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

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A B S T R A C T

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.

1. 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

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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 supero-posteriorly invading the fontal 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 Bourgine, 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). 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 found that people from latitudes with colder temperatures present smaller frontal (Koertvelyessy, 1972) and maxillary sinuses (Shea, 1977). Additionally, studies examining the interaction between nasal cavity and maxillary sinus volume in modern humans have 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, accommodating morphological adaptation of the nose to the environment. This has led several researchers to conclude that sinuses are not directly involved in air conditioning (Shea, 1977; Rae et al., 2003, 2006; O'Higgins 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 et al., 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 modeling the cranium as a bulk 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 adaption 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