

Ontogenetic Variation in the Mandibular Ramus of Great Apes and Humans

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ABSTRACT Considerable variation exists in mandibular ramus form among primates, particularly great apes and humans. Recent analyses of adult ramal morphology have suggested that features on the ramus, especially the coronoid process and sigmoid notch, can be treated as phylogenetic characters that can be used to reconstruct relationships among great ape and fossil hominin taxa. Others have contended that ramal morphology is more influenced by function than phylogeny. In addition, it remains unclear how ontogeny of the ramus contributes to adult variation in great apes and humans. Specifically, it is unclear whether differences among adults appear early and are maintained throughout ontogeny, or if these differences appear, or are enhanced, during later development. To address these questions, the present study examined a broad ontogenetic sample of great apes and humans using two-dimensional geometric morphometric analysis. Variation within and among species was summarized using principal component and thin plate spline analyses, and Procrustes distances and discriminant function analyses were used to statistically compare species and age classes. Results suggest that morphological differences among species in ramal morphology appear early in ontogeny and persist into adulthood. Morphological differences among adults are particularly pronounced in the height and angulation of the coronoid process, the depth and anteroposterior length of the sigmoid notch, and the inclination of the ramus. In all taxa, the ascending ramus of the youngest specimens is more posteriorly inclined in relation to the occlusal plane, shifting to become more upright in adults. These results suggest that, although there are likely functional influences over the form of the coronoid process and ramus, the morphology of this region can be profitably used to differentiate among great apes, modern humans, and fossil hominid taxa. *J. Morphol.* 275:661–677, 2014. © 2014 Wiley Periodicals, Inc.

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INTRODUCTION

In all primates, and more generally across mammals, the ramus of the mandible terminates superiorly in two processes: the condylar process, which forms the mandibular component of the

temporomandibular joint, and the coronoid process, to which the common tendon of the anterior and posterior temporalis muscles is attached. Between these two processes is the u-shaped sigmoid notch. The morphology of this region varies considerably both within and among extant primate taxa. Within the hominids, some authors suggest this morphological variation may reflect phylogenetic patterns (Rak et al., 2002, 2007) and/or functional demands of the masticatory apparatus (Hrdlicka, 1940a; Humphrey et al., 1999; Nicholson and Harvati, 2006; Ritzman and Spencer, 2009). However, the extent to which this morphology varies within and among great apes and humans remains relatively undocumented and the degree to which ontogeny contributes to this shape variation is unclear. This study seeks to examine mandibular ramus form throughout ontogeny in the great apes and humans, with the ultimate goal of addressing these potentially conflicting conclusions regarding the utility of mandibular ramal morphology for understanding phylogenetic relationships and/or functional variation within fossil and extant hominids.

Previous Morphological Descriptions of the Mandibular Ramus

The majority of previous work describing the mandibular ramus in extant hominids has focused on intraspecific human variation (e.g., Hrdlicka, 1940a, b, c; Humphrey et al., 1999; Nicholson and Harvati, 2006). Aitchison (1965) qualitatively observed that chimpanzees possess a coronoid

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process that is higher than those of gorillas and orangutans, which he related to the more oblique angle that the chimpanzee ramus made with the alveolar margin. In addition, he argued that great ape species could be clearly differentiated from each other in the height of the ramus above the occlusal plane, with *Gorilla* having the tallest ramus and *Pan* the shortest. This observation was supported by the work of Humphrey et al. (1999), who documented that the height of the mandibular ramus relative to the occlusal plane is lowest in humans and highest in *Gorilla*. They also found that humans exhibit a relatively greater distance between the coronoid and condyle (i.e., a wider sigmoid notch) than great apes.

Rak et al. (2002, 2007) recently performed a detailed analysis of ramal morphology in fossil hominins and extant hominids, with a particular focus on the shape of the sigmoid notch. In a dimensional (2D) analysis of ramal morphology, including the coronoid and condylar processes, Rak et al. (2002) identified different morphologies in Neanderthals and modern humans. Specifically, these authors demonstrated that Neanderthals possess a relatively lower condylar process (and correspondingly higher coronoid process), and a sigmoid notch with the deepest point situated closer to the condyle. These researchers linked this unique morphology to a "profound specialization of the masticatory system" in this taxon (Rak et al., 2002: 202), which they suggested may be linked to increased maximum jaw gape in Neanderthals compared to modern humans. Other studies comparing three-dimensional (3D) landmark configurations in modern humans and Neanderthals similarly described Neanderthals as having an "asymmetrical" sigmoid notch and a coronoid that is taller than the condyle (Nicholson and Harvati, 2006; Harvati et al., 2011). However, these authors found little support for the argument that the unique mandibular morphology of Neanderthals was related to mechanical demands placed on the mandible.

