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Godinho, Ricardo Miguel and O'Higgins, Paul orcid.org/0000-0002-9797-0809 (2018) The biomechanical significance of the frontal sinus in Kabwe 1 (*Homo heidelbergensis*). *Journal of Human Evolution*. pp. 141-153. ISSN 0047-2484

<https://doi.org/10.1016/j.jhevol.2017.10.007>

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The biomechanical significance of the frontal sinus in Kabwe 1 (*Homo heidelbergensis*)

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Keywords: Human evolution; Cranial form; Finite element analysis; Facial biomechanics; Palaeoanthropology

Abstract

Paranasal sinuses are highly variable among living and fossil hominins and their function(s) are poorly understood. It has been argued they serve no particular function and are biological 'spandrels' arising as a structural consequence of changes in associated bones and/or soft tissue structures. In contrast, others have suggested that sinuses have one or more functions, in olfaction, respiration, thermoregulation, nitric oxide production, voice resonance, reduction of skull weight, and craniofacial biomechanics. Here we assess the extent to which the very large frontal sinus of Kabwe 1 impacts on the mechanical performance of the craniofacial skeleton during biting. It may be that the browridge is large and the sinus has large trabecular struts traversing it to compensate for the effect of a large sinus on the ability of the face to resist forces arising from biting. Alternatively, the large sinus may have no impact and be sited where strains that arise from biting would be very low. If the former is true, then infilling of the sinus would be expected to increase the ability of the skeleton to resist biting loads while removing the struts might have the opposite effect. To these ends, finite element models with hollowed and infilled variants of the original sinus were created and loaded to simulate different bites. The deformations arising due to loading were then compared among different models and bites by contrasting the strain vectors arising during identical biting tasks. It was found that the frontal bone experiences very low strains and that infilling or hollowing of the sinus has little effect on strains over the cranial surface, with small effects over the frontal bone. The material used to infill the sinus experienced very low strains. This is consistent with the idea that frontal sinus morphogenesis is influenced by the strain field experienced by this region such that it comes to lie entirely within a region of the cranium that would otherwise experience low strains. This has implications for understanding why sinuses vary among hominin fossils.

Introduction

Paranasal sinuses are highly variable among living and fossil hominins and their function(s) are poorly understood. Here we investigate the extent to which the possession of large frontal sinuses impact on the ability of the cranium to resist forces generated by biting in a representative of *Homo heidelbergensis*, the Kabwe cranium, in which the frontal sinus is particularly large. This is of interest to students of human evolution not only with respect to this specimen but also because frontal sinus size varies markedly among late Pleistocene and Holocene hominins. Why this should be so and the consequences and causes of large versus small sinuses have been a constant subject of debate (Coon, 1962; Tillier, 1977; Seidler et al., 1997; Wolpoff, 1999, Rae and Koppe, 2004; O'Higgins et al, 2006; Laitman, 2008).

The human skull possesses maxillary, ethmoidal, sphenoidal, and frontal paranasal sinuses, named according to the bones they pneumatize. These are also differentiated according to the positions of their ostia in the nasal cavity (Rae and Koppe, 2004). Sinuses are first formed at different times during development, each by a two stage process (Sperber, 2001; Rae and Koppe, 2004; Smith et al., 2005; Rossie, 2006). Primary pneumatization occurs pre-natally and gives rise to nasal recesses that later develop into proper sinuses via secondary pneumatization (Smith et al., 2005; Rossie, 2006). The former consists of interstitial growth in the cartilaginous nasal capsule with no expansion to contiguous structures. Secondary pneumatization occurs via invasion of adjoining bones by osteoclasts and subsequent resorption (Smith et al., 2005; Rossie, 2006).

In modern humans, the frontal sinus begins primary pneumatization at 3–4 months post-conception and secondary pneumatization occurs postnatally, at 6 months to 2 years (Scheuer and Black, 2000; Sperber, 2001). Its subsequent growth results from resorption on the inner, and deposition on the outer, surfaces of the frontal bone tables, resulting in cortical

drift (Duterloo and Enlow, 1970; Tillier, 1977). Growth and development of the inner table is associated with changes in the growing brain (Moss and Young, 1960) and, as such, by about six years of age the inner table of the frontal bone presents approximately 95% of its total growth (Enlow and Hans, 1996; Lieberman, 2000). On the other hand, the external table, at the level of the browridge and frontal sinus, presents a somatic growth pattern (Enlow and Hans, 1996; Lieberman, 2000). Frontal sinus development is thought to occur secondarily to drift of the external table of the frontal bone, as the browridge grows and develops along with anterior growth of the face relative to the cranial vault (Enlow and Hans, 1996; Lieberman, 2000). The external table of the frontal achieves approximately 95% of its total growth by the end of puberty, completing growth after this period (Tillier, 1977). Thus, frontal sinus growth and development in modern humans is complete by approximately 18–20 years (Spaeth et al., 1997; Fatu et al. 2006; Park et al., 2010).

Among catarrhines, the frontal sinus is only present in African hominoids (Cave and Haines, 1940) and it has therefore been interpreted as a synapomorphy of the group (Rae and Koppe, 2004). In humans, it presents significant intra and inter population form variation (Buckland-Wright, 1970; Tillier, 1977) and may present high frequencies of absence in specific populations (Koertvelyessy, 1972; Greene and Scott, 1973). Fossil hominins also present significant form variation, with some individuals presenting very small frontal sinuses (e.g., Arago 21; Seidler et al., 1997), while others, such as Kabwe, Steinheim, and Petralona, show extremely enlarged sinuses that extend laterally beyond the supraorbital arch and superoposteriorly invading the frontal squama (Seidler et al., 1997; Prossinger et al., 2003; Zollikofer et al., 2008). Inter-specific variation in sinus form has been considered to be of taxonomic relevance, and it has been proposed that generally large sinuses are one of the distinctive cranial traits of *H. heidelbergensis* (Prossinger et al., 2003; Stringer, 2012a). In Neanderthals, the presence of large sinuses has been related to particular anatomical features, such as the

lack of the canine fossa and the presence of large supraorbital tori (Coon, 1962; Wolpoff, 1999), but more recent research shows that Neanderthals do not have large sinuses relative to modern humans when cranial size differences are taken into account (Rae et al., 2011).

Despite multiple studies, sinus function(s) are still poorly understood (Seidler et al., 1997; Laitman, 2008; Márquez, 2008). Some researchers consider that they are biological spandrels arising as a structural consequence of changes in other bones and/or structures, rather than because of a specific mechanism acting to create them or to serve any particular function (Enlow, 1968; O'Higgins et al., 2006; Zollikofer et al., 2008; Zollikofer and Weissmann, 2008). Irrespective of how they formed, others have suggested that sinuses have one or more putative functions, such as olfaction, respiration, thermoregulation, nitric oxide production, voice resonance, reduction of skull weight, and craniofacial biomechanics (Tillier, 1977; Blaney, 1990; Bookstein et al., 1999; Rae and Koppe, 2004; Laitman, 2008; Lundberg, 2008; Márquez, 2008). These views are not necessarily opposed since a 'spandrel' might subsequently take on a function.

As with most biological structures (Lesne and Bourguine, 2011), the morphogenesis of the frontal sinus is probably impacted by multiple factors. One such factor, which has been suggested to determine the morphology of the upper face, and so the morphogenesis of the browridge and frontal sinus, is the spatial relationship between the eyes and the brain (Moss and Young, 1960). This spatial hypothesis predicts that if the eyes are positioned substantially anteriorly relative to the brain, then big browridges develop to fill the 'gap' (Moss and Young, 1960) and frontal sinuses develop within them as a by-product of facial projection (Lieberman, 2011). Even though the spatial relationship between the neurocranium and the face, along with facial orientation, has been demonstrated to impact frontal sinus form in hominoids (Zollikofer et al., 2008), other studies have examined the extent to which paranasal sinus morphology is also impacted by environmental conditions and air

conditioning by investigating possible associations in humans, other primates, and non-primates between sinus size and environmental conditions. It was found that people from latitudes with colder temperatures present smaller frontal (Koertvelyessy, 1972) and maxillary sinuses (Shea, 1977). Conversely, other studies examining the interaction between nasal cavity and maxillary sinus volume in modern humans found that populations from cold-dry climates present larger sinuses, which are associated with narrower, taller, and longer nasal cavities, relative to populations from hot-humid climates (Holton et al., 2013; Butaric, 2015; Butaric and Maddux, 2016). Thus, maxillary sinus size appears to vary secondarily to nasal morphology as it accommodates morphological adaptation of the nose to the environment, leading several researchers to conclude that sinuses are not directly involved in air conditioning (Shea, 1977; Rae et al., 2003; O'Higgins et al., 2006; Rae et al., 2006; Holton et al., 2013; Butaric, 2015; Butaric and Maddux, 2016). Consistent with this, other species, such as macaques from cold climates (Rae et al., 2003; Ito et al., 2015) and cold raised rats (Rae et al., 2006), also present smaller maxillary sinuses due to increased nasal cavity size.

