Evaluating ontogenetic shape variation in the mandibular ramus of *Homo sapiens* and *Homo neanderthalensis*

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Introduction

Homo neanderthalensis has a suite of autapomorphic mandibular traits that have been used to distinguish this taxon from *H. sapiens* (e.g., Stringer et al., 1984; Trinkaus et al., 2003a,b; Wolpoff and Frayer, 2005; Cartmill et al., 2009). For example, Rak et al. (2002) proposed that the mandibular ramus, specifically the form of the sigmoid notch, is a useful diagnostic trait for differentiating adults of these two species. Using a canonical variate analysis (CVA), Rak et al. (2002) found significant differences in the sigmoid notch among adult *H. neanderthalensis*, fossil *H. erectus* and *H. sapiens*, and modern *H. sapiens*. However, it remains unclear when during ontogeny these differences in ramus form appear, and thus whether these features can be used as diagnostic traits for subadult Neandertals and modern humans is unknown. Ontogenetic data suggest hominoid taxa can be differentiated from one another prior to eruption of M_1 (Terhune et al., 2014). Thus, differences in ramus form appear early during ontogeny in extant hominoids, indicating that these traits are phylogenetically meaningful (Rak et al., 2002; Terhune et al., 2014). Here we use an ontogenetic analysis to extend these previous analyses. This analysis aims to identify when during ontogeny differences in Neandertal and modern human ramus form appear and compare the patterns of ontogenetic shape changes in these species.

Research Questions

To examine shape differences between *H. neanderthalensis* and *H. sapiens*, this study addresses three research questions:

1. **Does ramus shape differ significantly between *H. sapiens* and *H. neanderthalensis*?**
2. **When during ontogeny do significant differences in ramus form appear?**
3. **To what extent are patterns of ontogenetic shape change in the ramus similar or different between species?**

Materials and Methods

Sample: A total of 286 mandibles of *H. neanderthalensis* (*n*=15) and recent and fossil *H. sapiens* (*n*=271) were examined with age categories assigned based on dental eruption (Table 1). Recent *H. sapiens* were drawn from four geographically variable populations (Nubians, Alaskans, Southeast Asians, and Hungarians); fossil *H. sapiens* include Estelas (Age Category 2), Abri Lachaud and Laugerie Basse (Age Category 3), and Abri Pataud and L'Espugue (Age Category 4).

Table 1: Number of specimens in each age category for each species

	Category 1	Category 2	Category 3	Category 4	
	No permanent molars in occlusion	Only M_1 in occlusion	M_1 and M_2 in occlusion	All permanent molars in occlusion	Total
Homo sapiens	36	51	43	141	271
*Homo neanderthalensis**	2	1	3	9	15
*See below for Neandertal specimens used in this analysis					286

Data Collection: Two-dimensional landmarks (3 fixed landmarks, 41 sliding semilandmarks [Fig.1]) describing the anterior margin of the ramus and sigmoid notch were digitized on photographs of the lateral aspect of mandible in tpsDig (Rohlf, 2010a)(Fig. 1).

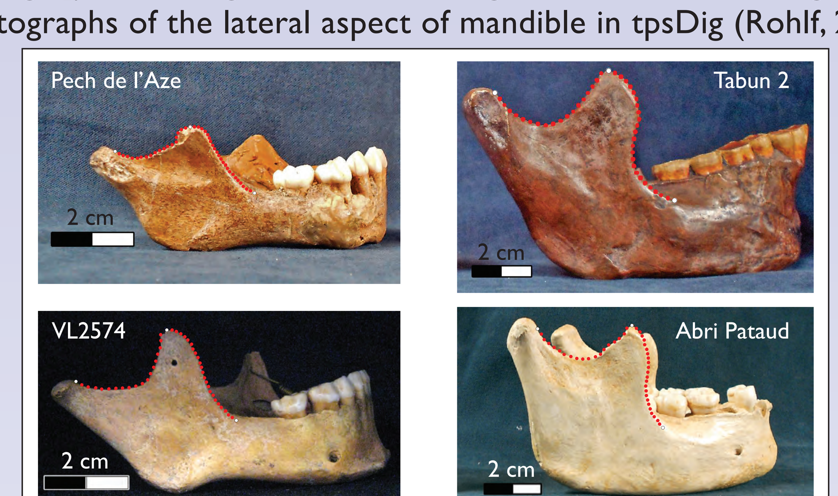

Fig. 1: Examples of Age Category 1 (left) and Age Category 4 (right) for both *H. neanderthalensis* (top) and *H. sapiens* (bottom). White circle denotes fixed landmark, red circle denotes sliding semilandmark

Data Analysis:

- Configurations were superimposed using Generalized Procrustes Analysis, and semilandmarks were allowed to slide to minimize bending energy in tpsRelw (Rohlf, 2010b).
- Principal components analyses (PCA) were performed for the entire sample, adults only, and subadults only to visualize variation in shape space.
- Procrustes distances were calculated among species and age groups and the significance of these distances was assessed using permutation tests (with 10,000 iterations).
- A multivariate regression of Procrustes residuals on the natural log of centroid size was used to examine the relationship between shape and size.
- Divergence of ontogenetic allometric trajectories was assessed by calculating the angle between vectors for each species calculated from a multivariate regression of shape on size; permutation tests (with 10,000 iterations) determined angle significance (following McNulty et al., 2006).