Rak et al. (2007) further documented the 2D-shape of the margin of the anterior ramus (i.e., the coronoid process) and the sigmoid notch in great apes and humans. Using these data, they were able to assign specimens to the correct taxon with approximately 82% accuracy, and they identified a set of traits unique to *Gorilla* relative to modern humans, chimpanzees, and orangutans. These traits include: 1) a coronoid process with a broad base that is taller than the condyle, which results in the deepest point of the sigmoid notch being positioned close to the condyle (i.e., similar to the morphology of Neanderthals); 2) a coronoid tip that is angled posteriorly, occasionally overhanging the sigmoid notch; and 3) a sigmoid notch that is narrow and deep. Importantly, these traits are also present in preserved mandibular rami of *Australopithecus afarensis* and *Paranthropus robustus*.

Given these analyses, Rak et al. (2002, 2007) suggested that aspects of ramus form, especially the shape of the coronoid process and sigmoid notch, may be useful characters for reconstructing phylogenetic relationships among great ape and fossil hominin taxa. Rak et al. (2007) argued that the utility of these features for phylogenetic analyses is strengthened by their finding that variation in these features is not related to the size and orientation of the temporalis. The basis of this argument rests primarily on the observation that, while chimpanzee and gorilla males and females differ in cranial cresting patterns (which largely reflect the orientation of the temporalis), males and females of these species do not differ in ramal morphology (Rak et al., 2007). In addition, they suggested that because *Au. afarensis* has been reconstructed as being dissimilar to *Gorilla* in its dietary behavior and habitat, early hominin taxa and gorillas were unlikely to have evolved these shared features because of adaptations to a similar dietary niche. Given these results, they argued that *Au. afarensis* and *P. robustus* (and *Au. africanus* as well, based on the preserved morphology of Sts 7) shared these characters as synapomorphies and that these synapomorphies unite these species in a clade, casting doubt on claims that *Au. afarensis* was basal to all later hominin species. Based on these traits, Rak et al. (2007) proposed instead that this clade was part of a side branch of hominins that did not contribute to the ancestry of the genus *Homo*.

Other researchers have argued that mandibular characters are generally poor indicators of taxonomic identity and phylogenetic relationships, primarily due to the high strains experienced by the mandible that may result in increased phenotypic plasticity (Wood and Lieberman, 2001; Schmittbuhl et al., 2007) and greater potential for homoplasy (e.g., Skelton and McHenry, 1992; Turner and Wood, 1993; Begun, 1994; McHenry, 1994; Lieberman et al., 1996; Asfaw et al., 1999). In contrast, some studies have found that homoplasy in characters related to mastication is no greater than in characters from other regions of the skull (Collard and Wood, 2001), and others suggested that including characters under high masticatory strain increases the accuracy of taxonomic analyses (Collard and Lycett, 2009). Furthermore, other researchers have found that variation among *Gorilla* and *Pan* subspecies in mandibular metrics is less than one would expect if the mandible were phenotypically plastic and, therefore, they did not support the contention that the mandible is of less taxonomic utility than other craniodental regions (Taylor and Groves, 2003). In contrast, Daegling (1996) suggested that the morphology of the coronoid exhibits considerable intraspecific variation in chimpanzees and gorillas because of functionally related differences in the size of the chewing muscles. Thus, there remains some question as to how reliable the morphology of the

mandibular ramus is for attributing individual specimens to a species and whether ramal morphology can be profitably employed in phylogenetic analyses.

Previous Studies of Mandibular Ramus Ontogeny

In light of the research described above, and particularly the conclusion by Rak et al. (2002, 2007) that the morphology of the mandibular ramus is phylogenetically meaningful, a consideration of how the ontogeny of the ramus contributes to adult variation is critical. If Rak et al. (2007) are correct and adult ramal morphologies primarily reflect genetically predetermined shapes (perhaps shaped by functional considerations through natural selection), then one would expect species-specific morphologies to be established early and taxa, even those with similar diets, to be readily differentiated. If, however, ramal morphology is a plastic response to mandibular remodeling as a result of stresses and strains experienced during an individual's lifetime, then species-specific ramal form should emerge later during development with or just before the onset of species-typical adult dietary behaviors and species with similar dietary behaviors should be more difficult to differentiate from one another. However, it is notable that these two scenarios are not mutually exclusive; functional differences among species may also track phylogenetic variation, and thus similar functional and phylogenetic signals in ramal morphology could be observed throughout ontogeny.

