

Sexual dimorphism in the shape of the extant hominid mandibular ramus

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INTRODUCTION

Other than studies on the robusticity of the mandibular symphysis and corpus (e.g., Weidenreich, 1936; Chamberlain and Wood, 1985; Kimbel and White, 1988; Daegling and Grine, 1991), there are few published data on sexual dimorphism in extant hominid mandibular shape. Those that have assessed mandibular shape dimorphism have typically found little or no significant dimorphism in *Pan* and *Homo*, and substantially greater amounts in *Pongo* and *Gorilla* (Wood et al., 1991; Taylor, 2006; Schmittbuhl et al., 2007; Robinson, 2012). By and large, however, sexual dimorphism in the great ape mandible is associated with differences in size rather than shape (Taylor, 2006). Notably, analyses investigating shape dimorphism have focused primarily on the overall shape of the mandible, mandibular corpus, and symphysis and have not specifically examined ramus shape dimorphism. As the region via which the mandible articulates with the cranium, and upon which the masticatory muscles (temporalis, masseter, medial pterygoid, and lateral pterygoid) insert, the shape of the ramus is biomechanically significant. For example, ramus height, and therefore temporomandibular (TMJ) height above the occlusal plane, varies among species in relation to diet, with taxa exploiting more resistant foods possessing superoinferiorly taller rami (e.g., Kinzey, 1974; Spencer, 1995; Anton, 1996; Taylor, 2002; Constantino, 2007). **Here we evaluate sexual dimorphism in ramus shape in four species of hominids.** Understanding these patterns of dimorphism is important due to the utility of the ramus for interpreting shape variation in extant and fossil hominids, and for evaluating differences in masticatory function between sexes and among taxa.

RESEARCH QUESTION

Do humans and great apes exhibit sexual dimorphism in the shape and size of the mandibular ramus, especially the coronoid process and sigmoid notch?

MATERIALS AND METHODS

Sample: A total of 219 specimens were examined; as much as possible, equal numbers of males and females were included in each group. All individuals are adult, with full eruption and occlusion of the third molar.



Lateral view of an adult male *Gorilla gorilla* mandible illustrating the landmarks used for this analysis.

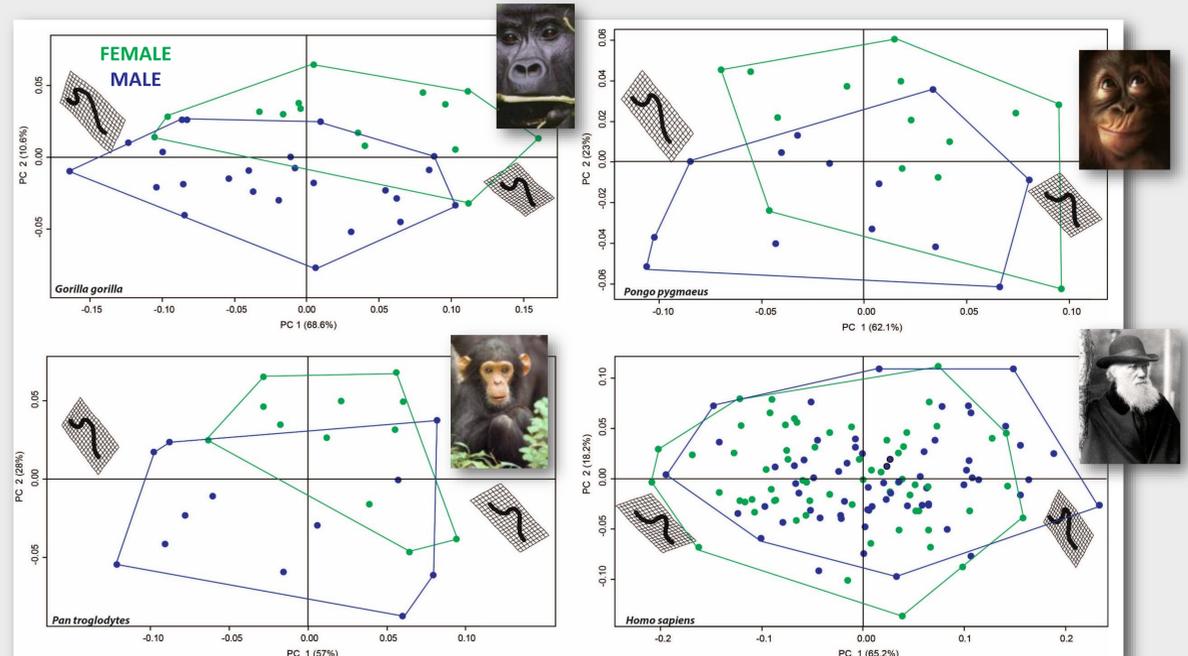
Species	Female	Male
<i>Gorilla gorilla</i>	15	24
<i>Pan troglodytes</i>	12	12
<i>Pongo pygmaeus</i>	14	13
<i>Homo sapiens</i>	63	66

Data collection: Two-dimensional landmarks and semilandmarks describing the anterior margin of the ascending ramus and sigmoid notch were digitized on photos of the lateral aspect of the ascending ramus of the mandible in tpsDig (Rohlf, 2010).

