the rapid 'eyebrow flash' , lasting around 1/6th of a second, found cross culturally as a sign of contact readiness and recognition[56]. A slow eyebrow raise is in contrast a sign of surprise and in particular social indignation[57]. The facial expression of sympathy, shown by pulling eyebrows up at the middle[58] has the advantage of removing need for the direct contact which is used to express sympathy in chimpanzees[59]. Subtle dynamic movements of eyebrows are also a key component of identifying trustworthiness[60] as well as identifying subtle indications of deception. Any constraints on 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 emotions[61].

When compared to our species, our nearest living relatives, chimpanzees, show minimal differences in underlying facial musculature[62], 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 conspecifics[53]. Similarly, other non-human primates, such as macaques[64], gibbons[65] and orangutans[66], 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 signalling[63].

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 space[67]. Even in modern hunter-gatherers more competitive and collaborative individuals tend to spatially locate together[68]. We should thus expect a long period of differing facial forms, reflecting differing social strategies, both within and between groups before the selective advantages of expressing complex pro-social emotions becomes stable. This pattern seems typical of archaic humans, with substantial variability in the definition of browridges amongst early modern humans at Jebel Irhoud for example[69].

METHODS

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

Skull reconstruction and model creation

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

Once the reconstruction was complete (model 1), the frontal sinuses were infilled to allow later excavation of this region to produce variant morphologies. Analysis of the impact of 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 sinus[38]. 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, VoxFE[71]. 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 cranium[72], a cranium of *Macaca fascicularis*[73] and a varanoid lizard mandible[74] 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 ration of 0.3. The modulus of elasticity was derived from nanoindentation studies of cortical bone in a cadaveric *Homo sapiens* skull[72]. The resulting value of 17 Gpa is within the range of values found in previous studies[75-76].

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 model[72] (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 5º 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 VoxFE[71]. The resulting deformations of the finite element models were compared through (1) visual assessment of strain magnitudes and directions of maximum ($\varepsilon 1$) and minimum ($\varepsilon 3$) principal strains, (2) plotting of $\varepsilon 1$ and $\varepsilon 3$ 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 coordinates[77-78]. 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

