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

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A B S T R A C T

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

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 process: 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 postcanine 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 gapes (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

this taxon. This morphology—i.e., a low condylar process relative to the higher coronoid process, and a sigmoid notch with the deepest point situated closer to the condyle—was posited by Rak et al. (2002) to represent a specialization for increased jaw gape in Neanderthals relative to modern humans. Three-dimensional (3D) geometric morphometric analyses conducted by Nicholson and Harvati (2006) and Harvati et al. (2011) also identified these features of the anterosuperior ramus and successfully distinguished between human and Neanderthal mandibular form (including the aspects of the ramus noted by Rak et al., [2002]). Allometric analysis by Harvati et al. (2011) further found that, although adult Neanderthals do (on average) have larger mandibular and cranial sizes than *H. sapiens*, morphological differences between modern humans and Neanderthals are largely unrelated to allometry. Moreover, there are some similarities in mandibular shape between Neanderthals and North American Arctic populations that could be related to (para)masticatory behaviors shared by these groups (Nicholson and Harvati, 2006). Wolpoff and Frayer (2005), however, disputed the unique nature of these features in Neanderthals, pointing out that coronoid process morphology, condyle position, and sigmoid notch shape are variable across Neanderthals and similar morphologies can also be found in modern humans.

Differences in adult mandibular form (and indeed craniofacial form in general) arise during ontogeny as a complex series of interactions between genetic and environmental factors, yet it is unclear how the observed differences in coronoid process and sigmoid notch shape between adult *H. sapiens* and *H. neanderthalensis* are manifested during ontogeny. Geometric morphometric analyses of cranial growth in modern humans and Neanderthals suggest that differences in facial shape are established early in development, either prenatally or very early in postnatal development (Ponce de León and Zollikofer, 2001; Krovitz, 2003; Bastir et al., 2007). However, these analyses have been mixed in regard to whether postnatal shape trajectories in *H. sapiens* and *H. neanderthalensis* are parallel (Ponce de León and Zollikofer, 2001) or diverge (Krovitz, 2003; Bastir et al., 2007). Detailed analyses of dental development in Neanderthals (Ramirez Rozzi and Bermudez de Castro, 2004; Smith et al., 2007a,b, 2010) suggest that the teeth of this species grew very rapidly, with crown formation times for the third molar (M3) as much as 2–4 years earlier than M3 crown formation in *H. sapiens* (Smith et al., 2010; but see Guatelli-Steinberg et al., 2005). As dental development patterns are tightly linked with overall maturation (Smith, 1989), these data suggest that somatic growth in Neanderthals was considerably accelerated relative to *H. sapiens* (perhaps also compared to *Homo heidelbergensis*; Ramirez Rozzi and Bermudez de Castro, 2004). Similarly, Neanderthal brain growth has been shown to be fast relative to *H. sapiens* (Ponce de León et al., 2008; Gunz et al., 2010; but see Ponce de León et al., 2016). Together, these prior studies suggest that the prolonged, "human-like" schedule of growth and development did not evolve until relatively late in human evolution, perhaps not until the emergence of *H. sapiens* (e.g., Bermúdez de Castro et al., 1999; Dean et al., 2001; Smith et al., 2007a,b; Ponce de León et al., 2008). This accelerated life history pattern has been suggested to be driven by high adult mortality rates in Neanderthals (Trinkaus, 1995; Pettitt, 2000; Ramirez Rozzi and Bermudez de Castro, 2004; Schwartz, 2012). Notably, however, recent analysis of a subadult Neanderthal skeleton from El Sidrón cave (Spain) has further complicated this picture of Neanderthal growth and development (Rosas et al., 2017). Analyses of cranial, dental, and postcranial maturity suggest that, although this individual displays dental development similar to that of comparably aged modern humans, brain growth would have continued past the developmental period typically observed for modern humans, as would some aspects of the postcranial growth

(i.e., the thoracic and cervical vertebrae). It is unclear if these patterns are representative of Neanderthals as a whole, but, if so, they would serve to demonstrate that there remains considerable uncertainty regarding Neanderthal life history patterns, particularly in comparison to modern humans.

Investigation of variation in and the ontogeny of the mandibular ramus in *H. sapiens* and *H. neanderthalensis*, particularly in those aspects that have been suggested to differ strongly between these two species, permits a closer examination of the similarities/differences between these species in craniofacial shape, ontogeny, and function. More specifically, an investigation of the mandibular ramus, especially aspects of the coronoid process and sigmoid notch, can provide insight into the relative importance of phylogeny and function in shaping ontogenetic patterns more generally, since this region is constrained by its functional role in mastication. As a structural link between the dentition and the facial skeleton—two anatomical regions for which the differences between Neanderthals and modern humans have been more widely studied with regard to the rate and duration of ontogeny—the mandibular ramus can also shed further light on overall developmental and life history differences between these species.

1.3. Aims of this study

In the light of previous research, which has identified significant differences in ramus shape between *H. sapiens* and *H. neanderthalensis*, this study assesses anterosuperior ramus shape (i.e., the coronoid process, sigmoid notch, and anterior margin of the ramus) in these two species. Specifically, we address two research questions, and discuss potential functional and/or biomechanical consequences of any such observed variation:

1. Does ramus shape differ significantly (a) among human populations, and (b) between *H. sapiens* and *H. neanderthalensis*?
2. To what extent are patterns of postnatal ontogenetic allometric shape change in the anterosuperior ramus similar or different among human populations and between *H. sapiens* and *H. neanderthalensis*?

2. Materials and methods

2.1. Data collection

A total of 292 specimens from two species, *H. sapiens* and *H. neanderthalensis*, were examined for this analysis (Table 1; Supplementary Online Material [SOM] Table S1). The recent human sample was divided among four populations: Alaskan Inuit, Hungarians, Nubians, and Southeast (SE) Asians. Human specimens are housed at the American Museum of Natural History or the School of Human Evolution and Social Change at Arizona State University. Whenever possible, approximately equal numbers of females and males were included for each group, though sexes were not analyzed separately since the majority of the subadults were unidentifiable to sex. A sample of 18 fossil *H. sapiens* specimens was also included to provide a similarly geologically aged comparison to the Neanderthal sample (Table 2). These fossil samples of *H. neanderthalensis* and *H. sapiens* are not representative of biological populations in the same general way that the recent modern human samples are, and therefore unavoidably incorporate considerable temporal and geographic variation. Further, although we avoided including specimens with considerable postmortem damage, the likelihood remains that some taphonomic effects may be present in the fossil samples. Though these sample sizes are somewhat small, they represent the bulk of Middle and Late Pleistocene fossil specimens assigned to

Table 1
Samples used in this analysis.

| | Sample size by age category | | | | |
| | 1 | 2 | 3 | 4 | |
Species	No permanent teeth erupted	Only M1 erupted and in occlusion	M1 and M2 erupted and in occlusion	All molars erupted	Total
Homo sapiens	37	53	44	140	274
Alaskan Inuit	13	21	12	47	93
Hungarians	5	13	21	48	87
Nubians	18	16	5	19	58
Southeast Asians	0	0	3	15	18
Fossil	1	3	3	11	18
Homo neanderthalensis	3	2	2	11	18
					Total *n*=292

H. sapiens and *H. neanderthalensis* in which the ramus and coronoid process are intact. Thus, although we acknowledge that our conclusions may be limited by the small samples currently available, we consider it important to document the shape variation represented by the current sample and suggest that our analysis provides an important first step in assessing the variation

Table 2
Fossil specimens included in this study.