In a recent study, Noback et al. (2016) assessed the association between maxillary and frontal sinus volume among Nubians and Greenlanders, finding no association with geographic origin (a proxy for climate) in the maxillary sinus but significantly smaller frontal sinus volumes in Greenlanders, which they noted could be due to factors such as population history rather than climate. They concluded “that using sinus volume to study climate adaptation in either *Homo sapiens* or *Homo neanderthalensis* is problematic” and that this remains the case “as long as the function and evolution of sinus volume and shape are not well understood in our own species” (Noback et al., 2016: 179).

Several studies suggest that masticatory mechanics influence sinus morphogenesis via bone mechanical adaptation to strains experienced during mechanical tasks. Strains can be

directly measured or predicted by Finite Element Analysis (FEA), a computational tool that can be used to simulate complex loading scenarios and the resulting straining of skeletal structures (Hutton, 2003). It has been used increasingly to investigate craniofacial biomechanics in human evolution (Strait et al., 2007, 2009, 2010; Wroe et al., 2010; Witzel, 2011; Smith, 2015; Ledogar et al., 2016) and was employed by Witzel and Preuschoft (2002) to investigate how masticatory system loading interacts with and influences skull morphology. When modelling the cranium as a block material and simulating biting, they found that the infilled regions where the sinuses are located experience low stresses and strains when compared to other regions of the craniofacial complex. Because bone adapts to the mechanical environment (Currey, 2006) these hollow spaces, arising in particular through secondary pneumatization, might be the consequence of biomechanical bone adaptation to these low stresses, enabling the cranium to resist mechanical loading while minimizing bone material (Witzel and Preuschoft, 2002; Witzel, 2011). The idea that sinuses occupy regions of low stress and so have no specific mechanical role is supported by the work of Fitton et al. (2015), who noted minimal effects on facial strains during FEA simulated biting in a macaque when the maxillary sinus is infilled. Bookstein et al. (1999) and Prossinger et al. (2000) note that *Petalona* has an extremely enlarged frontal sinus that is delimited by very thin internal and external tables of the frontal bone. Within the sinus there is a lamellar honeycomb-like structure that may be related to the resolution of masticatory loads, reinforcing this region against deformations arising during biting, while allowing a decrease in bone mass and subsequent thinning of the internal and external tables of the frontal bone. Greene and Scott (1973) also suggest bone mechanical adaptation of the frontal bone influences frontal sinus form in the Wadi Halfa Mesolithic population, proposing that the 95% frequency of frontal sinus absence is due to heavy masticatory loading.

In contrast, several researchers refute any association between sinus morphology and biomechanical loading. One of the main arguments has been that circumorbital structures, such as the browridge and frontal sinus, experience very low magnitude stresses and/or strains during masticatory system loading, thus precluding mechanical bone adaptation to masticatory loading (Picq and Hylander, 1989; Hylander et al., 1991; Ravosa et al., 2000; Hylander and Johnson, 2002). Rae and Koppe (2008) demonstrated that maxillary sinus volume is not significantly different between the frugivore *Cebus albifrons* and the hard object feeder *Cebus apella*, which are closely phylogenetically related. Thus, sinus size appears to be independent of different diets that lead to different masticatory system loads.

In hominins, sinus form variation has been considered to be related to air conditioning, bone mechanical adaptation to masticatory and paramasticatory loading, and spatial constraints between different anatomical components of the cranium. With respect to the latter, Zollikofer et al. (2008) examine the relationship between sinus morphology and cranial form using extant hominoids and mid-Pleistocene fossil hominins. They show that frontal sinus form correlates with the spatial relationship between the face and the cranial vault and the orientation of the face. While the results of Zollikofer et al. (2008) support the notion that sinuses are biological spandrels, consistent with the spatial hypothesis (Moss and Young, 1960), other studies examine the possible association between sinuses and climate. Much of this research has focused on Neanderthals, which lived during glacial periods and present postcranial characteristics consistent with cold adaptation (Holliday, 1997; Churchill, 1998; Steegman, et al., 2002). Thus several cranial features such as large nasal cavities and sinuses (Laitman et al., 1996; Churchill, 1998; Tattersall and Schwartz, 2006) have been hypothesized to be adaptations to conditioning of respired air. The notion of hyperpneumatization of this species has been challenged (Zollikofer et al., 2008; Rae et al., 2011). In fact, Rae et al. (2011) propose that Neanderthal crania are neither

hyperpneumatized nor cold adapted, suggesting that sinus form in *H. neanderthalensis* relates to other factors, such as paramasticatory mechanics (but see the response by Holton et al. [2011] to that study).

Although no studies have addressed the impact of paramasticatory behavior on sinus form, masticatory mechanics has been related to sinus morphology and morphogenesis. As mentioned above, the presence of bony struts inside the frontal sinus of the Petralona cranium and the thickness of the internal and external tables of the frontal bone circumscribing the sinus have been hypothesized to relate to biting mechanics (Bookstein et al., 1999; Prossinger et al., 2000). In another study, in which Witzel (2011) used FEA and modelled the cranium as a block with the brain, nasal, and orbital cavities, formation of sinuses was predicted in a Neanderthal based on masticatory mechanics alone. Thus, while there is evidence that sinuses in hominins are the result of the spatial relationship between different components of the cranium (i.e., the brain and eyes in the case of the frontal sinus; Zollikofer et al., 2008), there is also some evidence suggesting that masticatory mechanics impacts sinus morphogenesis (Witzel, 2011). These two views are not necessarily opposed and may work in concert, as the structural relationships among cranial components determine the space available for sinuses and local strain fields. These in turn influence sinus morphogenesis, enabling maximization of mechanical function while minimizing bone material (O'Higgins et al., 2006; Zollikofer et al., 2008).

The present study readdresses the impact of biting mechanics on frontal sinus form by assessing the biomechanical relevance of the frontal sinus in Kabwe 1, and if masticatory system mechanical loading might impact on its morphogenesis based on the principle of bone adaptation to loads. This middle Pleistocene (250–150 ka) male *H. heidelbergensis* cranium was recovered from Zambia (Schwartz and Tattersall, 2003; Stringer, 2012a). *Homo heidelbergensis* has been suggested to be hyperpneumatized (Seidler et al., 1997; Prossinger

et al., 2003; Zollikofer et al., 2008; Stringer, 2012a), presenting sinuses that are larger than average in hominins even when size is accounted for, making this species a good choice for the study of interactions between sinus form and masticatory system loading in human evolution.

Kabwe 1 is an extremely very well preserved specimen that displays a very prominent browridge (Fig. 1) containing a very well developed frontal sinus with a honeycomb-like structure within it. This is similar to the Petralona skull in which the presence of honeycombing is suggested to reflect loading history (Seidler et al., 1997; Bookstein et al., 1999; Prossinger et al., 2000). As such, it is to be expected that removal of these struts will lead to increased strains locally and plausibly more widely over the face and frontal. Beyond this, the preceding review has highlighted prior work that suggests the sinus itself may exist within a region of the facial skeleton that experiences very low strains, and these could in turn impact sinus morphogenesis (Witzel, 2011). In consequence, infilling of the sinus should have little or no impact on strains locally or more widely, and strains within the infilled sinus are expected to be very low.

Inevitably, modifications of the frontal sinus by adding or removing material will have a small effect at least locally on the ability to resist deformation when loaded. To assess whether any such effect is large or small, we compare differences in strains, due to sinus filling, to the peak strains achieved in each face during simulated biting and to the differences in modes and magnitudes of strains and large scale deformations that occur between different bite points. A small difference with respect to these would indicate that the frontal sinus is constructed in such a way that craniofacial strains are largely unaffected by its presence, while a large difference would indicate the opposite: that the frontal sinus comes at a ‘cost’ in terms of performance when resisting biting.