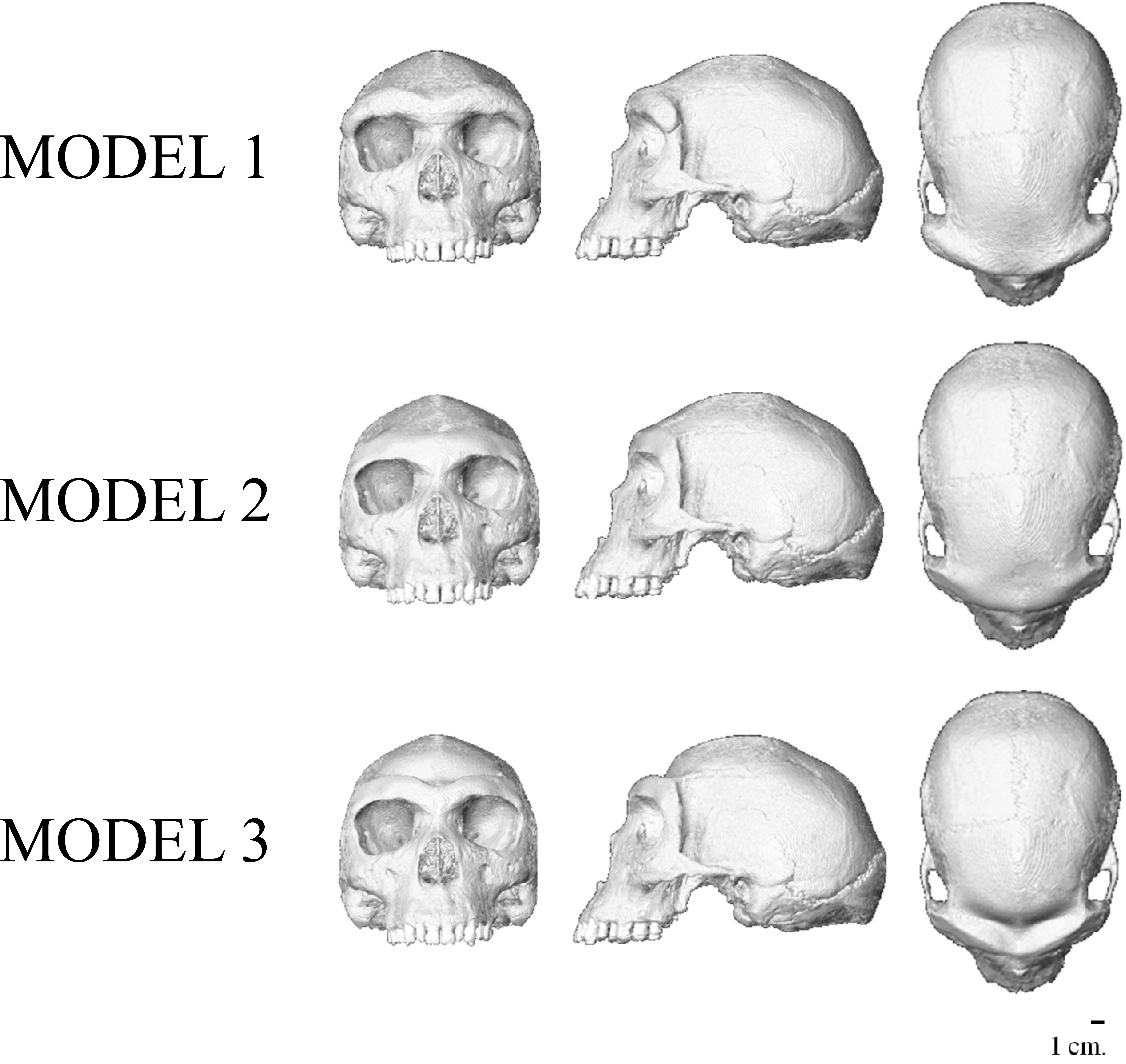
Figure 1: Models 1 - 3. Model 1 represents the original reconstruction of Kabwe 1; model 2 represents the reconstruction of Kabwe 1 with a reduced browridge; model 3 represents the reconstruction of Kabwe with a reduced browridge and a *post-orbital* sulcus.

