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# The contribution of subsistence to global human cranial variation

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ABSTRACT

Diet-related cranial variation in modern humans is well documented on a regional scale, with ample examples of cranial changes related to the agricultural transition. However, the influence of subsistence strategy on global cranial variation is less clear, having been confirmed only for the mandible, and dietary effects beyond agriculture are often neglected. Here we identify global patterns of subsistence-related human cranial shape variation. We analysed a worldwide sample of 15 populations ($n = 255$) with known subsistence strategies using 3-D landmark datasets designed to capture the shape of different units of the cranium. Results show significant correlations between global cranial shape and diet, especially for temporalis muscle shape and general cranial shape. Importantly, the differences between populations with either a plant- or an animal-based diet are more pronounced than those between agriculturalists and hunter-gatherers, suggesting that the influence of diet as driver of cranial variation is not limited to Holocene transitions to agricultural subsistence. Dental arch shape did not correlate with subsistence pattern, possibly indicating the high plasticity of this region of the face in relation to age, disease and individual use of the dentition. Our results highlight the importance of subsistence strategy as one of the factors underlying the evolution of human geographic cranial variation.



## Introduction

Modern human geographic cranial diversity is well documented (Howells, 1973; Lahr, 1996), but the mechanisms underlying it remain unclear (Lieberman, 2008). Although masticatory stress is generally accepted as a major driver of regional human cranial variation (Carlson and Van Gerven, 1977; Hylander, 1977a; Paschetta et al., 2010), the influence of subsistence on global cranial morphological variation is a matter of debate (Lieberman, 2011; von Cramon-Taubadel, 2011a). Regional studies comparing agriculturalists with non-agriculturalists have found that this dietary difference affects the shape, size and positioning of the masticatory muscle attachments, mandible, zygomatic bone, neurocranium and the dental arch (Carlson and Van Gerven, 1977; Hylander, 1977a, 1977b; Varrela, 1992; Larsen, 1995; González-José et al., 2005; Sardi et al., 2006; Pinhasi et al., 2008; Paschetta et al., 2010). On a global scale, however, such diet-related variation has only been confirmed for the mandible (von Cramon-Taubadel, 2011a). This is unexpected, as modern humans inhabit many different ecosystems where the types of food available, and consequently the strains posed on the cranium during mastication, can differ significantly. The possible influence of subsistence strategy on the pattern of global cranial variation therefore remains unclear.

Studies investigating the effects of diet on modern human cranial variation have mainly focused on differences between agriculturalists and hunter-gatherers. Nevertheless, dietary adaptations have been documented throughout the hominin fossil record. Diet is considered an important driver of cranial variation among early hominins (e.g., Teaford and Ungar, 2000), while the inclusion of meat in the diet likely marked an important step in human evolution (e.g., Stanford and Bunn, 2001). Among Pleistocene *Homo*, Neanderthals are often considered to have relied heavily on meat from medium and large size terrestrial mammals on the basis of both isotopic and zooarchaeological data (e.g., Hockett and Haws, 2005; Bocherens, 2009; Richards and Trinkaus, 2009; but see Henry et al., 2010), while modern humans might have had a more flexible subsistence strategy (e.g., Stiner, 2001; Hockett and Haws, 2005; Richards and Trinkaus, 2009). Food types have therefore been important throughout human evolution both in terms of the strain they posed on the cranium as well as the nutritional value they added. In order to understand possible effects of diet on the evolution of modern human cranial diversity it is

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thus important to study the relationship between cranial shape and detailed differences in diets, testing not only for effects of agriculture, but also for effects of animal- versus plant-based food intake.

Here we study a sample of 15 worldwide populations of *Homo sapiens* with different subsistence strategies. In addition to testing for correlations between diet and shape of particular cranial regions (upper dental arch, masseter and temporalis muscle, general cranium), we discuss overlap in effects of diet, climate and population history on global human cranial variation as well as the functionality of observed diet-related cranial variation.

*Subsistence strategy and cranial adaptation*

Central to the hypothesis that subsistence strategy affects global human cranial shape is the notion that differences in subsistence patterns result in different diets and therewith in different food types consumed. Diets including tougher and harder food items are generally thought to require more masticatory effort to break them down compared with tender and soft agricultural products that have a high component of processed grains (Carlson, 1976; Carlson and Van Gerven, 1979; Kohyama et al., 2004). With a more mechanically demanding diet, cranial adaptations are expected that enhance the production and dissipation of high bite forces (Hylander, 1972). The size of the masticatory muscles and the three-dimensional arrangement of those muscles are particularly relevant in this respect (e.g., Wroe et al., 2010). Proposed adaptations for the generation of high bite forces, needed for processing more mechanically resistant food items, include a more anterior positioning of the masticatory muscles (temporalis and masseter) and posterior position of the dental arch to enhance the mechanical advantage of the chewing muscles (Hylander, 1977a; Lieberman, 2011), as well as overall enlarged masticatory muscles, traceable on the cranium by enlarged attachment sites on the zygomatic arch (masseter) and lateral side of the cranium (temporalis), and a larger cross-section of the infratemporal fossa (temporalis) (Weijs and Hillen, 1984, 1986; Demes and Creel, 1988). Dissipation of masticatory stress and reduction of bending moments occurs via enlarged vertical facial dimensions (Hylander, 1977a), flaring of the cheekbones and thicker alveolar processes (Lieberman, 2011).