To investigate this, we assess the extent to which: (1) strain magnitudes and directions experienced by the cranium during simulated biting are affected by removing the honeycomb-like structure, and (2) strain magnitudes and directions experienced by the cranium are affected by infilling the frontal sinus.

Materials and methods

The Kabwe 1 skull was virtually reconstructed (Fig. 1) based on a computed tomography (CT) scan of the fossil that was provided by the Natural History Museum, London (courtesy of Robert Kruszynski). After reconstruction, the anatomy of the frontal sinus was modified. The unmodified and modified reconstructions were then directly converted into voxel based finite element models. These were used to simulate three different bites (left central incisor, left second premolar, left second molar) to assess the biomechanical performance of the facial skeleton with and without an infilled frontal sinus during biting.

Skull reconstruction and model creation

The reconstruction of Kabwe 1 is thoroughly described by Godinho and O'Higgins (2017) and briefly summarized here. A medical CT stack with originally anisometric voxel size (0.4687501 x 0.4687501 x 1 mm) was resampled to produce isometric voxels (0.35 mm). Automated, semi-automated, and manual segmentation of the cranium was then performed using Avizo[®] (version 8.0). Manual segmentation was required to exclude from the model sedimentary matrix present in the maxillary and sphenoidal sinuses. Despite outstanding preservation, several anatomical regions of the cranium required reconstruction to repair damage from taphonomic and pathological processes. These include the alveolar regions of

the maxilla, the right and left temporal bones, the occipital, the right parietal, the sphenoid, the orbital region of both maxillae, and several teeth. Where possible, reconstruction was performed by mirroring preserved contralateral elements and warping them to existing structures. When small gaps were present, Geomagic[®] (Studio 2013) was used to fill them using the surface of the surrounding structures as the reference for interpolation. Portions of a cadaveric *H. sapiens* skull were used to reconstruct part of the occipital and missing tooth crowns where no antimeres were present (Fig. 1). Reconstruction of the regions affected by pathological processes was minimal and localized, and so unlikely to have affected the results of the FEA simulations of this study.

Three models were then created based on this reconstruction: Model 1 represents the reconstruction with the honey-comb liked structure of the frontal sinus removed; Model 2 represents the original reconstruction, with no alteration of the sinus; and in Model 3, the sinus was completely infilled (Fig. 2). Voxel based finite element models were then generated by direct conversion using the bespoke vox2vec software tool and imported into VoxFE (Fagan et al., 2007) to be loaded and constrained.

Constraints

Constraints are used to fix the cranium in space and to reflect the loading of the temporomandibular joints and teeth during biting. Identical constraints were applied to all models using the FEA software VoxFE (Fagan et al., 2007) at each temporomandibular joint (24 nodes in the x, y and z axis), and a third constraint was applied successively at each of the bite points (left central incisor, left second premolar, left second molar; 21 nodes in the z axis).

Material properties

Prior sensitivity studies on a cadaveric human head (Toro-Ibacache et al., 2016) and in the cranium of *Macaca fascicularis* (Fitton et al., 2015) have shown only minor and localized effects when the same material properties (of cortical bone) are equally applied to cortical bone, trabecular bone, and teeth, rather than their own specific material properties. These studies show that, with the exception of the alveolus near the biting point, model simplification results in similar spatial distributions of regions experiencing high and low strain magnitudes, but strain magnitudes are reduced on average. Thus, simplification results in a ‘stiffer’ model that deforms less but in a similar way (mode of deformation) to a more complex model that distinguishes the material properties of cortical bone, trabecular bone, and teeth. This is relevant to the present study because trabecular bone is neither well preserved nor imaged at sufficient resolution in the fossil to accurately distinguish it from cortical bone in a finite element model. Thus, in the present study, teeth and trabecular bone (and the material that infills the frontal sinus in our experimental manipulations) were assigned the same material properties as cortical bone in all the models. All 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 nano-indentation studies of cortical bone in a cadaveric *H. sapiens* skull (Toro-Ibacache et al., 2016). The resulting value of 17 GPa is within the range of values found in previous studies (Dechow et al., 1993; Schwartz-Dabney and Dechow, 2003).

Muscle loads

Loads were applied to simulate the actions of six muscles active during biting: right and left temporalis, right and left masseters, right and left medial pterygoids. Lack of the mandible precludes direct estimation of the direction of muscle force vectors and the use of bony proxies to estimate anatomical cross sectional areas (and so maximum forces) of muscles that attach to the mandible (masseter and medial pterygoid). However, since this study is not concerned with magnitudes of bite forces nor with predicting real absolute strains, it matters little what actual forces are applied as long as they are identical in each model and approximate physiological vectors. As such, and because we did not have access to the Mauer mandible (the holotype specimen of *H. heidelbergensis*), we applied muscle forces to each model that were derived from a *H. sapiens* cadaveric head (Toro-Ibacache et al., 2016; see Table 1) and directions of the muscle force vectors (Fig. 3) were estimated by scaling a *H. neanderthalensis* mandible (Tabun 1 specimen) to the Kabwe 1 skull to provide estimates of the locations of muscle attachments on the mandible.

Model solution and data analysis

The finite element models were solved using VoxFE. Analysis and comparison of the results employed three different approaches. First, strains are used to describe local deformation (at each node) qualitative assessment of: (1a) maximum (ϵ_1) and minimum (ϵ_3) principal strain magnitudes over the cranial surface (on which these are the only two strains with meaningful magnitude—surface is two-dimensional [2D]); (1b) maximum (ϵ_1), second (ϵ_2), and minimum (ϵ_3) principal strain magnitudes through a mid-sagittal cross section (where, being a three-dimensional [3D] volume, there are three); and (1c) directions of ϵ_1 and ϵ_3 principal strains over the external surface of the frontal squama (results not shown because they differ little). Second, magnitudes are plotted of ϵ_1 and ϵ_3 at 42 points identically located

in each model on the surface of the frontal bones and 30 on the surface of the facial skeleton (Fig. 4). Third, a geometric morphometric (GM) analysis of global modes of deformation of the cranium is carried out using 67 landmarks on the craniofacial skeleton (Table 2).

Method 1 relies on visual assessment of changes in the strain contour plots and of the directions of the vectors. Method 2 visually compares strain magnitudes by plotting magnitudes arising from each simulated bite. Method 3 employs GM to compare large scale changes in size and shape between the unloaded and loaded models. This consists of an initial generalized Procrustes analysis, followed by rescaling by centroid size and then a principal components analysis (PCA) of the resulting size and shape coordinates (O'Higgins, 2000; Zelditch et al., 2012). This analysis leads to a quantitative appraisal of differences in global model deformations (here defined as changes in size and shape) in terms of vectors and magnitudes of deformation arising from loading.

Results

The strain contour plots (Figs. 5–7), the strain vector directions (Fig. 7), and the strain magnitudes extracted from the 42 points in the frontal bone and the 30 points in the face (Figs. 4 and 8) consistently show that hollowing out or infilling the frontal sinus has little effect. Thus, Figures 5, 6, and 8 show that, relative to the differences in strain magnitude manifest among anatomical regions that have not been manipulated, the effects on strain magnitudes are small over the frontal itself and extremely small or non-existent over much of the cranium. Further, compared to the small differences in strain vector directions over the frontal bone experienced by the unmodified cranium when simulating each of the three different bites (center column of Fig.7), the differences in strain directions due to hollowing out or infilling of the frontal sinus (left and right columns of Fig. 7) are, themselves, small.

The strain contour plots are very similar for each of the bites, with no marked differences, both in ϵ_1 and ϵ_3 , between the models with a completely hollow frontal sinus (model 1) and a frontal sinus with trabeculae forming a honeycomb-like structure (model 2). Slight, localized decreases in strain magnitude are observed between the hollow and honeycomb models and the infilled sinus model. This is apparent in the outer table of the frontal bone towards the midline for ϵ_1 (Figs. 5 [see arrow] and 7). It should also be noted that in the infilled sinus model strain magnitudes are consistently low within the material infilling the sinus during all simulated bites (Fig. 6 [see arrow]). These results are consistent with the plots of strain magnitudes extracted from the frontal bone (Fig. 8), where models 1 and 2 almost completely overlap both in ϵ_1 and ϵ_3 . Again, as in the strain contour plots, model 3 shows a decrease in the strain magnitudes experienced along, and close to, the midline of the frontal bone (Figs. 5 and 7), but when considering the full range of strain magnitudes experienced by the cranium, this decrease is proportionately very small. Changes in the frontal sinus have even less, indeed almost no, impact on the strain magnitudes extracted from the face (Fig. 8). It should be noted that the reaction force measured at each bite point in each model did not vary between models, indicating that the small differences in strains that we observe are not due to overall changes in cranial stiffness as a result of experimental manipulations.