Initial qualitative descriptions of human and chimpanzee mandibular ramus development by Aitchison (1963) suggested that these two species resemble one another more closely as infants and then diverge in morphology during ontogeny. In particular, Aitchison observed that humans develop an increasingly vertical ramus relative to the corpus, whereas chimpanzees develop in the opposite direction, having a ramus that becomes increasingly posteriorly inclined during ontogeny. In contrast, Schultz's (1969) extensive qualitative analysis of the chimpanzee skeleton found evidence of the opposite trend in chimpanzees, with the chimpanzee mandibular condyle described as shifting from "on a level with the alveolar margin" to a position "far above" the alveolar margin over the course of development. Schultz noted that this was a less extreme shift in the orientation of the ramus than is typical of orangutans, gorillas, and humans. More recent quantitative analyses of changes in the orientation of the ramus are also conflicting. For example, Taylor (2002) found evidence for a negative correlation between skull size (as a proxy for age) and the angulation of the ramus in *Pan* and *Gorilla*. These results suggest that the ramus becomes more vertically oriented during ontogeny in these taxa. However, in their analysis of ontoge-

netic changes in the 3D-structure of the mandible in *Pan*, Boughner and Dean (2008) found support for Aitchison's characterization of the ramus as becoming less vertically oriented during development. This work demonstrated that in *Pan*, particularly *Pan troglodytes*, the mandibular condyle becomes more posteriorly positioned later in development, which the authors argued orients the ramus as a whole more posteriorly.

Research based on linear dimensions of the mandible (Humphrey et al., 1999) suggested that differences in mandibular morphology among chimpanzees and gorillas are likely a result of differences in growth rate, while differences between apes and humans are likely explicable through changes in growth trajectory. Other work by Williams et al. (2002, 2003) found that, although values for some mandibular proportions diverge between both chimpanzees and bonobos and between Neanderthals and modern humans through ontogeny, "substantial" differences in shape are established early (i.e., either prenatally or early in postnatal development) and the overall morphological distance between the species remains constant throughout development. This interpretation would seem to suggest that these pairs of species develop along similar ontogenetic trajectories. Similarly, Boughner and Dean (2008) found that species-specific differences in mandibular form between *P. troglodytes* and *Pan paniscus* are established early in mandibular ontogeny (most likely prenatally), and that these species subsequently develop along parallel ontogenetic trajectories. Supporting this supposition, Coquerelle et al. (2010) provided evidence of observable differences in mandibular form between modern humans and chimpanzees in utero.

Rak et al. (2007) found that the morphology they identified as shared by gorillas, *Au. afarensis*, and *P. robustus*, was also present in quite young fossil hominin specimens (e.g., A.L. 333-43b). These authors argued that there is no significant change in the shape of the superior border of the ramus during ontogeny. Daegling (1996) agreed with respect to the sigmoid notch in gorillas, but found that the morphology of this structure changes over the course of development in chimpanzees. The suggestion that this region of the ramus does not change in gorillas and early hominins through ontogeny would seem to be at odds with much of the body of literature reviewed above describing shape change in the mandibular ramus during growth and development. This interpretation, therefore, raises the question of whether subadult morphology accurately predicts adult ramal morphology. Moreover, the conflicting arguments presented by the studies outlined above suggest that the patterns through which great ape and human mandibles achieve their adult form are poorly understood; it is this issue that this study seeks to address.

Research Questions

This study seeks to examine mandibular ramus shape variation in an ontogenetic sample of great apes and humans, with a subsequent goal of exploring the phylogenetic implications of this morphology for assessing fossil hominin variation. To this end, we ask four specific and interrelated research questions:

1. Are there diagnostic differences in the form of the mandibular ramus among adult great ape species and humans?
2. Can consistent differences be identified in the form of the mandibular ramus among individuals of different age classes in each species?
3. At what ontogenetic stage do morphological differences in ramus form among hominid species appear?
4. Are trajectories describing ontogenetic shape changes in the mandibular ramus of these species divergent or parallel?

MATERIALS AND METHODS

Data Collection

We examined a total of 463 specimens from four species of extant hominids, with approximately equal numbers of males and females (Table 1; for a detailed list of cataloged specimens please see the Supporting Information). Because the sample for *Homo sapiens* greatly outnumbered the samples for the great ape species, a reduced number of human specimens was used in most statistical tests and visualizations (i.e., the principal component, Procrustes distance, and discriminant function analyses, but not the ontogenetic angle calculations) so that the *H. sapiens* sample more closely approximated the sizes for the apes. Specimens in this reduced sample were drawn randomly from all of the human populations, and roughly equal numbers of males and females were included.

