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Mandibular ramus shape variation and ontogeny in *Homo sapiens* and *Homo neanderthalensis*

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ABSTRACT

As the interface between the mandible and cranium, the mandibular ramus is functionally significant and its morphology has been suggested to be informative for taxonomic and phylogenetic analyses. In primates, and particularly in great apes and humans, ramus morphology is highly variable, especially in the shape of the coronoid process and the relationship of the ramus to the alveolar margin. Here we compare ramus shape variation through ontogeny in *Homo neanderthalensis* to that of modern and fossil *Homo sapiens* using geometric morphometric analyses of two-dimensional semilandmarks and univariate measurements of ramus angulation and relative coronoid and condyle height. Results suggest that ramus, especially coronoid, morphology varies within and among subadult and adult modern human populations, with the Alaskan Inuit being particularly distinct. We also identify significant differences in overall anterosuperior ramus and coronoid shapes between *H. sapiens* and *H. neanderthalensis*, both in adults and throughout ontogeny. These shape differences are subtle, however, and we therefore suggest caution when using ramus morphology to diagnose group membership for individual specimens of these taxa. Furthermore, we argue that these morphologies are unlikely to be representative of differences in masticatory biomechanics and/or paramasticatory behaviors between Neanderthals and modern humans, as has been suggested by previous authors. Assessments of ontogenetic patterns of shape change reveal that the typical Neanderthal ramus morphology is established early in ontogeny, and there is little evidence for divergent postnatal ontogenetic allometric trajectories between Neanderthals and modern humans as a whole. This analysis informs our understanding of intraspecific patterns of mandibular shape variation and ontogeny in *H. sapiens* and can shed further light on overall developmental and life history differences between *H. sapiens* and *H. neanderthalensis*.

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1. Introduction

In primates, including humans and their fossil relatives, variation in mandibular morphology is patterned in large part according to the biomechanical demands of feeding behavior (i.e., configurations for producing muscle and/or bite forces required by specific diets), with these morphologies further influenced by phylogeny and constrained to maintain structural integrity (e.g., Greaves, 1974; Herring and Herring, 1974; Hylander, 1985; Spencer, 1995; Vinyard et al., 2003; Lague et al., 2008; Ross et al., 2012).

Although aspects of corpus morphology are frequently examined in both taxonomic and biomechanical analyses of fossil hominins (e.g., Leakey et al., 1995; Brunet et al., 1996; Ward et al., 2001; Skinner et al., 2006; Guy et al., 2008; Lague et al., 2008; Robinson and Williams, 2010; Robinson, 2012), ramus morphology is less frequently studied, likely in part due to the lack of preservation of this region in many fossils (but see Rak et al., 2007; Leakey et al., 2012). However, as the site of attachment of the masticatory muscles and the site of articulation between the mandible and cranium, the mandibular ramus is important for understanding patterns of masticatory and craniofacial variation across primates, including hominins. The goal of this study is to assess ramus shape variation in *Homo neanderthalensis* relative to modern and fossil

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Homo sapiens. We use these data to inform our understanding of intraspecific patterns of mandibular shape variation and ontogeny in *H. sapiens*, and for understanding ontogenetic differences between *H. sapiens* and *H. neanderthalensis* as indicated by the mandibular ramus.

1.1. Ramus morphology in extant primates and humans

In hominins, as in most mammals, the mandibular ramus terminates superiorly in two processes: the condylar process (which represents the mandibular component of the temporomandibular joint [TMJ]) and the coronoid process, on which the temporalis muscle inserts. Experimental analyses in which the temporalis attachment to the coronoid process has been partly or completely severed (Washburn, 1947; Avis, 1959), or where dental occlusion has been artificially manipulated (Isberg et al., 1990), have demonstrated that coronoid process morphology is highly dependent upon strains generated by the temporalis muscle, and, importantly, this morphology is labile during ontogeny. The position of the coronoid process (e.g., relative to the occlusal plane and/or mandibular condyle) is biomechanically relevant, since variation in this morphology leads to differences in temporalis lever arm length as well as the potential for muscle stretch (Maynard Smith and Savage, 1959; Greaves, 1974; Dubrul, 1977; Spencer, 1995; Vinyard et al., 2003; Ritzman and Spencer, 2009; Terhune et al., 2015).