The results of the GM analysis of global modes and magnitudes of deformation are, again, consistent with the pattern of differences in strain magnitudes predicted in the different models during the three simulated bites. Figure 9, with models tightly clustering by bite point rather than by type of sinus, shows that changes in bite point clearly impact much more on mode of deformation than changes in the sinus. The model that invariably deforms less (is closer to the unloaded model) in all bites is that with the infilled sinus, and the remaining two are very close to each other (indeed the markers in the plot overlap). These findings reflect

those from the analyses of strains in indicating only small and local effects of experimental manipulation of sinus anatomy.

Discussion

The present study has assessed the mechanical consequences of modification of the large frontal sinus of the Kabwe 1 fossil cranium. This is of interest because frontal sinus volume varies considerably in recent human evolution and the causes and associations of this variation have been debated extensively (see Introduction and below). One possibility, investigated here, is that they simply exist in regions of the frontal bone that would otherwise experience very low strains and simply reflect bony adaptation to low strains. The results show that experimentally manipulating frontal sinus anatomy in the Kabwe 1 cranium, by hollowing or infilling, has little to no impact on the strain magnitudes and directions and on the modes of deformation of the cranium in general. The strain magnitudes experienced over the frontal bone are consistently low compared to the peaks experienced elsewhere in the face. This finding mirrors the findings of studies of other primates that found low strain magnitudes in the frontal bone and/or circumorbital structures due to masticatory system loading (Picq and Hylander, 1989; Hylander et al., 1991; Ravosa et al., 2000; Hylander and Johnson, 2002; Kupczik et al., 2009).

Hollowing the frontal sinus results in only a small increase in strain magnitudes over the external surface of the frontal bone directly overlying the sinus. Infilling of the frontal sinus results in the opposite, a small decrease in strain magnitudes over the frontal. The infilled region shows low strains compared with the rest of the loaded cranium. Similar findings were made with respect to infilling of cancellous bone spaces and the maxillary sinus in a study of macaques (Fitton et al., 2015) and infilling of cavities in a varanoid lizard

mandible (Parr et al., 2012). These low strains within infilled spaces are consistent with the studies of Preuschoft and Witzel (2002) and Witzel (2011), who modelled crania as block materials with no hollow spaces, other than the brain cavity, nasal cavity, and orbits. They found low strains in the regions where sinuses arise, which led them to suggest that these hollow spaces might arise via bone adaptation to low strains via the mechanostat principle.

The mechanostat model (a refinement of ‘Wolff’s law;’ reviewed in the context of anthropology by Pearson and Lieberman [2004], and Ruff et al. [2006]) predicts that bone remodels according to strain magnitudes experienced relative to specific thresholds. If bone strains exceed a certain threshold bone deposition occurs, thus increasing bone mass. If bone strains are below another threshold then bone resorption occurs, thus decreasing bone mass (Frost, 1987, 1996, 2003; Turner, 1998). Even though it is not clear what that threshold is, and if it is generalized or site specific (Hillam et al., 1995; Skerry, 2000; Currey, 2006), it has been widely demonstrated that bone adapts to changes in mechanical loading via changes in mass (Jones et al., 1977; Kannus et al., 1995; Nordstrom et al., 1996; Goodship et al., 1998) and in mineral density (Kerr et al., 1996; Valdimarsson et al., 2005). As such, it is possible to hypothesize that the low strains experienced by the bone within the developing browridges influence the morphogenesis of the frontal sinus because low strains lead to osteoclastic activity and subsequent bone resorption.

Such adaptation of bony anatomy in relation to the frontal sinus is, nonetheless, compatible with the structural/spatial models that state that sinuses arise as a result of the spatial relationships of different components of the hominin cranium (Enlow, 1968; Zollikofer et al., 2008; Zollikofer and Weissmann, 2008; Smith et al., 2010; Smith et al., 2011). The primacy of spatial relationships is crystalized in the functional matrix hypothesis, which posits that the morphology of the upper face results from the spatial relationships between the eyes and the brain (Moss and Young, 1960).

While it is clear that spatial relationships between different cranial components impact browridge formation, in the Kabwe cranium the browridges are massive, larger than they need to be to simply accommodate the disjunction between the large face and frontal. This may indicate that the massive browridge arose for reasons that are additional to spatial relationships. It is, for instance, plausible that the browridge of Kabwe 1 might also be related to factors such as display and social signalling (Stringer, 2012b), which are important in primates and particularly so in humans (Ekman, 1979; Campbell et al 1999, Cieri et al., 2014).

If the large frontal sinuses of Kabwe 1 and variations in sinus morphology among hominins are explained by the mechanostat, the large frontal sinuses of *H. heidelbergensis*, and variations among other fossil hominins, need not have been specifically the target of selection, rather they may have arisen secondarily to changes in browridge and general cranial morphology that arose through adaptation or neutral evolutionary processes. In this scenario, sinus size is a secondary phenomenon, rather than an adaptive one. Whatever the cause of large browridges, the low strain magnitudes subsequently experienced within the browridge plausibly drove biomechanical bone adaptation via bone resorption, thereby sculpting the frontal sinus, as suggested by previous studies (O'Higgins et al., 2006; Zollikofer et al., 2008). This mechanism is also compatible with Witmer's (1997) hypothesis that paranasal sinuses form via opportunistic expansion of the epithelium under a given biomechanical regimen. If the frontal sinuses arise secondarily to browridge expansion, explanations of variations of sinus size of necessity need to focus on the browridges that house them.

As with the spatial hypothesis, biomechanical interpretations of frontal sinus morphogenesis do not preclude but rather may work in concert with other mechanisms that also underlie the initiation, presence, shape, and size of this structure, such as olfaction,

respiration, thermoregulation, nitric oxide production, and role in facial ontogeny (Tillier, 1977; Blaney, 1990; Bookstein et al., 1999; Rae and Koppe, 2004; Laitman, 2008; Lundberg, 2008; Márquez, 2008; Zollikofer and Weissmann, 2008; Smith et al., 2010). Thus, our results support Witmer's (1997) hypothesis, in that frontal sinus form is plausibly related to the interaction of loading history with the dynamics of the changing spatial arrangement of cranial components during ontogeny. Specifically, our results in Kabwe 1 are comparable to those of Witzel (2011) for Neanderthals. In that study, Witzel was able to predict sinus formation using biting mechanics and using a block cranium in which the spatial arrangement of the eyes, nasal cavity, dental arcade, and brain was specified. Thus, our results together with those of Witzel (2011) suggest that frontal sinus form and morphogenesis in recent hominins (i.e., *H. heidelbergensis* and Neanderthals) is probably explained by the shapes and relative sizes of cranial components, the spatial relationships among them during post-natal growth and development and the resulting biomechanical regimen arising during biting.

While this study has only used the Kabwe 1 cranium, it is likely that the form of cranial sinuses in other hominins is also impacted by the interaction of changing spatial arrangements, sizes, and shapes of cranial components (Zollikofer et al., 2008) with the strain regimen experienced by the bones throughout ontogeny. Thus, as the form and spatial relationships of different cranial components vary among different hominin species, so do the resulting stresses and strains experienced in the developing and growing frontal bone, and therefore brow and frontal sinus form change through alterations in mechanically regulated remodelling activity. This suggestion is based not only in our results but also on previous studies that have used comparable approaches and that have found low strains in the material that infills sinuses (Preuschoft and Witzel, 2002; Witzel, 2011; Fitton et al., 2015).