	Specimen	Abbreviation	Developmental age	Original or cast?	Photo source; institution[a]	Geological age and source	
Homo neanderthalensis	Gibraltar 2	G2	Category 1	Original	CET photo; BNHM	24—30 ka	Finlayson et al. (2006)[b]
	Pech de l'Aze	PdA	Category 1	Original	CET photo; MdlH	41—51 ka	Soressi et al. (2006)
	Roc de Marsal	RdM	Category 1	Original	Schwartz and Tattersall (2002)	60—70 ka	Guerin et al. (2012)
	Teshik-Tash	T-T	Category 2	Cast	CET photo; IPH	57—24 ka	Glantz et al. (2009)
	Scladina	Scl	Category 2/3[c]	Original	Smith et al., (2007a,b)	80—127 ka	Smith et al. (2007a,b)
	Ehringsdorf	Ehr	Category 3	Cast	CET photo; IPH	230 ka	Blackwell and Schwarcz (1986)
	Krapina C	KrC	Category 3	Cast	CET photo; IPH	130 ka	Rink et al. (1995)
	Amud 1	Am	Category 4	Cast	CET photo; IPH	53 ka	Rink et al. (2001)
	Krapina 59	Kr59	Category 4	Cast	CET photo; IPH	130 ka	Rink et al. (1995)
	La Ferrassie 1	LaF	Category 4	Original	CET photo; MdlH	43—45 ka	Guerin et al. (2015)
	La Quina 5	LaQ	Category 4	Original	CET photo; MdlH	48—42 ka	Higham et al. (2014)
	Le Moustier	LeM	Category 4	Cast	CET photo; AMNH	40—45 ka	Higham et al. (2014)
	Montmaurin	Mon	Category 4	Original	CET photo; MdlH	240—190 ka	Vialet et al. (2018)
	Regourdou 1	Reg	Category 4	Cast	CET photo; IPH	Uncertain (potentially MIS5)	Gomez-Olivencia et al. (2013)
	Shanidar 2	Sh2	Category 4	Cast	CET photo; NMNH	70—80 ka	Schwartz and Tattersall (2002)
	Tabun 1	Ta1	Category 4	Original	CET photo; BNHM	107—198 ka	Millard (2008)
	Tabun 2	Ta2	Category 4	Cast	CET photo; IPH	107—198 ka	Millard (2008)
	Zafarraya	Za	Category 4	Original	Schwartz and Tattersall (2002)	30—46 ka	Michel et al. (2013)
Homo sapiens	Rochereil (child)	RoC	Category 1	Original	CET photo; IPH	11 ka	Mafart et al. (2007)
	Estelas	Est	Category 2	Original	CET photo; MdlH	Unknown	Roule and Regnault (1895)
	Jebel Irhoud 3	JI3	Category 2	Original	Smith et al. (2007a,b)	315 ka	Hublin et al. (2017)
	Solutre	Sol	Category 2	Original	CET photo; IPH	12—25 ka	Banks (1996), Turner (2002)
	Abri Lachaud	AbLa	Category 3	Original	CET photo; IPH	Solutrean/ Magdalenian	Cheynier (1953), Ferembach (1957)
	Laugerie Basse	LaBa	Category 3	Original	CET photo; MdlH	Magdalenian	Boyle (1996)
	Dolní Vestonice XV	DV-XV	Category 3/4[c]	Original	Schwartz and Tattersall (2002)	27.64 ka	Klima (1988)
	Abri Pataud	AbPa	Category 4	Original	CET photo; MdlH	22 ka	Mellars et al. (1987)
	Barma Grande 5	BG5	Category 4	Original	Schwartz and Tattersall (2002)	20—30 ka	Formicola et al. (2004)
	Chancelade	Cha	Category 4	Original	Schwartz and Tattersall (2002)	Magdalenian	Sollas (1927)
	Dolní Vestonice XVI	DV-XVI	Category 4	Original	Schwartz and Tattersall (2002)	26.4—29 ka	Svoboda (1988)
	Fish Hoek	FH	Category 4	Original	Schwartz and Tattersall (2002)	12 ka	Schwartz and Tattersall (2002)
	Lespugue	L'Esp	Category 4	Original	CET photo; IPH	Gravettian	Petillon (2012)
	Rochereil (adult)	RoA	Category 4	Original	CET photo; IPH	Azilian	Ferembach (1974)
	Skhul V	SkV	Category 4	Cast	CET photo; UArk	59—115 ka	Millard (2008)
	Vogelherd	Vog	Category 4	Original	Schwartz and Tattersall (2002)	5 ka	Conard et al. (2004)
	Zhoukoudian Upper Cave 101	Zh	Category 4	Cast	CET photo; UArk	10—34 ka	Norton and Gao (2008)
	Oase 1[b]	Oa	Category 4	Original	Trinkaus et al. (2003)	37—42 kyr	Fu et al. (2015)

[a] Most photographs were taken by CET on the original specimens although some casts were also employed. In addition, published photographs of some specimens were taken from the literature. AMNH = American Museum of Natural History, BMNH = British Museum of Natural History, IPH = Institute de Paléontologie Humaine, MdlH = Musée de l'Homme, NMNH = National Museum of Natural History, Smithsonian Institution, UArk = University of Arkansas.

[b] Genetic analyses suggest partial Neanderthal ancestry for this individual (Fu et al., 2015).

[c] Data for these specimens suggest they are on the cusp of two different age categories. The second molar of Scladina is mostly erupted but is not quite in occlusion; this specimen was placed in Category 2 for statistical analysis. Descriptions of Dolní Vestonice by Trinkaus and Svoboda (2005) suggest that the third molars were either not fully in occlusion or had recently erupted into occlusion; this specimen was therefore placed in Category 3 for analysis.

in and phylogenetic valence of ramus morphology in *H. sapiens* and *H. neanderthalensis*.

Each individual was assigned to an age category based on dental eruption. Category 1 included individuals with no permanent teeth in occlusion, Category 2 individuals included those specimens with the first molar (M1) erupted and fully in occlusion, Category 3 individuals were those with the second molar (M2) fully erupted and in occlusion, and Category 4 individuals were those with M3 fully erupted and in occlusion. Previous work by our research team (Terhune et al., 2014) separated individuals in Category 4 into those with and without an unfused spheno-occipital synchondrosis (SOS). However, because our previous analysis suggests there is no significant difference in ramus shape between these age categories, we lumped these specimens into a single category. In humans, the age categories we use correspond roughly to chronological ages 0—6.5 years (Category 1), 6.5—12.5 years (Category 2), 12.5—18/20.5 years (Category 3), and greater than approximately 20 years of age (Category 4) (Ubelaker, 1989; White, 2000; AlQahtani et al., 2010).

Notably, dental maturation patterns in Neanderthals have been observed to differ from those of modern humans in that Neanderthals have shorter crown formation times that ultimately contribute to a comparatively rapid molar development in this species relative to *H. sapiens* (Smith et al., 2010; but see Rosas et al., 2017). Current estimates place the completion of M1 crown formation in Neanderthals at roughly six months earlier than modern humans, and the initiation of M3 crown formation as much as 2—4 years earlier in Neanderthals (Smith et al., 2007a,b, 2010). Thus, we acknowledge that it is likely that these age categories are not homologous across species; however, molar eruption patterns are important markers of weaning (M1) and the onset of sexual maturation (M3) across great apes and humans (Smith, 1991, 1994; Schwartz, 2012), and are therefore meaningful life history markers. Further, given uncertainties in estimating developmental age from dental eruption, we follow previous studies (e.g., O'Higgins and Collard, 2002; Mitteroecker et al., 2004, 2005; McNulty et al., 2006; McNulty, 2012; Singleton, 2012) and assess patterns of ontogenetic allometry (i.e., shape change in relation to size), rather than growth (change in size with age) or development (change in shape with age).

Ramus morphology was quantified using 44 two-dimensional semilandmarks and landmarks located along the anterior and superior margin of the ramus, the coronoid, and the sigmoid notch (Fig. 1). Photographs of the lateral aspect of the ramus were taken with the ramus oriented parallel to the lens of the camera. A scale

(placed at the same distance from the camera lens as the ascending ramus) was included in each photograph. Landmarks were collected on each photograph using the program tpsDig (Rohlf, 2013). All photographs were digitized by CET to minimize inter-observer error, which can potentially impact results, especially among closely related species (Robinson and Terhune, 2017). A sensitivity analysis conducted for this study determined that differences due to slight variation in the position of the camera relative to the specimen were negligible when compared to differences between specimens. To assess this, we photographed four specimens (two chimpanzees and two humans) at varying angles (approximately 3° intervals over an arc of 12°) and with the camera positioned either level to the specimen or slightly above. In no instances were photographs of one specimen more similar to another specimen than to different photos of the same specimen (i.e., inter-trial distances were smaller than inter-specimen distances). This result suggests that differences in the position of the camera relative to the specimen are minimal, which allowed us to use published lateral view photographs of fossil specimens that were otherwise not accessible to the authors. Full details of the sensitivity analysis can be found in the SOM, including Figures S1—3.

In addition to the 44 semilandmarks describing the anterior margin of the ramus, we also collected landmarks describing the alveolar margin: one landmark was placed on the most anterior point of the alveolar margin, and one was placed where the anterior ramal margin crosses the alveolar margin. Due to damage in some fossil specimens, the former landmark was not considered replicable enough across specimens to include in the geometric morphometric analyses. In other words, although we are confident that this landmark accurately captures the most anterior point on the alveolar margin in all specimens, we are not confident that this landmark is replicable enough (i.e., homologous across specimens) for a geometric morphometric analysis due to damage in several fossil specimens (i.e., this landmark is not always equivalent to alveolare). We did, however, employ these landmarks to measure the angle of the ramus (in degrees) relative to the alveolar margin, height of the coronoid above the alveolar margin, and height of the condyle relative to the alveolar margin for individual specimens (Fig. 1). Relative coronoid height was then expressed as a dimensionless ratio of coronoid height/condylar height for further analysis.

2.2. Data analysis

The landmark data were analyzed via geometric morphometric methods, with analyses conducted for the entire sample and separately for adult (Category 4) individuals only. Landmarks were superimposed via generalized Procrustes analysis (GPA) with the semilandmarks allowed to slide to minimize bending energy. Shape variation in the sample was examined using principal components analysis (PCA), and we examined the relationship of each principal component (PC) axis to size by regressing the PC scores on the natural log of centroid size and employing a permutation test with 9999 iterations to assess significance. To examine allometry in the entire sample, we performed a multivariate regression of shape on log centroid size. A permutation test with 9999 iterations was employed to assess significance of the multivariate regression model. Thin plate spline analysis (TPSA) was used to examine differences in shape between species and age categories and Procrustes distances were calculated between age groups and between species/geographic groups in shape space. A permutation test with 9999 iterations was used to determine the significance of differences in the Procrustes distances among age and taxonomic/geographic groups.
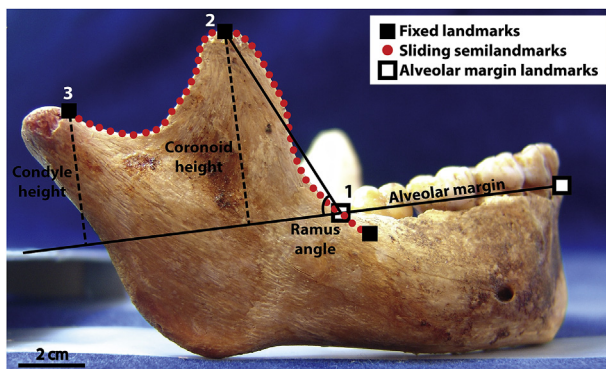

Figure 1. Lateral view of a subadult *H. sapiens* mandible showing the landmarks and measurements used in this study. Landmarks are identified as follows: 1) most inferior point on ramal root; 2) coronion; and 3) point at which the sigmoid crest meets the articular surface of the mandibular condyle. Note: alveolar margin landmarks were used to calculate ramus angle, and coronoid and condyle height, but were not included in the geometric morphometric analysis.