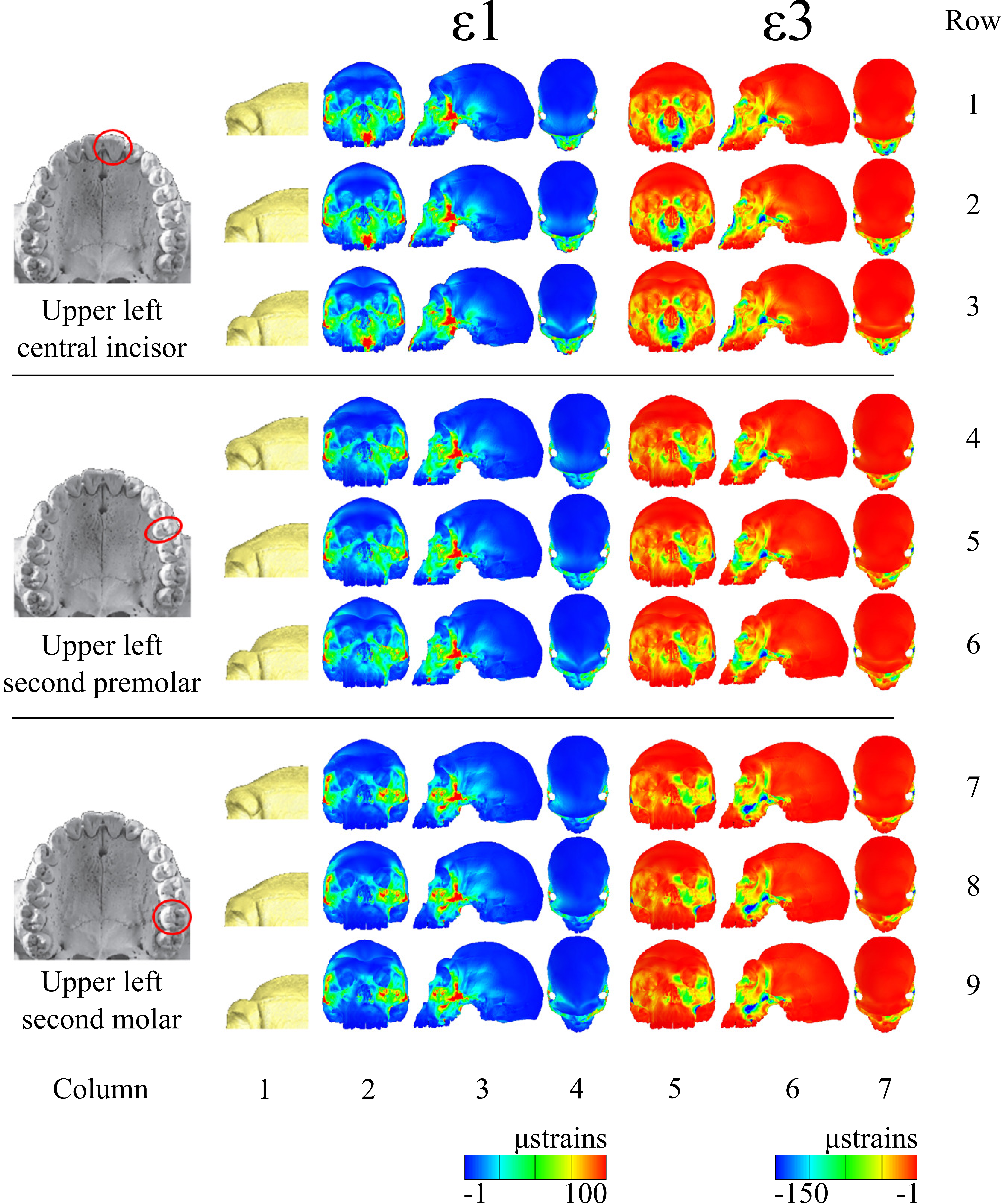
Figure 2: Strain contour plots of the biting simulations. Maximum principal strains (ε1) are represented in columns 3-5, and minimum principal strains (ε3) in columns 5-7. Model 1 is represented in rows 1, 4 and 7; model 2 in rows 2, 5 and 8; model 3 in rows 3, 6 and 9) under the different simulated bites.

Figure 3: Strain contour plots and strain directions of ε1 (rows 1, 3 and 5) and ε3 (rows 2, 4 and 6) over the maxilla (see inset frontal view for location) in the different models (model 1 in left column; model 2 in middle column; model 3 in right column) under the different bites simulated. The bottom left inset shows the anatomical region included in vector plots.