Because our study and that of Witzel (2011) are based on a single cranium, it will be of interest to further assess interactions between the form of the brow and frontal sinus and

functional loading in other hominins. Given the substantial variation in hominin brow and frontal sinus form, this is an important step to assess how changing browridge and frontal sinus form in different hominins impacts the deformations experienced by this region during biting similarly. As our ability to build accurate and reliable models improves, it will become feasible to test specific hypotheses concerning loading regimens and sinus form and to assess the extent to which loading and growth history can be retrodicted from such data. Thus, to test underlying biomechanical hypotheses of morphogenesis, FEA based simulations of bone adaptation to loads during growth (after the style of Witzel, 2011) could be used to ‘grow’ sinuses that can be compared with what is seen in life. The Neanderthals are an interesting case in point because it is plausible that their facial form and sinus morphology are in part a consequence of paramasticatory behavior (Rae et al., 2011). With improved methods, modelling detail and accuracy, this might be assessed by comparing what is seen in Neanderthals with the predictions of alternative loading scenarios, biting and chewing loads, or these loads plus simulated paramasticatory loads.

It should be noted that because infilling of the sinus did not markedly affect the strains experienced by nearby regions, and in the cranium as a whole, there are important consequences in relation to FE model simplification, which is always necessary. Particular issues arise with fossils, which are often imaged at resolutions that do not allow very detailed modelling of their internal anatomy and may be invaded by mineralized sedimentary matrix that is not distinguishable from bone in CTs. This study supports the application of simplifications, in particular infilling to the region of the frontal sinus in such circumstances. This study also supports the conclusions of a previous study in macaques, in which simplifications of models by infilling hollow trabecular bone and sinus spaces (Fitton et al., 2015) had little impact on mode, but greater impact on the magnitude of model deformation.

These results are also important in relation to the validity of the strategy of warping a base specimen to different target morphologies to speed up the model building process and to simplify building models of fossil material where parts may be fragmentary or missing (Sigal et al., 2008, 2010; Stayton, 2009; O'Higgins et al. 2011, 2012). Warping of cranial models will inevitably result in warped spaces within the bone that are very unlikely to represent the spaces that would arise as a result of mechanical adaptation. As such, models cannot be assured of reliably predicting deformations when submitted to FEA. By infilling and then warping, the issue might be circumvented, albeit predicted strain magnitudes will inevitably be lower than they should be, but modes of deformation can be expected to be approximately the same (Fitton et al, 2015). This potential strategy requires detailed sensitivity analyses before it can be adopted, but the evidence of this and previous studies (Fitton et al., 2015) leads us to be optimistic. Such studies, using warped solid models, would be explicit investigations of how skeletal form alone (excluding all internal anatomy) relates to function, rather than attempts to predict in vivo, physiological, strains. Such an approach is highly relevant in studies of human evolution where questions often exist about the functional and ecological implications of variations in craniofacial structures, such as facial pillars in australopiths (Rak, 2014) and midfacial prognathism or brow ridges in archaic *Homo* (Lieberman, 2011).

Conclusions

Hollowing or infilling the frontal sinus has little to no impact in strain vector magnitudes and directions experienced throughout the cranium under simulated masticatory loading. Moreover, low strains are experienced by circumorbital structures and, in particular, material infilling the frontal sinus. This supports the notion that sinus morphology may arise

at least in part by mechanical bone adaptation during growth, and that hominin frontal sinus form changes as the relative sizes, the spatial arrangement of different cranial components, and the subsequent biomechanical loading regimen changes. It would be of interest to test this prediction by performing similar studies in other hominins with different cranial morphologies or to use a single cranium in which midfacial projection is experimentally manipulated. Our results do not exclude possible (secondary) functions that have been suggested in the literature.

Acknowledgments

We thank Robert Kruszynski, Natural History Museum, London, UK, for access to the CT scan of Kabwe I and to the original fossil. Laura C. Fitton, Hull York Medical School, UK, for suggestions for the experiment and reconstruction. We are also grateful to Dr. William Sellers, University of Manchester, UK, for providing us with access to software in his laboratory to facilitate mesh reconstruction of fossils. We also thank the editors and reviewers for useful comments and suggestions.

Funding

Ricardo Miguel Godinho is funded by the Portuguese Foundation for Science and Technology (FCT; Ph.D. funding reference: SFRH/BD/76375/2011).

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Figures

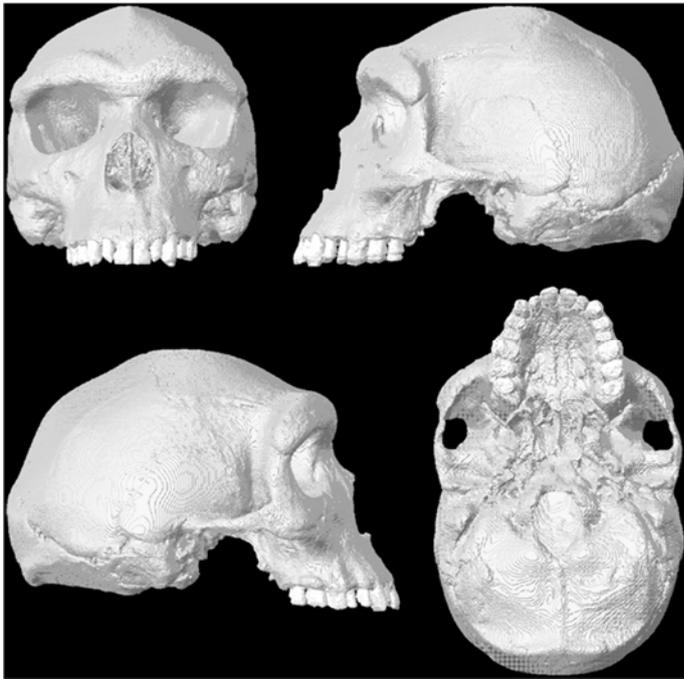


Figure 1. Reconstruction of the Kabwe 1 cranium.

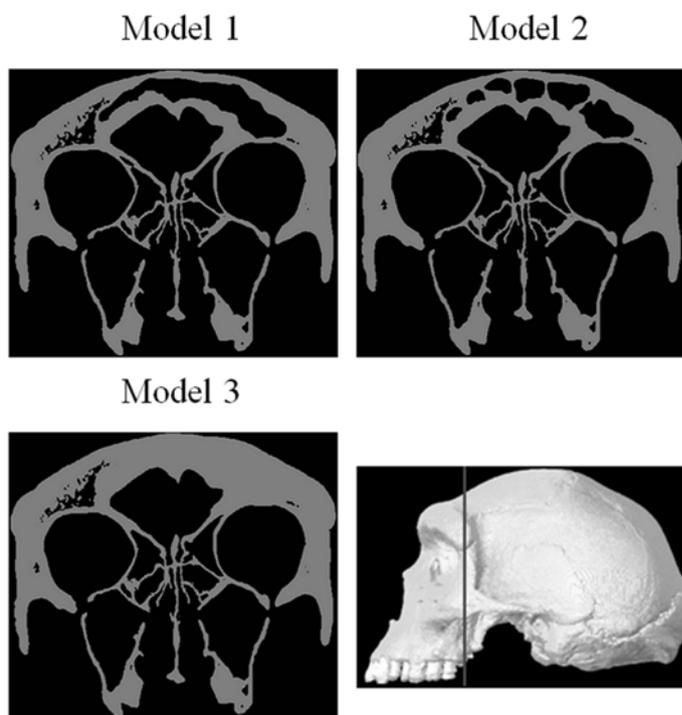


Figure 2. Coronal cross-section of models 1–3 used in biting simulations. Model 1 presents a hollow frontal sinus in which the original bony struts were removed. Model 2 presents the original frontal sinus with bony struts as captured by the CT scanner. Model 3 presents an infilled frontal sinus. The lower right frame shows a lateral view of the cranium with a vertical line indicating the plane of section used in the other frames.