The divergence of the ontogenetic allometric trajectories between *H. sapiens* and *H. neanderthalensis*, and among populations of *H. sapiens*, was assessed by calculating the angle between the regression coefficients produced by a multivariate linear regression of shape (i.e., the Procrustes rotated coordinates) onto the natural log of centroid size. First, all populations and species were included in a single GPA so that all specimens were in a common morphospace. Next, a multivariate regression of the Procrustes residuals onto the natural log of centroid size was conducted separately for each population and species, and the regression coefficients were extracted to form a trajectory vector (Anderson and Ter Braak, 2003; Collyer and Adams, 2007; Adams and Collyer, 2009; Piras et al., 2010). The angle between pairs of taxa was then calculated as the arccosine of the dot product of the vectors. Angle significance was evaluated via a permutation test (9999 iterations) of the regression residuals, where group membership was randomly shuffled but the sample sizes in age categories were held constant (following McNulty et al., 2006). Holding sample sizes constant ensures that age categories with small samples are not artificially increased during this shuffling; this method provides a more conservative estimate of the significance between ontogenetic trajectories than if group sizes were allowed to fluctuate during the permutation process (McNulty et al., 2006). Geometric morphometric analyses were conducted in the software MorphoJ (Klingenberg, 2011) and in the program R (R Development Core Team, 2008) using the package "geomorph" (Adams and Otárola-Castillo, 2013); ontogenetic trajectory analyses were conducted in the program R using code modified from geomorph (Otárola-Castillo, personal communication). Although our subadult sample sizes are admittedly small, the use of permutation tests for assessing differences between groups and the significance of our regression models allows us to circumvent many assumptions that would otherwise be involved in parametric tests. We further guard against Type I error by employing a sequential Bonferroni adjustment (Rice, 1989).

Data describing the angle of the ramus relative to the alveolar margin and relative coronoid height were visualized using box and whisker plots and statistically evaluated via one-way analysis of variance (ANOVA). Because the ramus angle data are circular, we employed a circular ANOVA for this variable from the R package "circular" (Agostinelli and Lund, 2017), performing both a single overall circular ANOVA for each species, and a series of pairwise circular ANOVAs to examine whether age categories within each species were significantly different for this variable. For these pairwise comparisons, *p*-values were adjusted using the "p.adjust" function in R with the method "fdr" (Benjamini and Hochberg, 2001). Box plots and the ANOVA for relative coronoid height (with Tukey's Honestly Significant Difference [HSD] tests for multiple comparisons) were conducted in IBM SPSS Statistics (Version 22) (IBM Corp., 2013). Correlations (*r*) and *p*-values were calculated to describe the relationship between ramus angle and relative coronoid height; again, because ramus angle is circular, we employed methods outlined in Zar (1999) for angular—linear correlation analysis. We protected from Type I error in our correlation analysis by performing a sequential Bonferroni adjustment (Rice, 1989).

3. Results

3.1. Variation in morphospace

Principal components analysis of the entire sample (Fig. 2) illustrates shape variation within and between species (i.e., *H. sapiens* versus *H. neanderthalensis*) and among age categories. Shape variation along PC 1 (which represents 56.5% of the variance in the sample) is primarily related to the overall height of the ramus

as well as the relative height of the coronoid process and width of the sigmoid notch. However, there is no notable separation among age categories or species along this axis. There is a slight trend for the Alaskan Inuit sample (and to a lesser extent the fossil *H. sapiens*) to fall more negatively along this axis, with the SE Asian, Hungarian, and Nubian samples falling more positively on this axis, but there is overlap among groups. On PC 2 (21.8% of sample variance), shape variation is primarily linked to the shape of the anterior border of the ramus and the size and superior projection of the coronoid process; again there is little to no consistent separation among age categories, human populations, or species along this axis. Principal component 3 (8.3% of the sample variance), however, does separate *H. sapiens* and *H. neanderthalensis*, although there is still some overlap between these species on this axis. Notably, there is no clear pattern related to age category on PC 3. Further, fossil *H. sapiens* specimens are no closer to *H. neanderthalensis* specimens than their modern counterparts, as might be anticipated if variation was related to dietary differences between hunter-gatherer populations (i.e., fossil *H. sapiens* and *H. neanderthalensis*) and agricultural populations (e.g., Carlson and Van Gerven, 1977; Katz et al., 2017). Shape variation along this axis is linked to the anteroposterior width of the coronoid process; specimens on the positive end of the axis (where *H. sapiens* primarily resides) show a thinner coronoid process with a wide sigmoid notch, whereas specimens (i.e., Neanderthals) at the negative end of this axis tend to have coronoid processes that are wider anteroposteriorly, a morphology that consequently causes the sigmoid notch to appear compressed. Although both PC axes 1 and 3 are significantly correlated with size (at $p < 0.005$) the r^2 values for these relationships are very small (PC 1 $r^2 = 0.025$; PC 3 $r^2 = 0.024$). There is no significant relationship between PC 2 and centroid size.

Shape differences among age categories and modern human populations are subtle, as revealed by the TPSA (Fig. 3). Although more marked shape change occurs during ontogeny in both fossil *H. sapiens* and *H. neanderthalensis*, little shape change between age categories is observable in most modern human populations. It is possible that these changes in the fossil groups represent noise in the data due to the small samples sizes for each of these groups. Procrustes distances calculated between populations and species and between age categories within populations and species, however, indicate that there are significant shape differences among populations and species even after Bonferroni adjustment (Table 3). Procrustes distances between Neanderthals and all of the modern human populations are statistically significant. Interestingly, however, the distance between the Neanderthal and fossil *H. sapiens* sample is not significant. Notably, all of the Procrustes distances between the Alaskan Inuit sample and the fossil and modern human samples, as well as the *H. neanderthalensis* sample, are significantly different at ($p \leq 0.0003$). This is also true when the populations are broken down by age category (SOM Table S2). Thus, the shape of the Alaskan Inuit ramus seems to be significantly different in morphospace from all other groups, regardless of age. As can be seen in the TPSA plot, the Alaskan Inuit ramus displays a less superiorly projecting coronoid process that is positioned at approximately the same level as the mandibular condyle. This is not true of the other modern human samples, fossil modern humans, or the Neanderthals. Examination of Procrustes distances between age categories within each species (Table 4) reveals that there are no significant differences in Procrustes distance between *H. neanderthalensis* individuals in any age category. *H. sapiens* in age categories 1 and 2 differ significantly from those in age categories 3 and 4. However, these significant differences in age categories for *H. sapiens* are only present when the sample is pooled; when human populations are examined separately, the pattern of differences in shape between
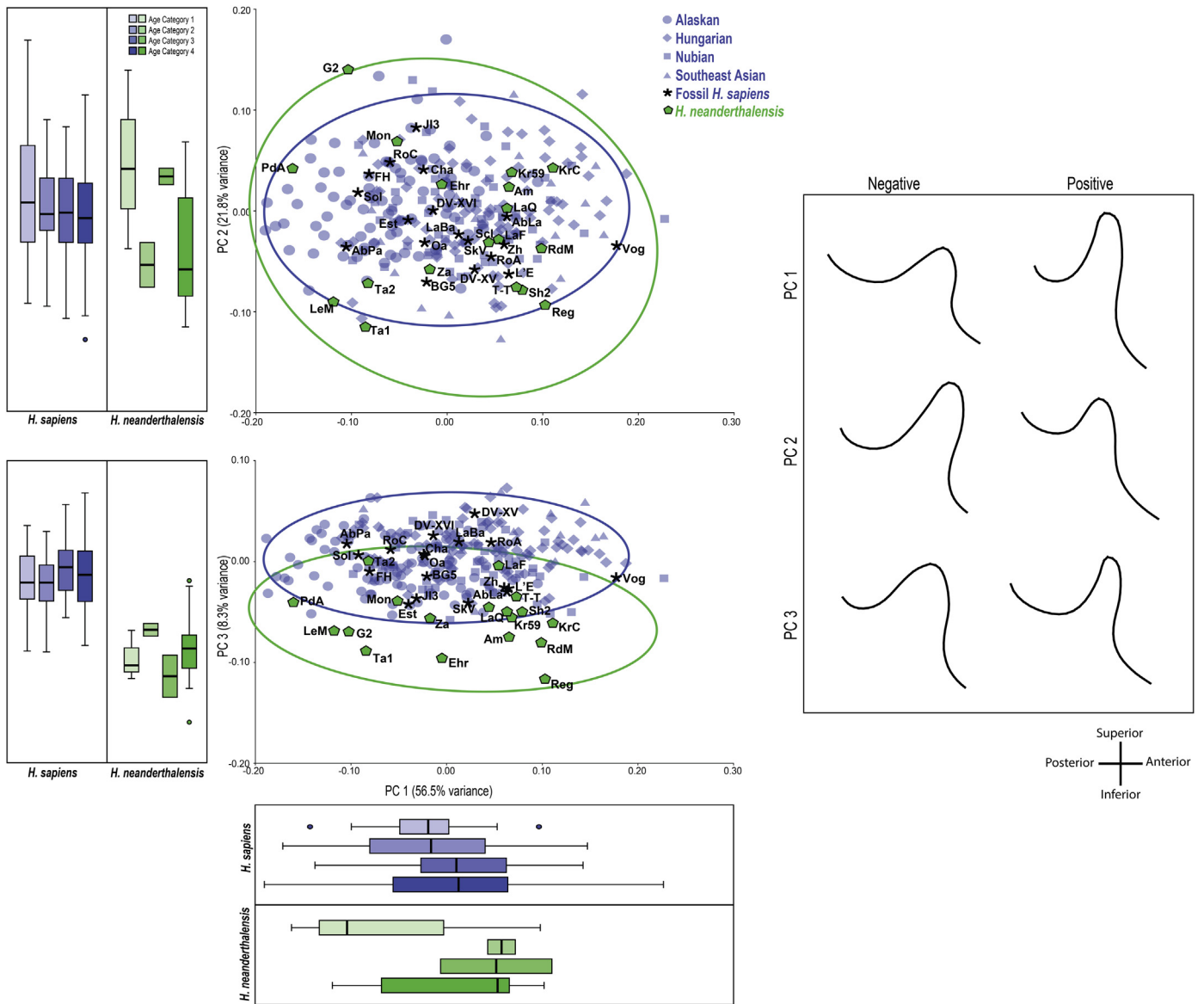
Figure 2. Bivariate plots of principal component (PC) axes 1, 2, and 3 along with corresponding box plots illustrating the distribution of individuals in different age categories along those PC axes, and wireframe diagrams showing shape variation along these axes. Darkened bars represent the median value for each group, boxes show the interquartile range (25th to 75th percentile), and the whiskers extend to 1.5 times the interquartile range. Outliers are designated by circles. Circles on PC plots represent 95% confidence ellipses for *H. sapiens* and *H. neanderthalensis*. Please see Table 2 for specimen abbreviations.