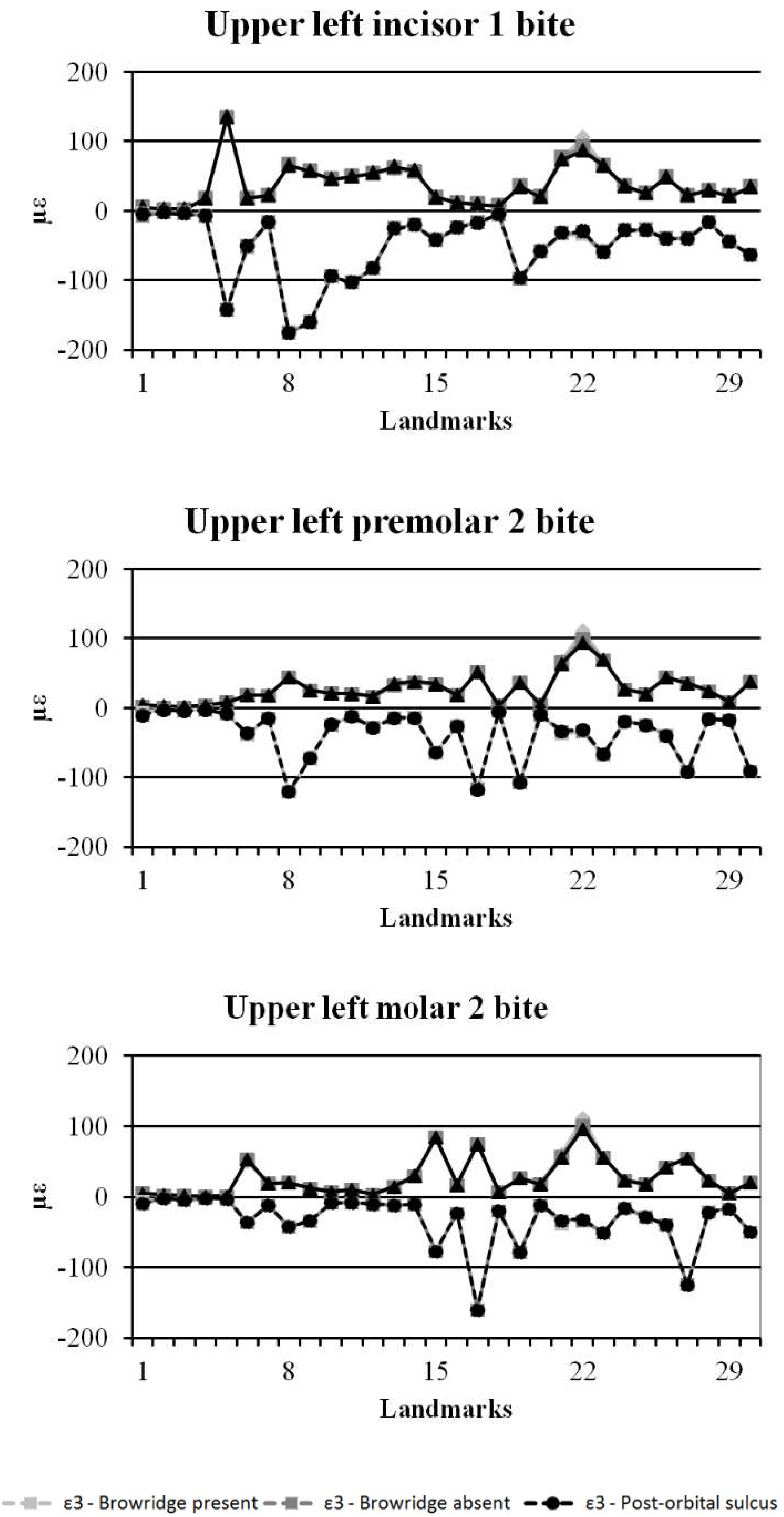
Figure 4: Plots of facial strains experienced by the models at 30 anatomical points.

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


MODEL 1
MODEL 2
MODEL 3
1 cm.


ε1
ε3
Row
1
2
3
4
5
6
7
8
9
Upper left central incisor
Upper left second premolar
Upper left second molar
Column
1
2
3
4
5
6
7
µstrains
-1
100
µstrains
-150
-1