To attempt to achieve approximately equal sampling throughout ontogeny, each individual was assigned to an age category based on dental eruption patterns and fusion of the

spheno-occipital synchondrosis (SOS). Category 1 included individuals with no permanent teeth in occlusion; Category 2 individuals were those specimens with M1 erupted and in occlusion; Category 3 contained individuals with both M1 and M2 erupted and in occlusion; Category 4 included individuals with M1, M2, and M3 erupted and in occlusion, but without a fused SOS; and Category 5 contained specimens with all permanent molars erupted and in occlusion, and with a fused SOS. In humans, these stages 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), 18/20.5–<25 years (Category 4), and >25 years (Category 5) (Ubelaker, 1989; White, 2000; AlQahtani et al., 2010). Known eruption times for the permanent molars in the African apes (*P. troglodytes* and *G. gorilla*) are approximately 3–3.5 years for M1, 6.5–7 years for M2, and 10.25–11 years for M3 (summary data presented in Smith et al., 1994); eruption of the molars is generally considered to be relatively later in *Pongo* (M1 = 4.6 years) (Kelley and Schwartz, 2014). These age categories are unlikely to be exactly homologous across species; however, the sequence of molar eruption is similar among hominids (Godfrey et al., 2001) and these eruption patterns are important markers of weaning (M1) and the onset of sexual maturation (M3) in all of these taxa (Smith, 1991, 1994). 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), although we also explore whether the results differ when examining development.

The morphology of the ramus was quantified using 2D-landmarks and semilandmarks that were collected from photographs of the lateral aspect of the ascending ramus. Photographs were taken so that the lens of the camera was oriented parallel to the ascending ramus of the mandible, and a scale (placed at the same distance from the camera lens as the ascending ramus) was included in each image. Landmarks were collected using the program tpsDig (Rohlf, 2010a) and were used to describe the orientation of the alveolar margin; because of changes in the number of teeth during ontogeny, only two landmarks were collected for this purpose: the most anterior point on the alveolar margin, and the point at which the anterior margin of the ramus crosses the alveolar margin. The anterior border of the ascending ramus and the form of the coronoid process and sigmoid notch were further quantified

TABLE 1. Samples used in this analysis

Species	Category 1	Category 2	Category 3	Category 4	Category 5	Museum Source*
	No permanent teeth erupted	Only M1 erupted and in occlusion	M1 and M2 erupted and in occlusion	All molars erupted, SOS unfused	All molars erupted, SOS fused	
<i>Pan troglodytes</i>	12	16	11	5	23	AMNH, NMNH
<i>Gorilla gorilla</i>	11	3	8	17	27	AMNH, NMNH
<i>Pongo pygmaeus</i>	9	7	11	11	17	AMNH, NMNH
<i>Homo sapiens</i>						
Nubians	19	16	5	0	21	ASU
Alaskans	13	21	12	3	47	AMNH
Southeast Asians	2	0	3	3	16	AMNH
Hungarians	5	14	23	4	48	AMNH
Reduced sample [†]	14	12	13	10	24	n/a

*AMNH = American Museum of Natural History, New York, NY; NMNH = National Museum of Natural History, Washington DC; ASU = Department of Anthropology, Arizona State University, Tempe, AZ.

[†]Because the sample for *H. sapiens* greatly outnumbered the samples for the great ape species, a reduced number of humans drawn randomly from all of the human populations was used in most statistical tests (i.e., the principal component, Procrustes distance, and discriminant function analyses but not the ontogenetic angle calculations) and visualizations so that the *H. sapiens* sample more closely approximated the sizes for the apes.

using sliding semilandmarks anchored by three fixed Type II landmarks (Bookstein, 1991; Fig. 1). All photographs were digitized by CET to minimize interobserver error.

Data Analysis

Data were analyzed using geometric morphometric methods. First, landmark configurations were superimposed using generalized procrustes analysis (GPA) so that the effects of size, rotation, and specimen position were removed. During superimposition, semilandmarks were allowed to slide to minimize bending energy [performed using the program *tpsRelw* (Rohlf, 2010b)]. All landmarks were then subjected to principal component analysis (PCA) so that variation in morphospace could be summarized and examined visually. Separate PCAs were performed for the entire sample and for each age category. Wireframe diagrams were employed to visualize shape variation in morphospace. Shape change during ontogeny was examined for each species by calculating the average landmark configuration for each age class within each species. A thin plate spline analysis (TPSA) was then performed where the average configuration for Category 1 was warped to the average configuration for each subsequent age category. To assess how ramus shape changed with size, a multivariate regression of the rotated Procrustes coordinates was performed for the entire sample onto the natural log of ramus centroid size. The angle between the alveolar margin and the ramus was further calculated (Fig. 1) and a least-squares regression of this angle on the natural log of centroid size was performed to specifically examine how orientation of the ramus changed in relation to size. Here, we follow previous work (O'Higgins et al., 2001; Ponce de León and Zollikofer, 2001; O'Higgins and Collard, 2002; Cobb and O'Higgins, 2004; McNulty et al., 2006) that has employed linear models to approximate these relationships, although it is likely that the entirety of pre- and postnatal ontogenetic shape change is best represented by a curvilinear model.