age categories varies considerably (SOM Table S2). In the Alaskan sample, age category 1 was significantly different from categories 2 and 4; in the fossil *H. sapiens* sample, significant differences were observed between age categories 1 and 3 and between age categories 2 and 3, and in the Nubian sample there was only one significant difference (i.e., between age categories 1 and 4). There were no significant differences between age categories in the Hungarian sample.

Separate analysis of the adult sample (i.e., age category 4 individuals only) reveals a pattern of variation that is very similar to analyses that included the entire sample (SOM Fig. S4). These results also corroborate conclusions drawn from previous studies by Rak et al. (2002) and Harvati et al. (2011) with regard to the differences between Neanderthals and modern humans—i.e., they demonstrate that, compared to modern humans, Neanderthals possess sigmoid notches with the deepest point located more posteriorly and coronoid processes that are anteriorposteriorly

wider and slightly taller (refer to SOM Fig. S5). Due to the similarities with the analysis including the entire sample, the results of the adult-only analyses are presented in the SOM.

3.2. Regression analysis and ontogenetic trajectories

Multivariate regression of the entire sample on the natural log of centroid size (Fig. 4) indicates that, although ramus shape and ramus size are significantly related ($p = 0.0005$), only 2.5% of the sample variance is explained by this relationship. Thus, there is considerable variation in ramus shape that is unexplained by ramus size. In general, however, compared to smaller individuals, larger individuals possess more anteriorly and superiorly projecting coronoids with a scooped-out anterior margin of the ramus. There is no difference between *H. sapiens* and *H. neanderthalensis* in the relationship between shape and size. Roc de Marsal, a Neanderthal subadult with no permanent dentition erupted, is a
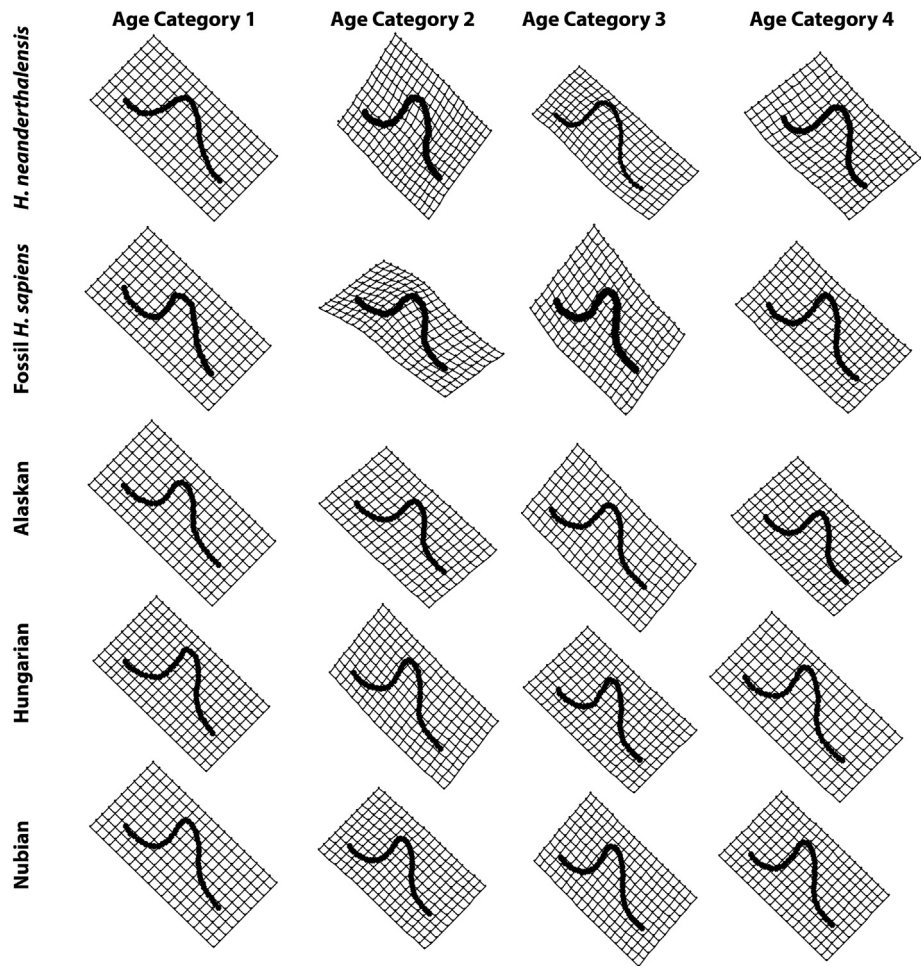
Figure 3. Thin plate spline analysis showing ontogenetic shape change within each population examined (except the Southeast Asian sample which has been excluded since it is represented by Age Categories 3 and 4 only). The reference configuration for each plot is the Age Category 1 average for that population, while the target configuration is for the Age Category in the column header. All configurations have been rotated so that the ramus is vertical.

Table 3
Procrustes distances and permutation test results for differences among populations/species. Age categories in each population are pooled for analysis.[a]

	Fossil *H. sapiens*	Alaskans	Hungarians	Nubians	SE Asians
Neanderthals	0.056	0.086	0.081	0.061	0.081
	$p = 0.076$	**$p < 0.0001$**	**$p < 0.0001$**	**$p = 0.002$**	**$p = 0.008$**
Fossil *H. sapiens*		0.062	0.049	0.032	0.051
		$p = 0.0003$	**$p = 0.012$**	$p = 0.139$	$p = 0.101$
Alaskans			0.096	0.080	0.102
			$p < 0.0001$	**$p < 0.0001$**	**$p < 0.0001$**
Hungarians				0.028	0.020
				$p = 0.025$	$p = 0.591$
Nubians					0.036
					$p = 0.112$

[a] Bolded p-values are significant at $p < 0.05$; bolded and highlighted p-values are also significant after sequential Bonferroni adjustment.

notable outlier, but removal of this specimen does not greatly alter the regression statistics (2.77% variance explained, $p = 0.0002$).

Calculation of the ontogenetic allometric trajectories in morphospace indicate that there is no significant difference in the trajectories of *H. neanderthalensis* and the pooled sample of *H. sapiens* (angle = 27.3, $p = 0.36$), although when the populations of *H. sapiens* are analyzed separately there is a significant difference in trajectory between fossil *H. sapiens* and all other groups, including *H. neanderthalensis* (Table 5).

3.3. Ramus angle and relative coronoid height

Damage to the anterior-most aspect of the mandible on multiple fossil specimens precluded the inclusion of landmarks representing the anterior edge of the alveolar margin from the geometric morphometric analyses described above (as employed in Terhune et al., 2014). Coronoid height, condyle height, and ramus angulation relative to the alveolar margin (as a proxy for the occlusal plane), are biomechanically relevant, however, and were investigated here as angles (ramus angle) and ratios (coronoid/condyle

Table 4
Procrustes distances between age categories within each species examined.[a]

Age category	Homo neanderthalensis			Homo sapiens		
	1	2	3	1	2	3
2	0.160			0.022		
	$p = 0.195$			$p = 0.327$		
3	0.120	0.099		0.044	0.038	
	$p = 0.466$	$p = 0.332$		$p = 0.003$	$p = 0.019$	
4	0.115	0.063	0.089	0.040	0.030	0.012
	$p = 0.121$	$p = 0.743$	$p = 0.440$	$p = 0.009$	$p = 0.039$	$p = 0.700$

[a] Bolded p-values are significant at $p < 0.05$; bolded and highlighted p-values are also significant after sequential Bonferroni adjustment.

ratio). Values for these measures varied primarily in relation to age category, with older individuals having relatively more angled rami (as previously observed in Terhune et al., 2014) and lower coronoid/condyle ratios (i.e., the coronoid and condyle were closer to the same height relative to the alveolar margin) (Table 6, Fig. 5). Furthermore, these variables were significantly correlated with each other in all groups except Neanderthals (Table 7; though note that the p-value for this correlation in fossil *H. sapiens* is <0.05, but is not significant after sequential Bonferroni adjustment). ANOVAs examining differences between age categories within each population/species were significant for all groups for ramus angle, although significant differences among age categories for coronoid/condyle ratio were found only in the Alaskan, Hungarian, and Nubian samples (Table 8).