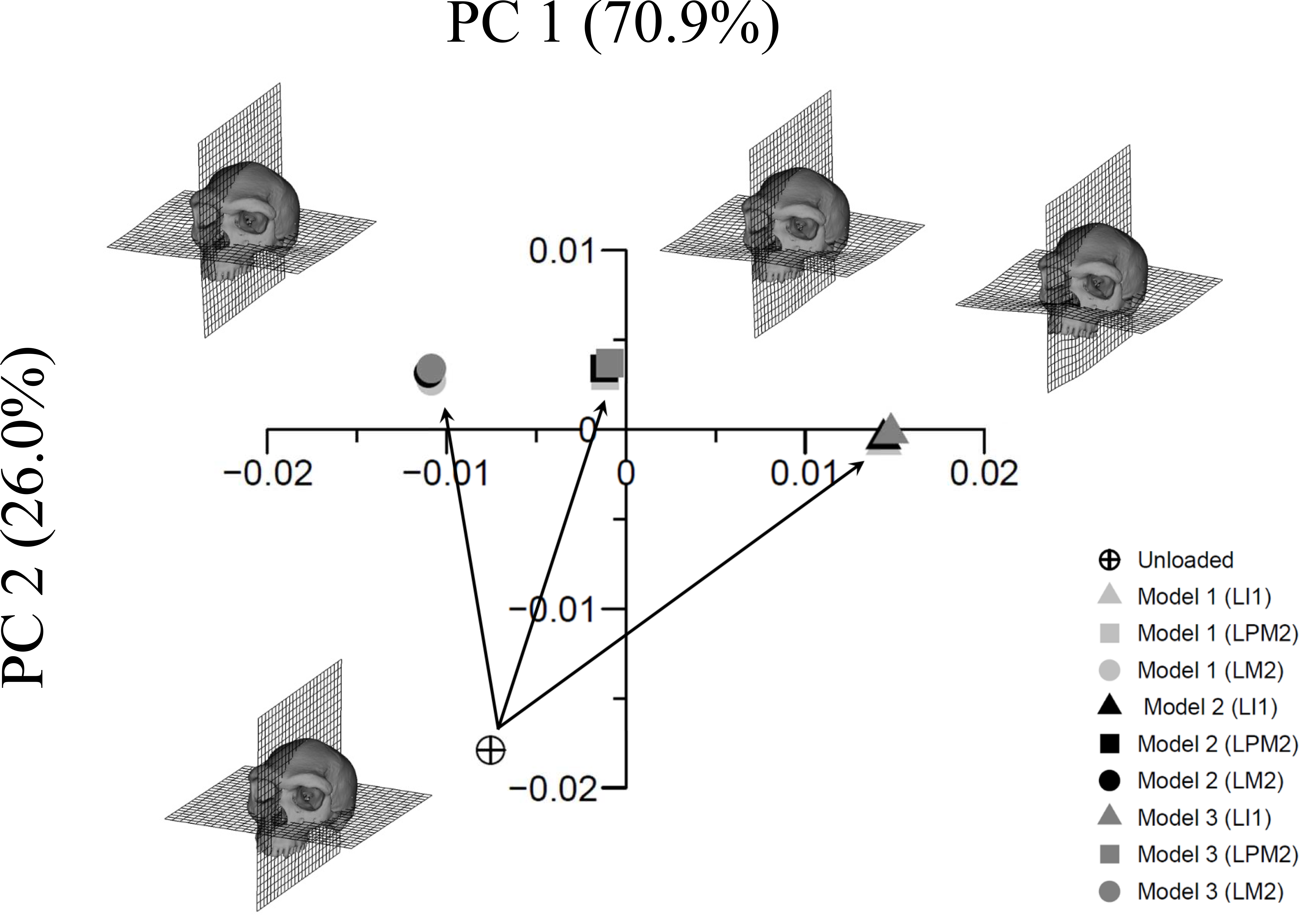

Row
Upper left central incisor
ε1
1
ε3
2
Upper left second premolar
ε1
3
ε3
4
Upper left second molar
ε1
5
ε3
6
Column
1
2
3
ε1 (μstrains)
-1
100
ε3 (μstrains)
-150
-1



Upper left incisor 1 bite

Upper left premolar 2 bite

Upper left molar 2 bite


PC 1 (70.9%)
PC 2 (26.0%)
0.01
0
−0.01
−0.02
−0.02
−0.01
0
0.01
0.02
⊕ 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)