Research Question 1

Does ramus shape differ significantly between *H. sapiens* and *H. neanderthalensis*?

Rak et al. (2002) concluded that ramus form is a diagnostic trait based on a CVA of all specimens; our results replicate this finding (Fig. 2). However, with a PCA, the species overlap considerably along PC1 and PC2 (Fig. 3), but there is some separation along PC3 (Fig. 4).

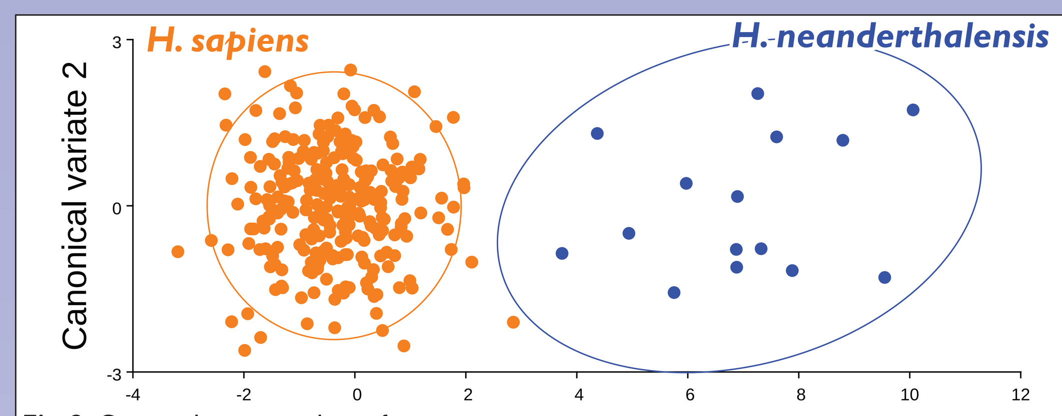

Fig. 2: Canonical variate analysis of all ages following Rak et al. (2002).

Procrustes distances between *H. neanderthalensis* and *H. sapiens* species are significant. All ages (Fig. 3, 4): $p = 0.001$ Adults only: $p = 0.012$ Subadults only: $p = 0.020$

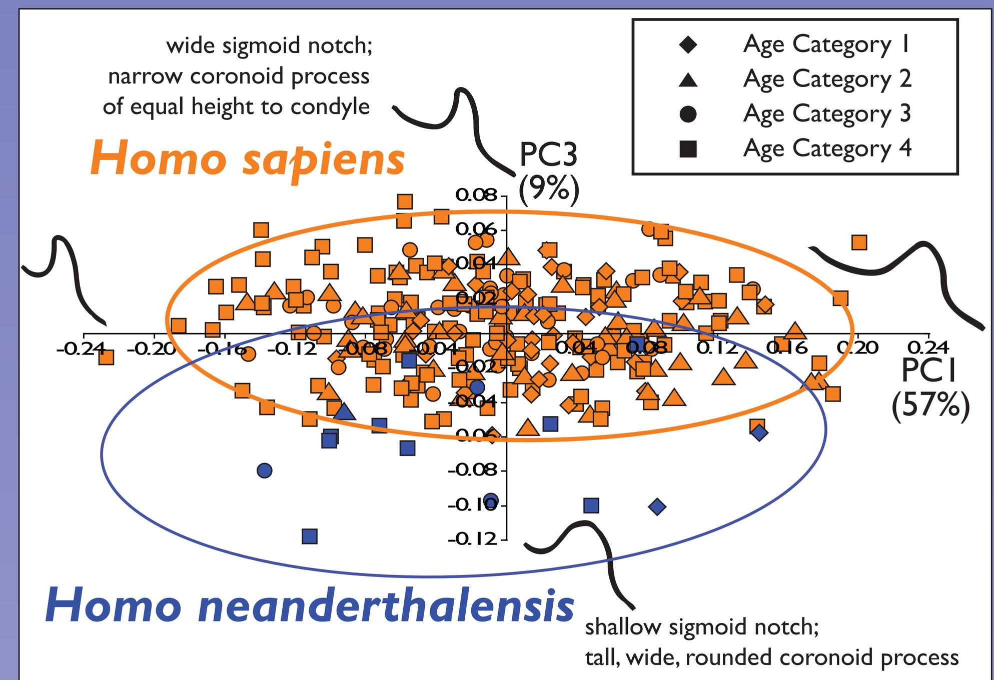

Fig. 4: PCA of all specimens. Ramus form for each PC represented along the appropriate axis. Ellipses represent 95% confidence intervals. Descriptions for PC1 in Fig. 2.