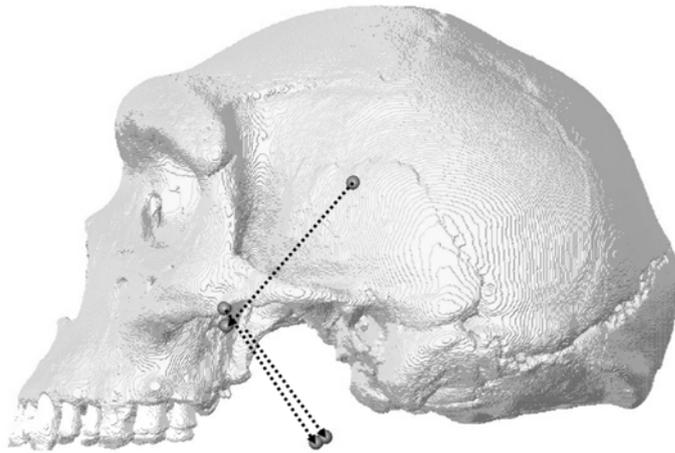


Figure 3. Left lateral view of the Kabwe 1 reconstructed cranium with estimated orientations (black dashed arrows) of modelled jaw elevator muscles (temporalis, masseter, and medial pterygoid) in the FEA simulations. The right muscle vectors are not shown for clarity purposes.



Figure 4. Thirty facial points (left) and 42 points in the frontal bone (right) used for extraction of ϵ_1 and ϵ_3 . The points are labelled according to the X axis of Figure 8.

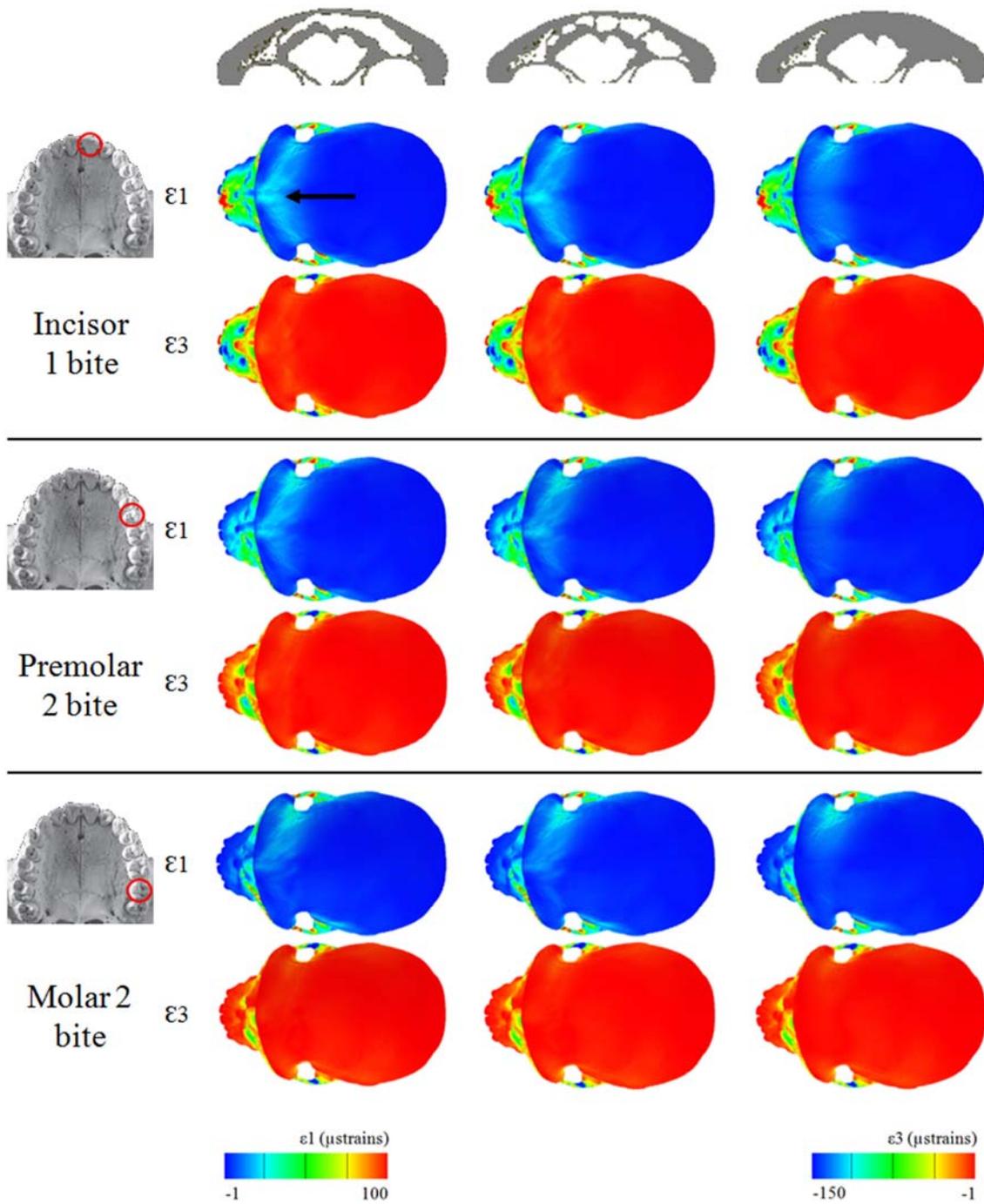


Figure 5. Maximum (ϵ_1) and minimum (ϵ_3) principal strain contour plots showing the strain magnitudes experienced over the cranium (norma superioris) under the three simulated bites. Rows 1 and 2 show the incisor bite; rows 3 and 4, the second premolar bite; rows 5 and 6, the second molar bite; left column shows the hollow sinus model; central column, the honeycomb model; right column, the infilled sinus model. The arrow indicates the region of the frontal bone where strain magnitudes, especially ϵ_1 , differ slightly between models.