4. Discussion

The morphology of the mandibular ramus is functionally significant in that it is the interface between the mandible and cranium, the site associated with a variety of muscles and ligaments, and the conveyance through which multiple nerves pass. In primates, and particularly in great apes and humans (including fossil hominins), the morphology of the anterosuperior ramus is highly variable, particularly in the shape of the coronoid process and the

Table 5
Angles between ontogenetic allometric trajectories (shape regressed on the natural log of centroid size) with the human sample broken down by population.[a]

	Neanderthals	Fossil *H. sapiens*	Alaskans	Hungarians	Nubians
Fossil *H. sapiens*	157.5				
	$p = 0.001$				
Alaskans	31.8	126.0			
	$p = 0.28$	$p = 0.001$			
Hungarians	47.9	110.6	20.2		
	$p = 0.19$	$p = 0.001$	$p = 0.315$		
Nubians	19.5	138.1	13.2	29.1	
	$p = 0.56$	$p = 0.001$	$p = 0.49$	$p = 0.24$	
SE Asians	24.0	135.4	16.6	32.5	13.1
	$p = 0.7$	$p = 0.001$	$p = 0.78$	$p = 0.52$	$p = 0.88$

[a] Bolded and highlighted p-values are significant at $p < 0.05$.

relationship of the ramus to the alveolar margin (Humphrey et al., 1999; Schmittbuhl et al., 2007; Terhune et al., 2014; Ritzman et al., 2016). The analyses presented here suggest that ramus, especially coronoid, morphology also varies considerably within and among modern human populations and differs between *H. sapiens* and *H. neanderthalensis*, both in adults and throughout ontogeny.

4.1. Variation in ramus shape

Within modern humans, there are significant differences among some populations in ramus shape. These differences, however, are subtle, and there is also substantial variation within populations. The shape variation we observed within *H. sapiens* was related to the shape of the sigmoid notch, the height of the coronoid process relative to the mandibular condyle, the angulation of the ramus relative to the alveolar margin, and the anteroposterior length of the coronoid process. Notably, in agreement with previous research on mandibular form (e.g., Nicholson and Harvati, 2006), the
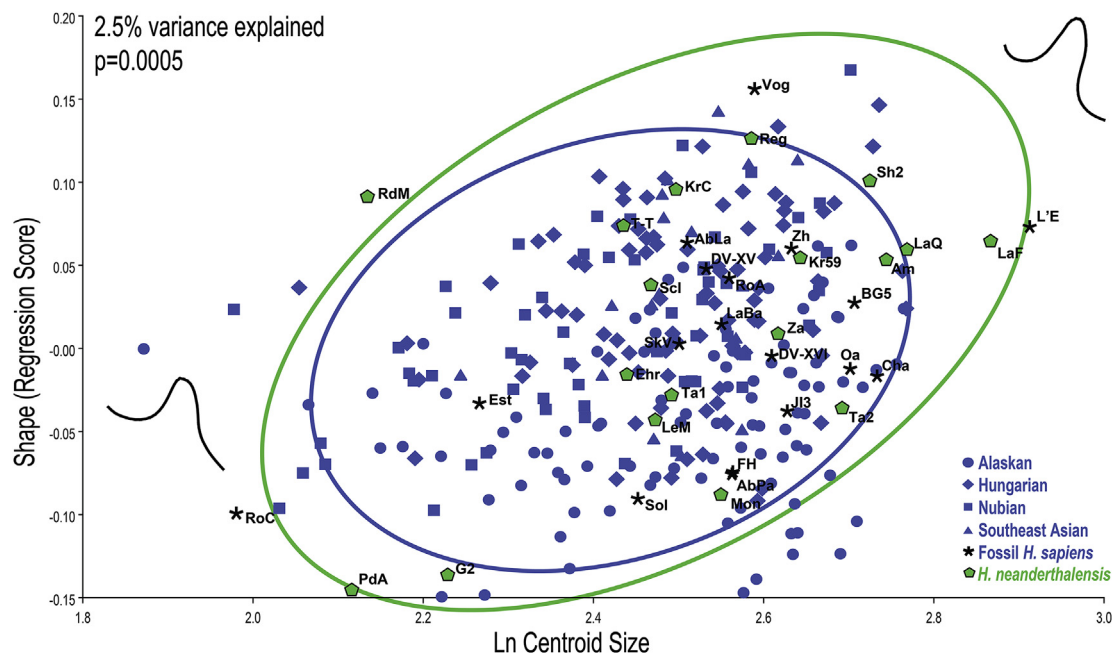

Figure 4. Multivariate regression of the Procrustes residuals (i.e., shape) of the entire sample on the natural log (Ln) of centroid size with 95% confidence ellipses around the human and Neanderthal samples. Wireframe images represent small and large specimens at either end of the regression relationship. Please see Table 2 for specimen abbreviations.

Table 6
Descriptive statistics for coronoid/condyle ratio and ramus angle in degrees for each age category in species/population (SD = standard deviation).

	Age category	Coronoid/condyle ratio		Ramus angle	
		n	Mean (SD)	n	Mean (SD)
H. neanderthalensis	1	3	1.51 (±0.48)	3	52.11 (±7.28)
	2	2	1.64 (±0.16)	2	62.00 (±0.43)
	3	2	1.32 (±0.05)	2	65.78 (±1.94)
	4	11	1.25 (±0.19)	11	74.38 (±5.43)
Fossil *H. sapiens*	1	1	1.70 (NA)	1	36.59 (NA)
	2	3	1.13 (±0.14)	3	65.59 (±0.70)
	3	3	1.33 (±0.27)	3	71.15 (±5.35)
	4	11	1.18 (±0.22)	11	75.51 (±3.57)
Alaskan	1	13	1.66 (±0.39)	13	47.12 (±5.61)
	2	21	1.32 (±0.16)	21	59.63 (±5.36)
	3	12	1.30 (±0.13)	12	61.45 (±3.79)
	4	47	1.13 (±0.17)	47	70.79 (±4.25)
Hungarian	1	5	1.64 (±0.18)	5	61.23 (±3.54)
	2	13	1.43 (±0.19)	13	63.95 (±5.62)
	3	21	1.31 (±0.18)	21	69.29 (±4.17)
	4	48	1.18 (±0.13)	48	71.17 (±3.53)
Nubian	1	14	1.76 (±0.36)	18	46.91 (±9.87)
	2	16	1.60 (±0.33)	16	56.56 (±4.88)
	3	5	1.39 (±0.15)	5	62.51 (±5.77)
	4	19	1.25 (±0.15)	19	70.99 (±4.37)
SE Asian	3	3	1.19 (±0.09)	3	68.18 (±5.55)
	4	15	1.33 (±0.19)	15	68.37 (±5.65)

Alaskan Inuit sample stood out as distinct from other modern human populations in analyses of the entire sample as well as in the adult-only sample (and regardless of whether differences were judged in PC plots or using Procrustes distances). Specifically, the Alaskan sample is distinct in its possession of a superoinferiorly shorter ramus with a wide, shallow sigmoid notch and coronoid process that is roughly level with the mandibular condyle. Similar analyses of variation in modern human craniofacial morphology have also highlighted the distinctiveness of the Alaskan/Arctic samples (e.g., Harvati and Weaver, 2006; Smith et al., 2007a,b, 2013), with this distinctiveness generally attributed to dietary specializations in these populations, and particularly to paramasticatory behaviors documented in these groups (e.g., Hylander, 1977).

In general, all humans tend to have a wide sigmoid notch with a superiorly and/or anteriorly (rather than posteriorly) projecting coronoid process, a finding which is consistent with our previous work (Terhune et al., 2014). Importantly, this finding is true across age categories. In comparison, Neanderthals tend to have coronoid processes that are more anteroposteriorly elongated and more "bulbous" in outline (consequently causing the deepest point in the sigmoid notch to be posteriorly shifted), the ramus is slightly more upright relative to the alveolar margin, and the coronoid process projects slightly higher above the level of the mandibular condyle than is typical of at least some modern human groups. This result is generally in agreement with the findings of Rak et al. (2002), which were also supported by Nicholson and Harvati (2006). However, our analyses found little support for Rak et al.'s (2002) conclusion that the Neanderthal coronoid relative to the condyle is statistically significantly higher than that of *H. sapiens* as a whole. In fact, for both coronoid/condyle ratio and ramus angle, the fossil *H. sapiens* sample showed very similar values to the Neanderthals. Importantly, the shape differences we observed between Neanderthals and modern humans are subtle, and given the high levels of intraspecific variation observed here, we suggest that caution should be exercised when using ramus morphology to diagnose group membership for specimens of these taxa.