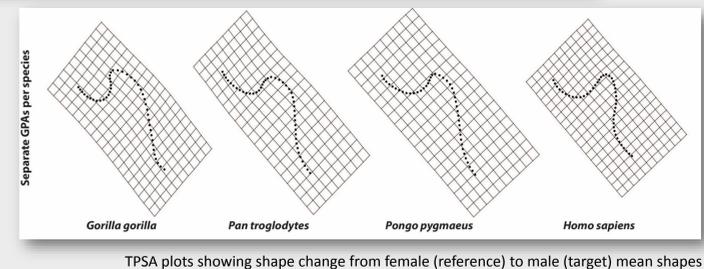
Data analysis: Data were analyzed using geometric morphometric methods. Semilandmarks were allowed to slide to minimize Procrustes distances, and all landmarks were subjected to principal components analysis (PCA) (separately by species and for the entire sample). Specimens were regressed on the natural log of centroid size to assess the influence of size on shape. Mean forms per sex for each species were calculated, and thin plate spline analysis (TPSA) was used to demonstrate shape differences between sexes. Procrustes distances between the centroids of sexes within each species were calculated and a permutation test was performed to assess their significance.

RESULTS

- Males and females are separated (though still overlapping) in PC plots of all species except humans.



- However, only subtle differences were exhibited between the mean male and female ramus shapes, with males exhibiting slightly more superiorly and posteriorly oriented coronoids in all taxa.

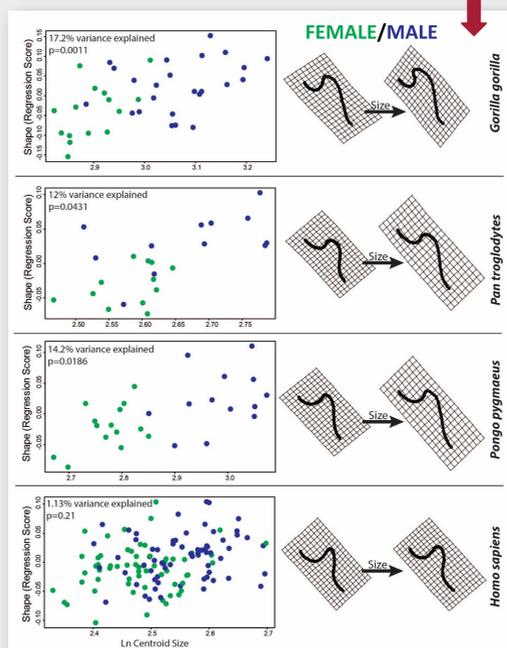


TPSA plots showing shape change from female (reference) to male (target) mean shapes

- Procrustes distances between sexes were significant for all taxa (including humans), with the largest distances between males and females in the African apes.

	Procrustes distance	p-value
<i>Gorilla gorilla</i>	0.0624	0.0055
<i>Pan troglodytes</i>	0.0677	0.0153
<i>Pongo pygmaeus</i>	0.045	0.0616
<i>Homo sapiens</i>	0.0447	0.0059

- Results of the multivariate regressions indicate a significant relationship between ramus shape and size in all taxa except humans.



CONCLUSIONS

These results demonstrate **slight but significant shape dimorphism in ramus morphology in great apes and humans**. In all taxa, males exhibit more superiorly and posteriorly oriented coronoids, and males tend to have larger rami than females. Thus, **much of this shape dimorphism likely represents allometric variation**. These differences may also indicate **important functional differences between males and females in the temporalis muscle**. A more superiorly projecting coronoid process is likely impacted by the angulation of the temporalis muscle relative to the occlusal plane (and therefore the line of action of the muscle), and may increase the length of the temporalis moment arm (Ritzman and Spencer, 2009). Analyses modeling temporalis function at different coronoid positions, as well as analyses linking temporalis architecture to coronoid morphology, would be beneficial.

These data are also relevant to interpreting mandibular variation in fossil hominins, including *Australopithecus sediba*. Considerable variation in ramus shape between *A. sediba* specimens MH1 (a subadult presumed male) and MH2 (an adult presumed female) has been suggested to represent normal variation in age and/or sex. The results presented here, however, are inconsistent with this interpretation as they suggest that only subtle differences exist in ramus shape between sexes. Moreover, the **specific differences between MH1 and MH2 are largely inconsistent with the less marked shape differences between males and females identified in this study**.

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