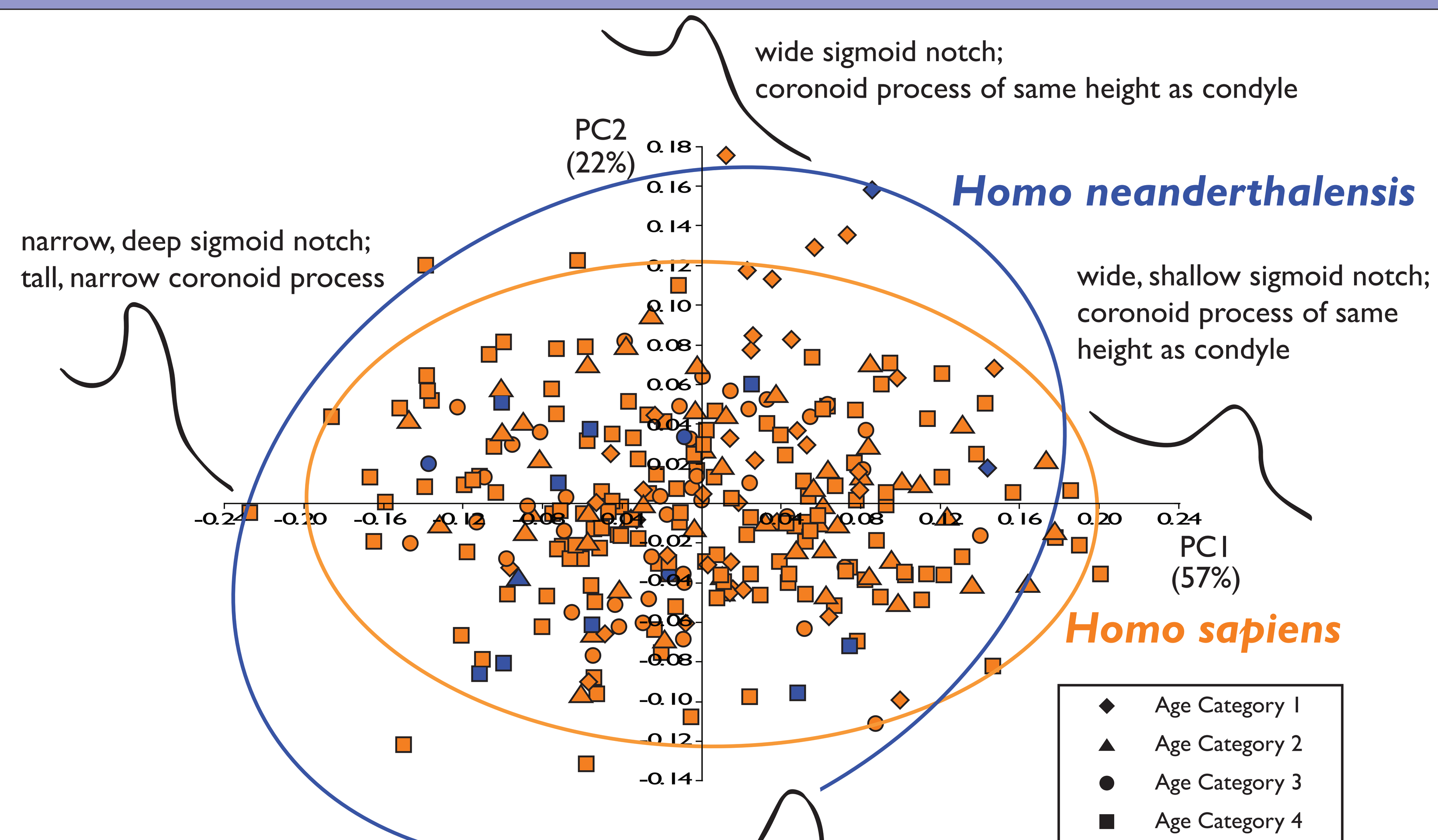

Fig. 3: PCA of all specimens. Ramus form for each PC represented along the appropriate axis. Ellipses represent 95% confidence intervals.

Research Question 2

When during ontogeny do significant differences in ramus form appear?