The differences between our results and those of Rak et al. (2002) could be due in part to differences in the specimens employed in these two analyses and/or to methodological differences. Although we included seven out of the nine adult Neanderthal specimens used by Rak et al. (2002) in our sample, we were also able to include additional adult and subadult specimens that increase the range of ramus shape variation in our analysis (total adult $n = 11$, total $n = 18$). Further, although we included Tabun 2 in our analysis as did Rak et al. (2002), we classified this specimen as a Neanderthal following Schwartz and Tattersall (2003). The taxonomic attribution of this specimen has been debated (Quam and Smith, 1998; Rak, 1998; Stefan and Trinkaus, 1998), and Rak et al. (2002) consider this specimen to be best attributed to *H. sapiens*. However, there is no substantive difference in our results when Tabun 2 is classified as a fossil *H. sapiens* rather than a Neanderthal. Our method of quantifying ramus morphology (i.e., using landmark and semilandmark data combined with geometric morphometric analysis) also differed from that employed by Rak et al. (2002), who traced the outline of the sigmoid notch and registered these outlines on a x, y grid. Notably, however, Rak et al. (2002) did not incorporate a consideration of the position of these morphologies relative to the occlusal or alveolar plane. Regardless of these sampling and methodological differences, it is noteworthy that our results and those of Rak et al. (2002) identified the same general pattern of morphological differences in ramus shape between Neanderthals and *H. sapiens*.

4.2. Ontogeny of the mandibular ramus

In our previous work (Terhune et al., 2014) we found that ramus shape in modern humans was indistinguishable after age category 1 (i.e., only category 1 was significantly different from all other age categories); in contrast, the results of this study found that adult shape of the anterior ramus in *H. sapiens* (at least when pooled for the entire species) was not reached until age category 3. The human samples for these two analyses were identical, although we did not include the alveolar margin in the geometric morphometric analysis here due to lack of preservation of these landmarks in the fossil materials. These different results reveal that a large component of ramus shape variation among different ontogenetic stages is linked to the angulation of the ramus relative to the alveolar margin. The separate univariate analyses of ramus angulation presented here indicate that all *H. sapiens* populations in our sample have a strong correlation between ramus angle and coronoid/condyle ratio, and nearly all age categories within populations differ significantly in these variables.

Importantly, in our preliminary analyses for this study we compared results in which ramus angulation was included in the landmark data (though sample sizes were reduced), and found that, at least when examining differences between *H. sapiens* and *H. neanderthalensis*, separation between species was clearer when ramus angulation was not included in the landmark data. Thus, we feel that our treatment of these two datasets (i.e., the landmarks describing the shape of the anterior ramus versus the univariate data describing ramus angulation) allows us to assess both of these two distinct sources of variation while decreasing noise in the geometric morphometric analysis.

It is notable that, once the *H. sapiens* sample was divided by population, there was no consistent pattern of differences in shape between age categories. Thus, although the Neanderthal sample showed no significant differences in ramus shape between age categories, it is not unique in this regard. The Neanderthal sample is unique, however, in the combination of the outcomes of the Procrustes distance analysis and the analysis examining ramus angle and coronoid/condyle ratio. Although our sample sizes for several age categories are small, Procrustes distances among age categories were not significant for Neanderthals, and our analysis of
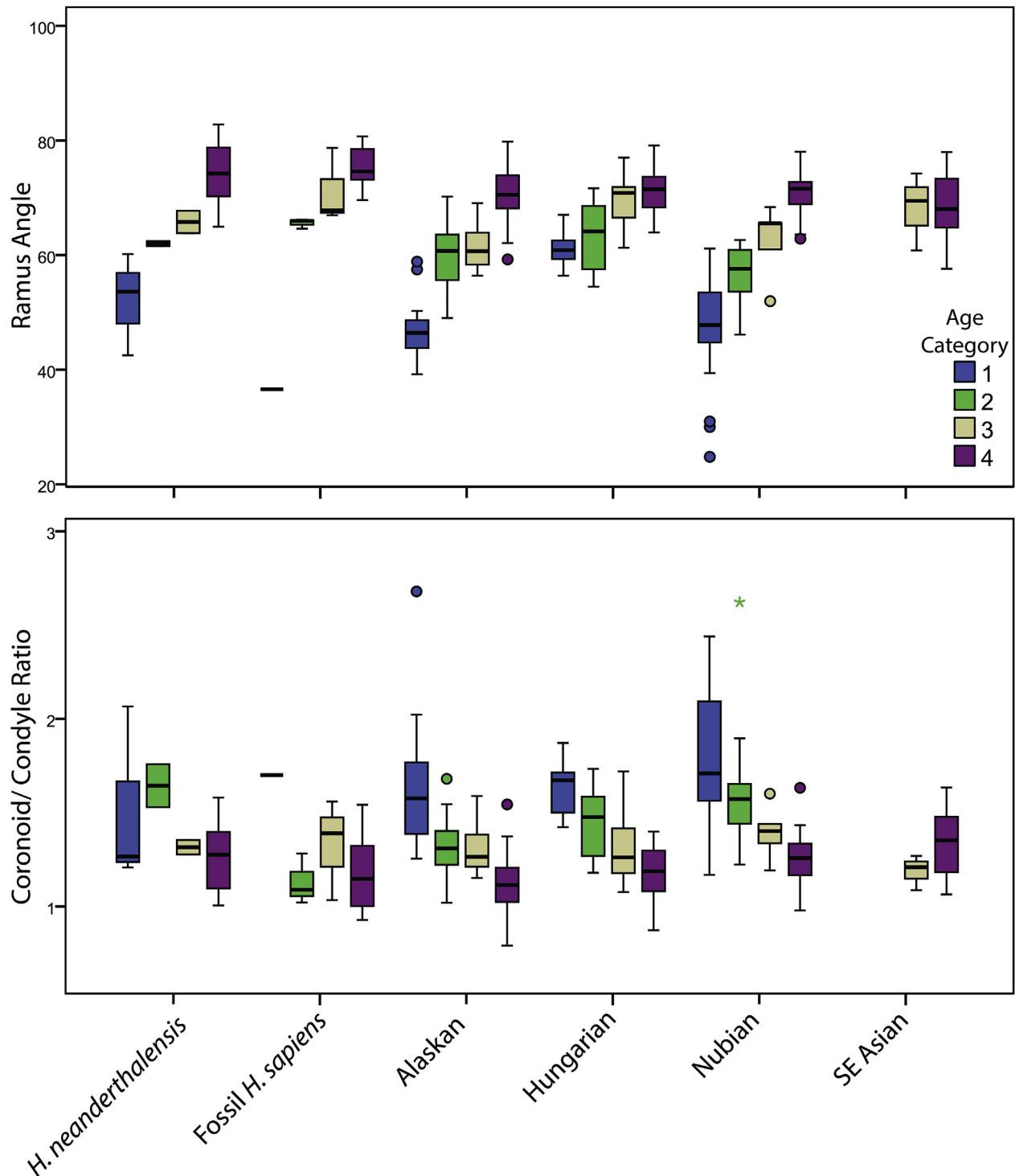
Figure 5. Box plot of ramus angle in degrees (top) and coronoid/condyle ratio (bottom) for each of the age categories in each group. Darkened bars represent the median value for each group, boxes show the interquartile range (25th to 75th percentile), and the whiskers extend to 1.5 times the interquartile range. Outliers are designated by circles and extremes are represented by stars.

differences in ramus angle and coronoid/condyle ratio among Neanderthal age categories found that the only significant difference is between age category 1 versus 4. This is not true of the modern human populations, all of which differ considerably in both ramus angle and coronoid/condyle ratio across age categories. Thus, Neanderthal ramus morphology seems to be relatively homogeneous throughout ontogeny, with few significant differences

in either coronoid/ramus shape, ramus angulation, or relative heights of the coronoid and condyle between subadult and adult Neanderthals. This result suggests that the adult *H. neanderthalensis* morphology is established early in ontogeny, perhaps even prenatally, whereas adult *H. sapiens* morphology (particularly in relation to the angulation and height of the coronoid process relative to the condyle) tends to emerge later in ontogeny, though there is

Table 7
Results of the correlation analysis showing the relationship between ramus angle and coronoid/condyle ratio.[a]

	n	r	p-value
H. neanderthalensis	18	−0.46	0.152
H. sapiens	270	−0.73	**<0.0001**
Alaskans	93	−0.79	**<0.0001**
Hungarians	87	−0.65	**<0.0001**
Nubians	54	−0.74	**<0.0001**
SE Asians	18	−0.68	**0.0160**
Fossil	18	−0.61	0.035

[a] Correlation analyses were conducted separately for each species/population, with specimens from all age categories included. Bolded and highlighted p-values are significant after sequential Bonferroni adjustment.

considerable variation in these features across populations. The early establishment of ramus shape in Neanderthals suggests that this morphology may be phylogenetically significant, though the considerable amount of variation in this feature in both humans and Neanderthals limits its diagnostic utility. Furthermore, the early establishment of this ramus shape in Neanderthals could reflect the hypothesized accelerated growth in Neanderthals relative to modern humans and potentially also *H. heidelbergensis* (Ramirez Rozzi and Bermudez de Castro, 2004; Smith et al., 2007a,b, 2010; Ponce de León et al., 2008; Gunz et al., 2010; but see Ponce de León et al., 2016 and Rosas et al., 2017).