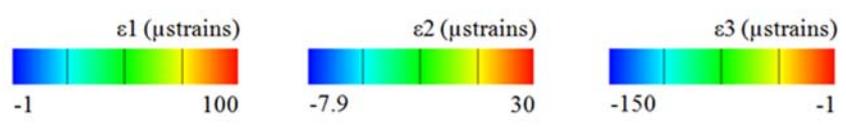
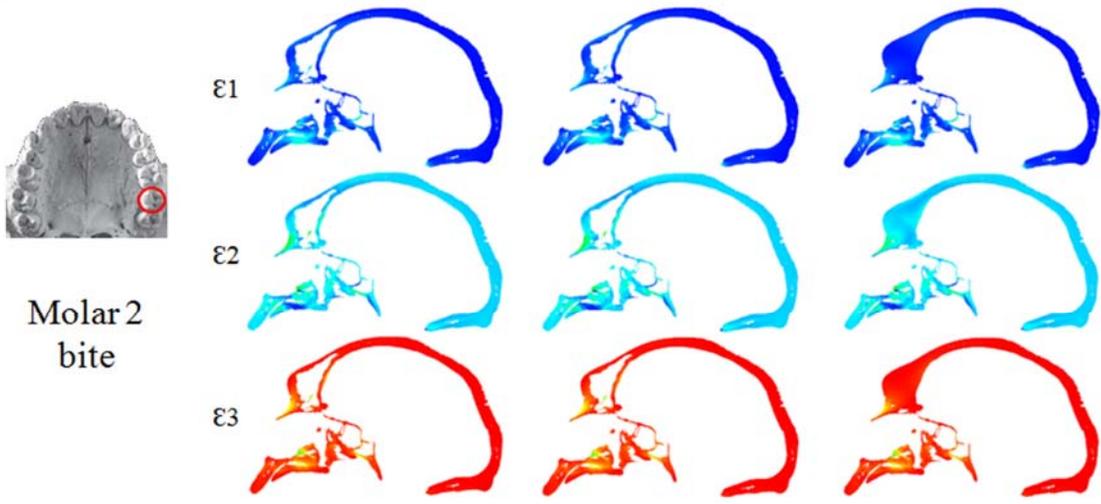
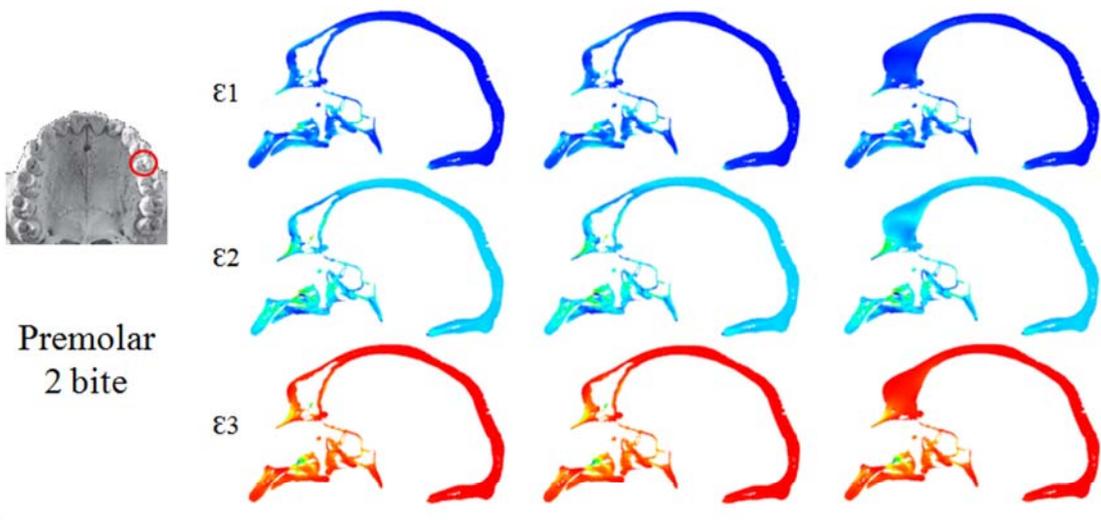
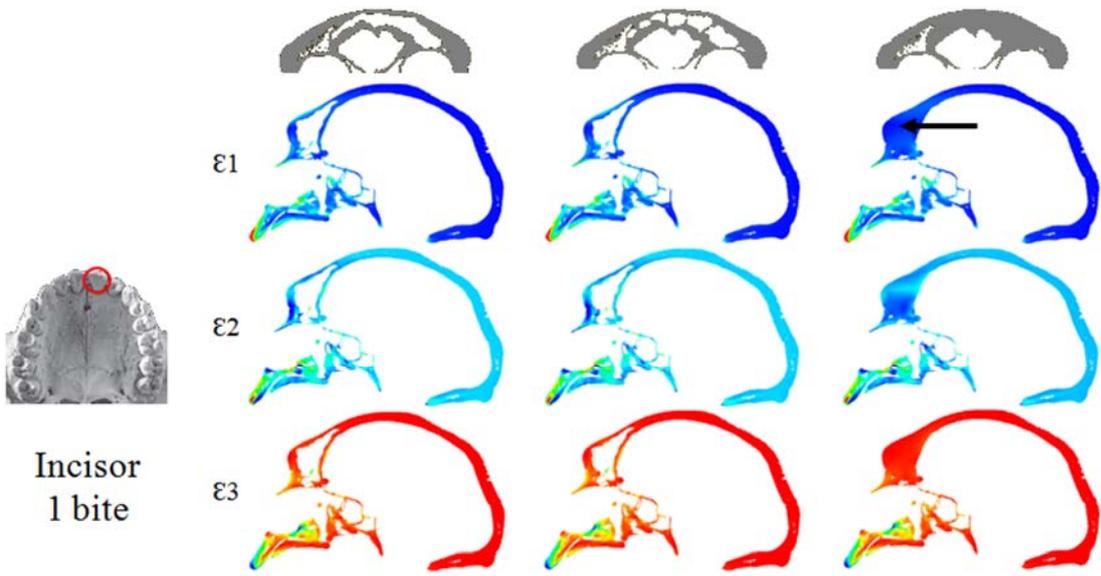


Figure 6. Principal strain contour plots from the three simulated bites in the three models. Rows 1, 2, and 3 show the incisor bite; rows 4, 5, and 6, the second premolar bite; rows 7, 8, and 9, the second molar bite; left column shows the hollow sinus model; central column shows the honeycomb model; right column shows the infilled sinus model. The arrow indicates the region of the frontal sinus (infilled). The reader is referred to the digital version of the article for a color version of the contour plots and to the text for interpretation.

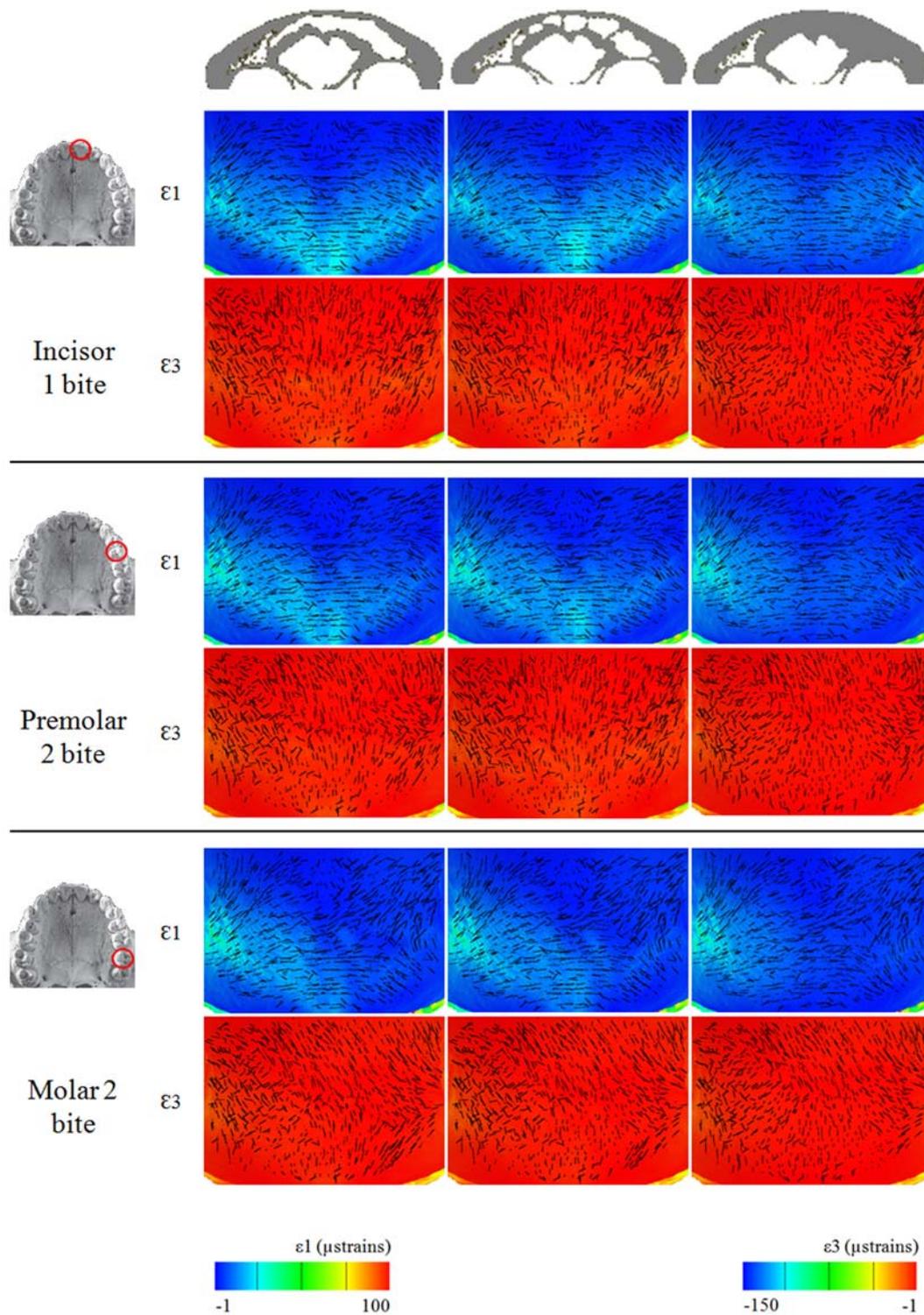


Figure 7. Maximum (ϵ_1) and minimum (ϵ_3) principal strains experienced by the browridge region of the frontal bone (norma superioris). The black lines depict strain directions. The reader is referred to the digital version of the article for a color version of the contour plots and to the text for interpretation.