Among great apes and humans, the ramus varies in relation to the occlusal plane, both in height and angulation. *Gorilla* tends to have the highest ramus, situated well above the occlusal plane, which is hypothesized to be biomechanically advantageous for increasing muscle attachment area (Freeman, 1988), increasing the moment arms of the masseter and temporalis muscles (Maynard Smith and Savage, 1959; Greaves, 1974; Dubrul, 1977; Spencer, 1995), and/or more evenly distributing bite forces along the post-canine tooth row (Herring and Herring, 1974; Greaves, 1980; Ward and Molnar, 1980; Spencer, 1995). In *Pan* and *Homo*, by contrast, the superior border of the ramus is closer to the occlusal plane (the ramus in *Pongo* is intermediate in height) (Humphrey et al., 1999; Schmittbuhl et al., 2007); this morphology is linked to increased jaw gaps (Herring and Herring, 1974; Vinyard et al., 2003; Terhune et al., 2015). In all taxa, angulation of the ramus relative to the occlusal plane decreases during ontogeny, with the ramus becoming more vertical with increasing age (e.g., Aitchison, 1963; Schultz, 1969; Taylor, 2002; Terhune et al., 2014). Coronoid process shape also varies across taxa, with *Gorilla* (and, to a lesser extent, *Pongo* and *Pan*) possessing a more hook-like, posteriorly oriented coronoid process that compresses the sigmoid notch and results in the deepest point in the sigmoid notch being more posteriorly positioned (Rak et al., 2007; Terhune et al., 2014). Humans, on the other hand, have more anterosuperiorly angled and projecting coronoid processes, with a wide, uncompressed, sigmoid notch (e.g., Nicholson and Harvati, 2006; Schmittbuhl et al., 2007; Terhune et al., 2014). A number of analyses have established that these species-specific morphologies appear early in ontogeny, perhaps as early as eruption of the first molars (Daegling, 1996; Williams et al., 2002, 2003; Boughner and Dean, 2008; Coquerelle et al., 2010; Singh, 2014; Terhune et al., 2014), and then are exaggerated by diverging ontogenetic trajectories (Terhune et al., 2014). This early divergence in mandibular morphology among great apes is consistent with the patterns of early shape divergence and non-parallel ontogenetic trajectories in craniofacial form (e.g., O'Higgins and Collard, 2002; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004, 2005; Strand Viðarsdóttir and Cobb, 2004; Terhune et al., 2013).

Similarly, several studies have quantified intraspecific variation in mandibular form in modern humans. Work by Humphrey et al.

(1999) examined mandibular shape variation (via caliper measurements) among 10 populations of humans and concluded that, although there is high intraspecific diversity in humans (particularly in height and breadth of the ramus and the distance between the coronoid process and condyle) there was no obvious geographic patterning of this shape variation. However, these researchers did find that individuals were correctly classified to geographic region 78.4% of the time using data from mandibular shape variables. Following on from this research, Nicholson and Harvati (2006) and Harvati et al. (2011) performed geometric morphometric analyses of mandibular shape in 10 populations of modern humans and found a number of shape differences among populations, including in aspects of ramal shape, such as the shape of the coronoid process. Nicholson and Harvati (2006) and Harvati et al. (2011) also noted that their two African populations (South Africans and East Africans) tended to have higher coronoid processes relative to the condyle when compared to other groups (though this difference was slight). Importantly, Nicholson and Harvati (2006) found that both geography and climate (i.e., cold versus warm adapted populations) influenced shape variation in modern human mandibular form. They also identified allometric variation in mandibular shape in modern humans, with larger individuals having superoinferiorly taller rami with more anteriorly-oriented and higher coronoid processes (with a corresponding deeper sigmoid notch). Nicholson and Harvati (2006) called particular attention to the divergence in shape of the North American Arctic population (i.e., populations from Alaska, Greenland, and Northern Canada), which tended to have a relatively lower and wider ramus than the other populations. Divergence in craniofacial shape of Arctic populations from other modern human groups has previously been noted by a number of researchers (e.g., Hrdlička, 1940a,b,c; Hylander, 1977; Harvati and Weaver, 2006; Smith et al., 2007a,b, 2013) and has most consistently been linked to unique paramasticatory behaviors in these populations (Hylander, 1977). These previously observed patterns in ramus variation were also supported in recent work by Katz et al. (2017), who found differences in ramus shape among populations of modern humans that practiced different subsistence strategies. Specifically, farming populations tend to have a taller mandibular coronoid process and narrower mandibular ramus than foraging populations. As with differences among hominid genera, these craniofacial shape differences among modern human populations appear to be established quite early in ontogeny, though the extent to which differences in postnatal ontogenetic trajectory contribute to ultimate adult differences among populations varies (Strand Viðarsdóttir et al., 2002; Smith et al., 2013). Notably, no previous analyses have specifically examined between-population variation in modern human mandibular ontogeny.

1.2. Neanderthal mandibular ramus shape and ontogeny

Variation in ramus shape has been assessed less frequently than other parts of the mandible in fossil hominins, primarily due to issues with preservation of this region. Only a handful of intact rami have been recovered from *Australopithecus* (e.g., *Australopithecus afarensis*: A.L. 822-1, A.L. 333-43; *Australopithecus sediba*: MH 1), *Paranthropus* (e.g., *P. robustus*: SK 23, SK 63), early *Homo* (e.g., KNM-ER 60000), and *Homo erectus* (e.g., KNM-WT 15000). Ramus morphology is better represented for later species in the genus *Homo*, and this is particularly true for *H. neanderthalensis*. In fact, ramus shape in Neanderthals—especially the shape of the coronoid process and sigmoid notch—has featured prominently in discussions of masticatory apparatus configuration in this species. Specifically, Rak et al. (2002:202) suggested that, compared to other hominins, the unique morphology of the ramus in Neanderthals is linked to a “profound specialization of the masticatory system” in

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