One unexpected finding of our analysis was the strong divergence of the fossil *H. sapiens* ontogenetic allometric trajectory from those of all other samples (i.e., both Neanderthals and the modern human populations). Notably, Neanderthals and the recent *H. sapiens* samples did not have significantly different trajectories, and none of the recent modern human samples differed from each other. It is unclear why the fossil *H. sapiens* sample is so strongly divergent, except perhaps that this may be the result of small samples and combining relatively heterogeneous fossil populations, genetic lineages, and/or geological ages of specimens. Notably, however, this averaging is similarly true of the Neanderthal sample, though to a lesser extent. Additionally, we would anticipate that sampling error would be more likely to result in a

lack of statistical significance, rather than such a strong divergence. At least in regard to the ontogenetic allometric trajectories for the recent modern human populations and the Neanderthal sample, these results suggest that the differences in ramus shape that exist between populations (e.g., the distinctive morphology of the Alaskan Inuit sample) appear early during ontogeny, as do differences between *H. sapiens* and *H. neanderthalensis*, and that postnatal ontogenetic allometric trajectories for the ramus are largely parallel. To some extent, these results echo those of Strand Viðarsdóttir et al. (2002) for the face and Smith et al. (2013) for the temporal bone (both studies on *H. sapiens*), though those analyses did identify some populations that demonstrated divergent postnatal trajectories. Additionally, these findings identifying an early establishment of species-specific morphologies in *H. neanderthalensis* relative to *H. sapiens* and parallel postnatal growth trajectories are consistent with work by Ponce de León and Zollikover (2001) examining the cranium and mandible (including some aspects of ramus shape).

4.3. Functional shape variation in the ramus

The unique ramus morphology in Neanderthals has been argued to reflect an extreme adaptation in the jaws and associated musculature (Rak et al., 2002). If this argument is correct, what is this specialization, and what are the functional implications of the ramus morphologies observed here? Coronoid process morphology has been shown to respond to experimental manipulations of the masticatory system, and particularly to changes in temporalis function (Washburn, 1947; Avis, 1959; Soni and Malloy, 1974; Isberg et al., 1990). Further, increased ramus height serves to increase the distance from the mandibular condyle to the occlusal plane, which has been linked to more even distributions of bite forces along the postcanine tooth row (Herring and Herring, 1974; Greaves, 1980; Ward and Molnar, 1980; Spencer, 1995) and to increased moment arms of the temporalis, masseter, and medial pterygoid muscles (Maynard Smith and Savage, 1959; Greaves, 1974; Dubrul, 1977; Spencer, 1995). Increased surface area of the ramus may also serve to increase muscle attachment area, and therefore potentially increase the physiological cross-sectional area (i.e., force output) of

Table 8
One-way ANOVA with multiple comparison tests for differences among age categories within each population/species.[a]

	Ramus angle		Coronoid/condyle ratio	
	F	p-value	F	p-value
H. neanderthalensis	12.21	**0.0003**	1.92	0.17
Fossil *H. sapiens*	30.29	**<0.0001**	2.17	0.14
Alaskans	92.66	**<0.0001**	22.99	**<0.0001**
Hungarians	16.60	**<0.0001**	20.03	**<0.0001**
Nubians	37.41	**<0.0001**	10.18	**<0.0001**

Tukey's HSD summaries (upper triangle = ramus angle, lower triangle = coronoid/condyle ratio)

H. neanderthalensis Age category	1	2	3	4	Alaskans Age category	1	2	3	4
1	–	0.41	0.41	**0.0001**	1	–	**<0.0001**	**<0.0001**	**<0.0001**
2	0.94	–	0.41	0.06	2	**0.0001**	–	0.32	**<0.0001**
3	0.82	0.57	–	0.26	3	**0.0002**	0.99	–	**<0.0001**
4	0.41	0.22	0.99	–	4	**<0.0001**	**0.0036**	0.06	–

Hungarians Age category	1	2	3	4	Nubians Age category	1	2	3	4
1	–	0.60	**0.003**	**<0.0001**	1	–	**0.007**	**0.008**	**<0.0001**
2	0.07	–	**0.013**	**<0.0001**	2	0.38	–	0.044	**<0.0001**
3	**0.0003**	0.11	–	0.32	3	0.06	0.47	–	0.007
4	**<0.0001**	**<0.0001**	**0.01**	–	4	**<0.0001**	**0.003**	0.75	–

[a] Bolded and highlighted values are significant at $p < 0.05$. No post-hoc results are shown for fossil *H. sapiens* since there were less than two samples for at least one age category, and no ANOVAs were performed for the SE Asian sample since this group only had specimens from age categories 3 and 4.

the masticatory muscles (Freeman, 1988). Thus, these previous studies make it clear that the configuration of the mandibular ramus has functional significance across primates and mammals. Notably, analyses of masticatory variation in primates and non-primate mammals suggest that mandibular condyles that are closer to the occlusal plane help to increase jaw gape (Herring and Herring, 1974; Vinyard et al., 2003; Terhune et al., 2015), and, based on this relationship, Rak et al. (2002) propose that Neanderthals must have experienced some selection for increased gape. However, there is little evidence from the data presented here to suggest that Neanderthal mandibular condyles are significantly closer to the occlusal plane relative to the coronoid process when compared to humans. Therefore, if Neanderthal ramus morphology is adaptively important for increasing gape, the resulting increase in gape would have been very small.

Other potential consequences of variation in ramus morphology, particularly the position of the coronoid process, relate to the moment arm of the temporalis muscle, as well as the orientation of the temporalis force vector. The effect of this feature can be demonstrated by imagining a comparison of two specimens one with a wide sigmoid notch and a coronoid process that is anteriorly oriented and/or non-projecting (Fig. 6A), and the other with a narrower sigmoid notch and a coronoid process that is superiorly projecting (Fig. 6B) (i.e., the two ends of the extremes on PC 1 in Fig. 2). Holding constant all other aspects of the masticatory apparatus, the moment arm of the temporalis will be longest in the individual with the wider sigmoid notch and anteriorly projecting coronoid (Ritzman and Spencer, 2009). This morphology would also serve to change the angle of the temporalis force vector relative to the occlusal plane. However, considering the major shape differences between *H. sapiens* and *H. neanderthalensis* (Fig. 6C, D) (i.e., shape variation along PC 3 in Fig. 2) reveals that a more bulbous coronoid and asymmetric sigmoid notch (as found in Neanderthals) actually functions to slightly decrease the moment arm of the temporalis, and the change in orientation of the temporalis force vector is minor. Thus, at least in the absence of other changes to the craniofacial skeleton, the shape differences in ramus morphology observed between humans and Neanderthals are unlikely to have a substantial effect on masticatory biomechanics.

Of course, there are substantial differences in the craniofacial skeleton of *H. sapiens* and *H. neanderthalensis* beyond the mandibular ramus, and considerable attention has been paid to the unique morphology of the Neanderthal skull, particularly the face and mandible. A number of authors have hypothesized that the Neanderthal face was adapted to generating relatively high forces on the anterior dentition (e.g., Smith, 1983; Rak, 1986; Demes, 1987; Spencer and Demes, 1993). While this hypothesis—the anterior dental loading hypothesis (ADLH)—has garnered support, it is still contentious (see O'Connor et al., 2005; Weaver et al., 2007; Weaver, 2009). Notably, work by Spencer and Demes (1993) found that, relative to more archaic forms of *Homo* (e.g., *H. heidelbergensis*), Neanderthals were able to more efficiently produce bite forces at the anterior dentition. Specifically, they found that the masseter, medial pterygoid, and temporalis muscles were all more anteriorly positioned relative to the TMJ in Neanderthals, giving Neanderthals greater mechanical advantage relative to an incisal moment arm. Evidence opposing the ADLH has come from studies that have calculated forces in the Neanderthal masticatory apparatus. These studies suggest that Neanderthals were unable to produce bite forces that were unusually high for their cranial size (e.g., Antón, 1990; O'Connor et al., 2005). However, strong wear patterns on the anterior dentition of Neanderthals (e.g., Brace, 1962; Trinkaus, 1978; Smith, 1983; but see Clement et al., 2012), have frequently been interpreted as resulting from use of these teeth for

paramasticatory behaviors (e.g., Brace, 1962; Fox and Frayer, 1997). Thus, some authors have suggested that Neanderthals may not necessarily have been generating high magnitude bite forces on their anterior teeth, but instead may have been more frequently loading their anterior teeth at low magnitudes (Antón, 1990; O'Connor et al., 2005).

Although the data presented in this study cannot bear directly on the ADLH and we have not performed a biomechanical analysis, our assessment of coronoid process and ramus morphology in Neanderthals offers little support for the suggestion that increased temporalis moment arms in this species was a result of selection for increased mechanical efficiency when loading the anterior dentition. One potential alternative explanation for the more anteroposteriorly elongated and bulbous coronoid process morphology observed in Neanderthals relative to *H. sapiens*, is that it is related to decreasing the bending moments exerted by differences in the orientation of the temporalis muscle as also recently suggested by Marom and Rak (2018). For example, a more posteriorly angled temporalis force vector may be more likely to place the anterior margin of the coronoid process in tension and the posterior margin of the coronoid process in compression. Widening the coronoid process via additional deposition of bone in these areas may therefore function to decrease strains in this region. However, while analyses of muscle attachment sites in the cranium of Neanderthals suggest that they may have possessed stronger and/or larger masticatory muscles than modern humans (Antón, 1996), particularly the anterior temporalis and deep masseter, our ability to correctly infer the size, orientation, and attachment of the Neanderthal temporalis muscle is limited. Additionally, if the coronoid process and ramus morphology of Neanderthals is strongly plastically shaped by masticatory forces placed on the mandible during development, we might expect to see this distinctive morphology appear relatively late in ontogeny, likely post-weaning. However, as discussed above, this is not the case.