Changes in diet are also shown to relate to changes in cranial size (Sardi et al., 2006; Perez et al., 2011), where less demanding diets correlate with smaller sized crania. In Nubian populations with a soft, agricultural diet, the size of the face decreased relative to total cranium size (Carlson and Van Gerven, 1977). Perez et al. (2011) found that in South American populations, the effect of diet on size is larger than the effect of diet on facial and neurocranial shape variation. Size differences are thus to be expected between groups with different subsistence patterns.

Importantly, not only adaptation, but also cranial plasticity might play an important role in diet-related shape variation. Studies on non-human mammals have indicated cranial shape changes induced by differences in food types during rearing (e.g., Lieberman et al., 2004; Menegaz et al., 2010; Ravosa et al., 2010). Human cranial regions under masticatory stress (zygotemporal and palatomaxilla) show higher variability than regions less affected by mastication (basicranium, upper face, vault), which might indicate higher plasticity in the masticatory regions of the cranium (von Cramon-Taubadel, 2009a). Nevertheless, the masticatory regions have been found to be equally reliable for inferring population history patterns (von Cramon-Taubadel, 2009a). Although environmental plasticity and adaptation to diet can be difficult to disentangle (O'Higgins et al., 2006), it has been shown in humans that typical diet related morphology of the mandible can already be traced in children before they start on their adult foods (Fukase and Suwa, 2008) and that population differentiation in craniofacial shape is already detectable at an early ontogenetic stage (e.g., Viðarsdóttir et al., 2002; Viðarsdóttir and Cobb, 2004; Gonzalez et al., 2010).

*Population history and climate*

Beyond such considerations relating cranial shape to masticatory behaviour, there is clear evidence that population history has a significant influence on global patterning of cranial morphology (e.g., Relethford, 1994; Roseman, 2004; Roseman and Weaver, 2004; Harvati and Weaver, 2006a, 2006b; Hubbe et al., 2009; Smith, 2009, 2011; von Cramon-Taubadel, 2011b). Regions of the human cranium have been found to preserve the signal of population history to varying extents, also depending on how the cranium is divided into separately studied compartments (von Cramon-Taubadel, 2014). Overall cranial shape reflects population history, and specifically the regions of the basicranium and the temporal bone shape show a very clear correlation with neutral genetic data (Harvati and Weaver, 2006a, 2006b; Smith, 2009; von Cramon-Taubadel, 2009a, 2009b). The vault shows varying results, depending on the populations studied and the landmarks included, being either strongly (Harvati and Weaver, 2006a, 2006b; von Cramon-Taubadel, 2009b) or weakly (Smith, 2009) related to neutral genetic distances. The mandible, maxilla, zygomatic bone and occipital bone are generally considered to perform less well as indicators of past population history (Smith, 2009; von Cramon-Taubadel, 2009b, 2014), which might be related to the fact that these parts of the cranium are involved in shaping overall facial morphology and/or relate to muscle attachment sites (masseter, temporalis and nuchal muscles) (von Cramon-Taubadel, 2014). The overall face and especially the region around the nasal opening shows stronger influences from climate (Roseman and Weaver, 2004; Harvati and Weaver, 2006a, 2006b; Hubbe et al., 2009; Noback et al., 2011). Although neutral evolution thus plays an important role in human variation (Relethford, 1994), part of craniofacial variation remains unexplained (Roseman and Weaver, 2004; Smith, 2009; von Cramon-Taubadel, 2009b, 2014). Furthermore, observed population differences in cranial shape and size are too large to be caused by genetic drift alone (Perez and Monteiro, 2009; Perez et al., 2011).

In addition to population history, climate also plays an important role in cranial diversity. A relationship has been found between climatic factors and morphology of the face in general (Roseman, 2004; Harvati and Weaver, 2006a; Hubbe et al., 2009), the midface (Evteev et al., 2014), nasal aperture and cavity (e.g., Wolpoff, 1968; Noback et al., 2011), sinus volume (Shea, 1977; but see Rae et al., 2003; Butaric et al., 2010) and cranial size (Beals et al., 1984; Harvati and Weaver, 2006a), suggesting adaptive selection. This selection signal is strongly influenced by populations from extremely cold regions (Roseman, 2004; Harvati and Weaver, 2006a, 2006b; Hubbe et al., 2009). The latter observation is important, as Arctic populations are also linked with extreme dietary adaptations (Hylander, 1972). Global studies specifically focussed on effects of climate versus population history on cranial variation have generally not included factors of subsistence differences (e.g., Harvati and Weaver, 2006a; von Cramon-Taubadel, 2009b; Betti et al., 2010).

*Closely linked: diet, climate and population history*

In order to detect diet-related cranial variation it is essential to correct for the effects of population history/genetic drift to prevent overestimating the effects of natural selection (Betti et al., 2010). As there is a very strong correlation between genetic and geographic distances (Manica et al., 2005; Ramachandran et al., 2005; Romero