Procrustes distances for all age categories with appropriately large sample sizes are significant between *H. neanderthalensis* and *H. sapiens*.

Age Category 1: $p = 0.012$ Age Category 3: $p = 0.042$
Age Category 2: N/A Age Category 4: $p = 0.019$

Morphological differences in ramus form appear early in ontogeny, prior to the eruption of M_1, with significant differences in ramus shape between *H. sapiens* and *H. neanderthalensis* present starting in Age Category 1.

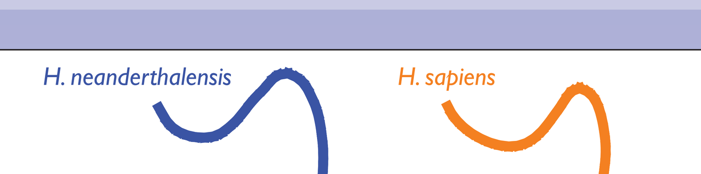

Fig. 6: Average ramus form of adult *H. neanderthalensis* (left) and *H. sapiens* (right).

Research Question 3

To what extent are patterns of ontogenetic shape change in the ramus similar or different between species?

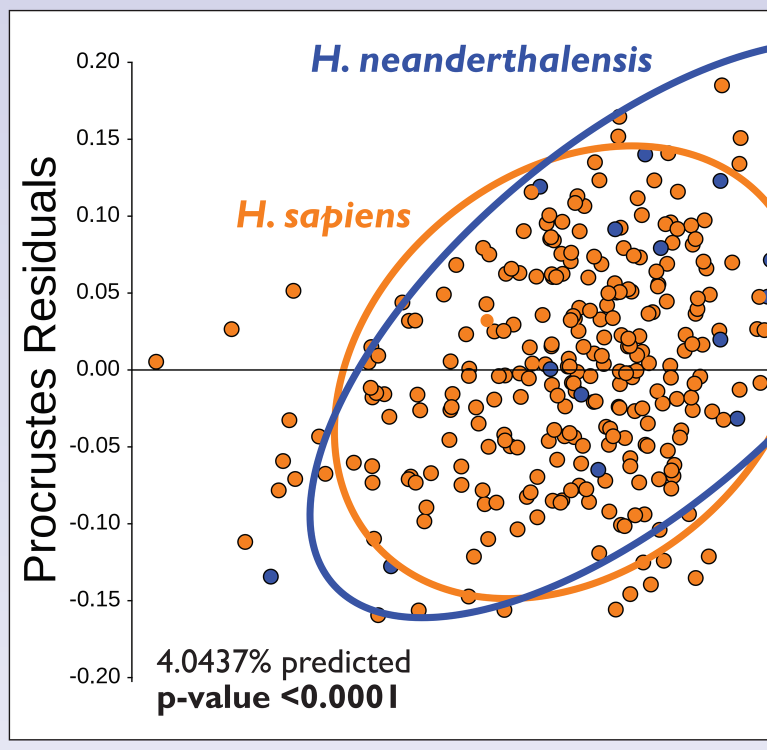

Fig. 5: Regression of Procrustes residuals against the natural log of centroid size to assess the effects of size on shape.

The angle between the ontogenetic allometric trajectories of *H. neanderthalensis* and *H. sapiens* is 27.72° (p=0.8933).

The lack of significance differences between ontogenetic allometric trajectories for *H. neanderthalensis* and *H. sapiens* suggests that the trajectories are parallel rather than divergent (Fig. 5).

Discussion

The results of this analysis suggest that ramus form is significantly different between *H. neanderthalensis* and *H. sapiens*, supporting Rak et al.'s (2002) conclusion. However, these differences are subtle. The average adult form of the ramus in *H. neanderthalensis* has an anterioposteriorly wider coronoid process that is taller than the mandibular condyle, while the average form of the *H. sapiens* ramus displays a narrower coronoid process that is more equal in height to the mandibular condyle (Fig. 6). Our data indicate that differences in ramus form in *H. neanderthalensis* and *H. sapiens* appear early during ontogeny. However, there is considerable variation within both species at each age category throughout ontogeny, and the species overlap substantially in morphospace. One explanation for this discrepancy is that Rak and colleagues base their interpretations on the use of a CVA rather than a PCA. By warping shape space to maximize differences between *a priori* defined samples (Klingenberg and Monteiro, 2005; Mitteroecker and Bookstein, 2011), the CVA obscures the overlap in variation between the two species. **These data therefore suggest that, despite the statistical significance of differences between mean ramus form in Neandertals and modern humans, some degree of caution should be exercised when using this trait for taxonomic or phylogenetic analyses as the overlap in ramus morphology in these taxa is relatively large.**

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