A number of studies have compared Neanderthal masticatory morphology to the morphology of the Inuit (e.g., Spencer and Demes, 1993; Antón, 1996; Rak et al., 2002; Nicholson and Harvati, 2006; Harvati et al., 2011; Clement et al., 2012) because ethnographic, archaeological, and dental evidence suggest the Inuit practiced paramasticatory behaviors and possess climate adaptations similar to those of Neanderthals (e.g., Hrdlička, 1945; Hylander, 1977; Ungar and Spencer, 1999; Spencer and Ungar, 2000). In particular, historical accounts indicate that Alaskan Inuit habitually used their anterior teeth for processing and ingesting tough, dried meat (Hrdlička, 1945). Several of these studies have identified similarities in the overall masticatory configurations of Neanderthals and Alaskan Inuit, including anteriorly shifted masticatory muscles relative to the TMJ and increased mechanical advantage of the masticatory muscles relative to the incisal moment arm (Spencer and Demes, 1993), a low position of the coronoid process and height of the ramus (Nicholson and Harvati, 2006), and a well-developed anterior temporalis (Antón, 1996). However, although we identified the same low, non-projecting coronoid process with an anteroposteriorly wide sigmoid notch in our Alaskan Inuit sample as Nicholson and Harvati (2006) did, we did not observe marked similarities between the Alaskan and Neanderthal samples. In fact, Neanderthals were found to be more similar to other human populations in relative coronoid height (although they were not significantly different from any *H. sapiens* group). Rak et al. (2002) also found that their sample of Canadian Inuit was not different from the rest of their *H. sapiens* sample, and did not resemble Neanderthals.

We did, however, identify several similarities between the Neanderthal and fossil *H. sapiens* samples that were not shared
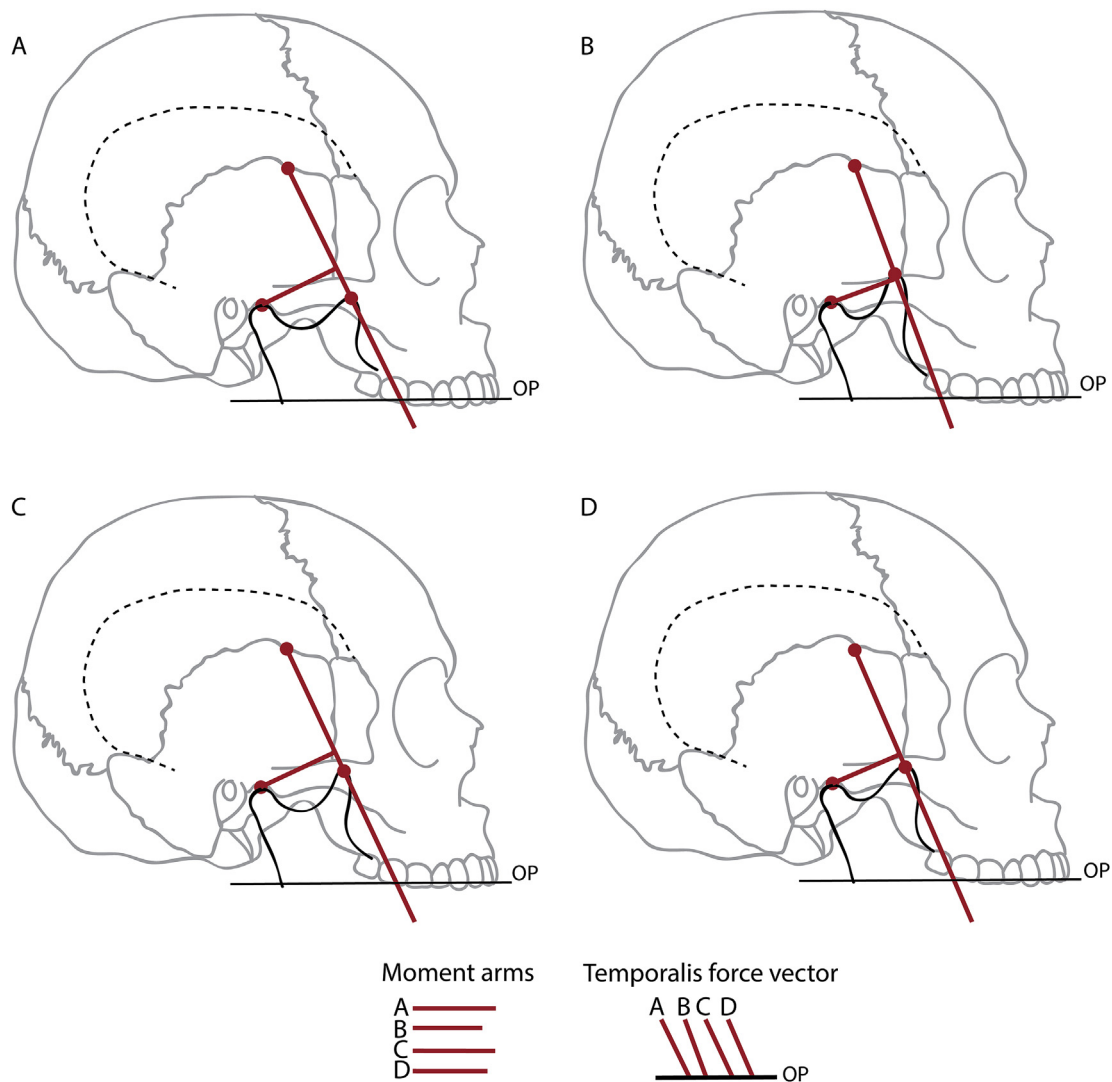
Figure 6. Simplified models of a human cranium showing changes in temporalis moment arm length and force vector orientation resulting from different coronoid/ramus morphologies. Moment arms are represented as the perpendicular distance from the center of the mandibular condyle to the line connecting the temporalis insertion (coronion) and origin (here represented as the centroid of the anterior temporalis; entire outline of temporalis indicated by the dashed line). A) Ramus morphology showing a wide, shallow sigmoid notch and small, anteriorly oriented coronoid process (this morphology is most common in the Alaskan sample; corresponds to the negative end of PC 1 in Fig. 2). B) ramus morphology showing a narrow sigmoid notch along with a superiorly projecting coronoid process (corresponds to the positive end of PC 1 in Fig. 2). C) ramus morphology showing a wide sigmoid notch and a superoanteriorly oriented coronoid process (i.e., the generalized *H. sapiens* morphology; corresponds to the positive end of PC 3 in Fig. 2). D) ramus morphology showing an asymmetric sigmoid notch with a bulbous, superiorly projecting coronoid process (generalized Neanderthal morphology; corresponds to the negative end of PC 3 in Fig. 2). Insets at the bottom of the figure compare the relative lengths and orientations of the moment arms and force vectors for each model. OP = occlusal plane.

with the other populations. For example, Procrustes distances between all recent modern human populations and the Neanderthals were statistically significant (though the SE Asian sample was not significant after Bonferroni adjustment). This was true for both the adults-only sample and when all ages were combined. Notably, however, Neanderthals and the fossil *H. sapiens* samples were not statistically significantly different in morphospace. This may be a reflection of similarities in food processing and/or dietary behaviors in fossil *H. sapiens* and *H. neanderthalensis* (e.g., Clement et al., 2012) rather than similarities among more recent populations of modern humans (e.g., hunter-gatherers versus agriculturalists). However, this does not explain the dissimilarity of the Alaskan samples from the fossil *H. sapiens* and *H. neanderthalensis* samples, unless the Alaskan Inuit practiced markedly different masticatory and/or paramasticatory behaviors from the fossil humans and Neanderthals as well as from the other human populations.

5. Conclusion

The present study sought to address two research questions related to 1) ramus shape variation among human populations and between *H. sapiens* and *H. neanderthalensis*, and 2) postnatal ontogenetic shape change in the ramus of these species. Our results suggest that, although subtle, there are ramus shape differences among some modern human populations, and between *H. sapiens* and *H. neanderthalensis*. These findings are consistent with similar previous work (e.g., Rak et al., 2002; Nicholson and Harvati, 2006; Harvati et al., 2011). However, where previous studies have suggested that differences between Neanderthal and modern human mandibular shape may be linked to differences in masticatory behaviors, we find little evidence for such a relationship, at least in the ramus. Additional work is needed to establish the extent and nature of the link between variation in anterosuperior ramus, particularly coronoid, shape and masticatory function, particularly with respect

to the size and orientation of the temporalis muscle. Furthermore, our results suggest that researchers should be cautious about using ramus morphology to diagnose group membership in *H. neanderthalensis* and *H. sapiens*. The influence of ontogeny on mandibular ramus shape is also important to consider in evaluations of *H. sapiens* and *H. neanderthalensis*. In particular, we observe ontogenetic variation in mandibular ramus angulation and relative coronoid/condyle height among modern human populations, although our data suggest that Neanderthal ramus shape is established earlier in ontogeny. This analysis informs our understanding of intraspecific patterns of mandibular ramus 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*. These potentially different ontogenetic patterns in ramus shape between humans and Neanderthals are consistent with suggestions that Neanderthals experienced an accelerated life history pattern compared to the prolonged, modern human life history schedule, which seems to have appeared relatively late in hominin evolution.

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Supplementary Online Material

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