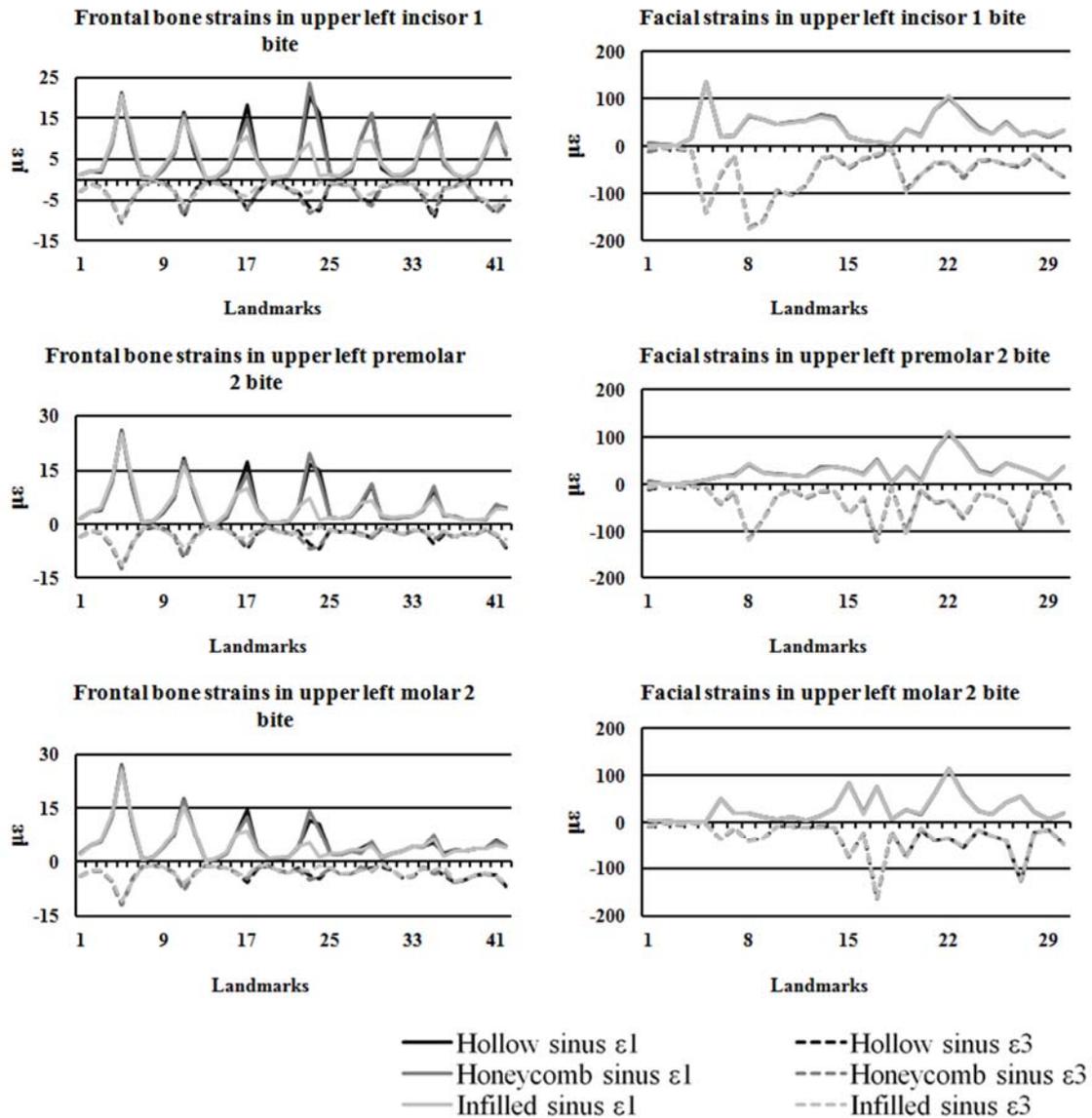


Figure 8. Maximum (ϵ_1) and minimum (ϵ_3) principal strain magnitudes experienced by the frontal bone, at 42 points (left column; see Fig 4), and over the face, at 30 points (right column; see Fig 4). The first row shows the results from simulation of the incisor bite; the second, of the second premolar; and the third, of the second molar bite. The labels in the x axis (named landmarks) correspond to the numbers in Figure 4.

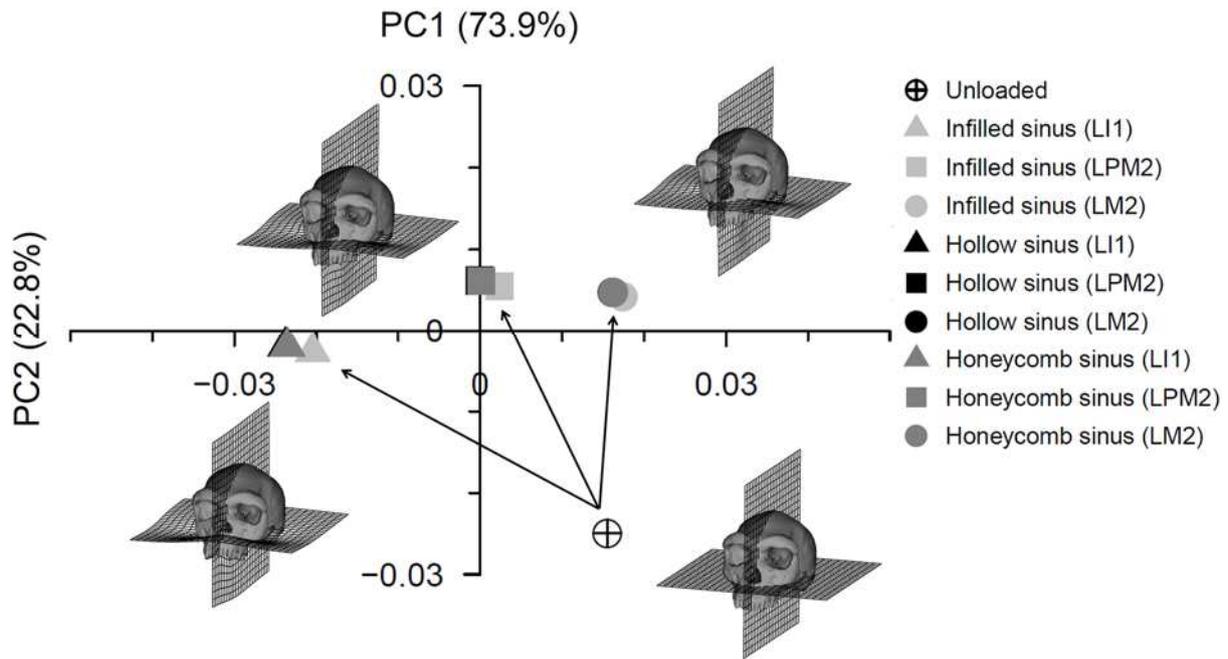


Figure 9. Principal components analysis of the modes of deformation (changes in size and shape when loaded) of the different models in all biting simulations. The inset, lower right cranium with overlain regular grids is the unloaded cranium (the reference form). The loaded crania with overlain deformed transformation grids (target forms) are shown adjacent to the load cases they visualize. Thus lower left represents the incisor bite, upper left, premolar and upper right, molar bites. The deformations of the grids and crania are multiplied by a factor of 1000 to facilitate visualisation.

Table 1: Forces applied by each muscle.

	Left	Right
Temporalis	168.02	170.67
Masseter	134.06	124.01
Medial pterygoid	124.01	117.49

Table 2: Landmarks used in the GM analysis of modes of deformation.

1	Bregma
2	Lambda
3	Inion
4 & 42	Asterion
5 & 43	Porion
6 & 44	Pterion
7 & 45	Frontomalare orbitale
8 & 46	Frontomalare temporale
9 & 47	Jugale
10 & 48	Zygotemporale superior
11 & 49	Zygotemporale inferior
12 & 50	Maxillofrontale
13 & 51	Zygoorbitale
14 & 52	Zygomaxillare
15 & 53	Superior rim of orbit
16 & 54	Infraorbital foramen
17	Nasion
18	Rhinion
19 & 55	Lateral Nasal Suture
20	Nasospinale
21 & 56	Alare
22	Alveolare
23 & 57	External Alveolar Incisor 2

24 & 58	External Alveolar Canine
25 & 59	External Alveolar Premolar 4
26 & 60	Zygomatic take-off
27 & 61	Inferior Distal Alveolar
28	Incisive Foramen
29	Palate maximum
30	Staphylion
31 & 62	Infratemporal crest
32	Basion
33	Opisthion
34 & 63	Lateral Edge of Foramen Magnum
35	Hormion
36	Glabella
37	Supra-glabella
38 & 64	Inferolateral choanal corner
39 & 65	Anterior edge of anterior ethmoid foramen
40 & 66	Posterior edge of posterior ethmoid foramen
41 & 67	Inferiormost margin of nasal aperture