To assess whether taxa and age categories differed significantly in morphospace, pairwise Procrustes distances among the centroids of each of the species and among age categories in each species were calculated and a permutation test (4,999 iterations) was performed to assess the significance of each distance. Discriminant function analysis (DFA) with jack-knife

cross validation was conducted to determine whether individuals could be reliably assigned to species and/or age class. The top ten principal component (PC) axes (accounting for >98% of sample variance) were used in this DFA and prior probabilities were set equal to group size. All of the analyses described above were performed using the programs Morphologika (O'Higgins and Jones, 1998), MorphoJ (Klingenberg, 2011), and SPSS (IBM Corp., 2012).

Divergence of ontogenetic allometric trajectories among species 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 taxa were included in a single GPA so that the entire sample was placed into a common morphospace. Next, a multivariate regression of the Procrustes rotated coordinates onto the natural log of centroid size was conducted separately for each 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. The significance of these angles was evaluated via a permutation test (9,999 iterations) of the regression residuals, where group membership was randomly shuffled but age category sizes were held constant (McNulty et al., 2006); we further compared these results to those obtained when age category sizes were not held constant. All angular analyses were conducted in the program *R* (*R* Development Core Team, 2008) using code modified from the package "geomorph" (Adams and Otárola-Castillo, 2013). In addition to angles between ontogenetic allometric trajectories, we calculated developmental trajectories using the approach of McNulty et al. (2006), where shape was regressed against age category.

Because of the high number of statistical tests employed across this study, Type I error was minimized by performing a sequential Bonferroni adjustment (Rice, 1989).

RESULTS

Principal Components Analysis

Entire sample. PCA of the entire sample (Fig. 2) illustrates substantial shape variation both within and among the taxa examined here. Shape variation along PC 1 (which explains approximately 47% of the sample variation) primarily reflects differences in the width and depth of the sigmoid notch and height and orientation of the coronoid process; loading most positively are humans, with comparatively very wide, shallow sigmoid notches and lower, superiorly angled coronoid processes. In contrast, gorillas tend to load more negatively and have high, posteriorly angled coronoid processes and deep, anteroposteriorly (AP) compressed sigmoid notches. *Pongo* and *Pan* tend to fall intermediately along this axis. Principal component 2 (21% of sample variation) reflects similar features, especially exhibiting differences in the height of the coronoid process. Loading positively on PC 2 are humans, with very high coronoid processes, whereas loading negatively on PC 2 are the apes, with comparatively lower coronoid processes and shallow, asymmetric sigmoid notches. Thus, along these two PC axes, the primary separation is between humans (with wide sigmoid notches and generally more projecting and anteriorly/superiorly angled coronoid processes) and great apes (with AP

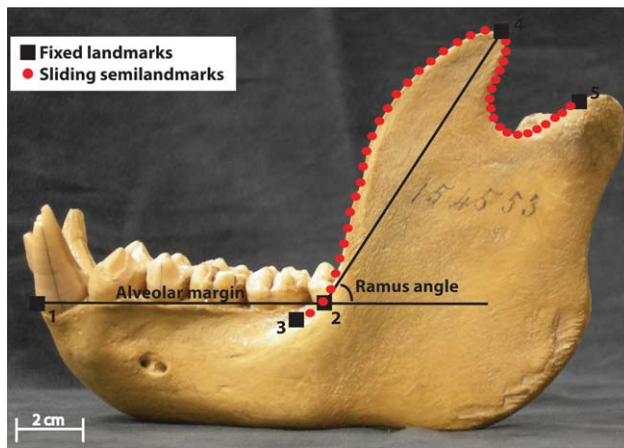


Fig. 1. Photograph of an adult male *G. gorilla* mandible in lateral view showing the landmarks utilized in this study. Black squares indicate fixed Type II landmarks and red circles indicate sliding semilandmarks. Landmarks are identified as follows: (1) most anterior point on the alveolar margin; (2) point at which the anterior margin of the ramus crosses the alveolar margin; (3) most inferior point on ramal root; (4) coronion; and (5) point at which the sigmoid crest meets the articular surface of the mandibular condyle.

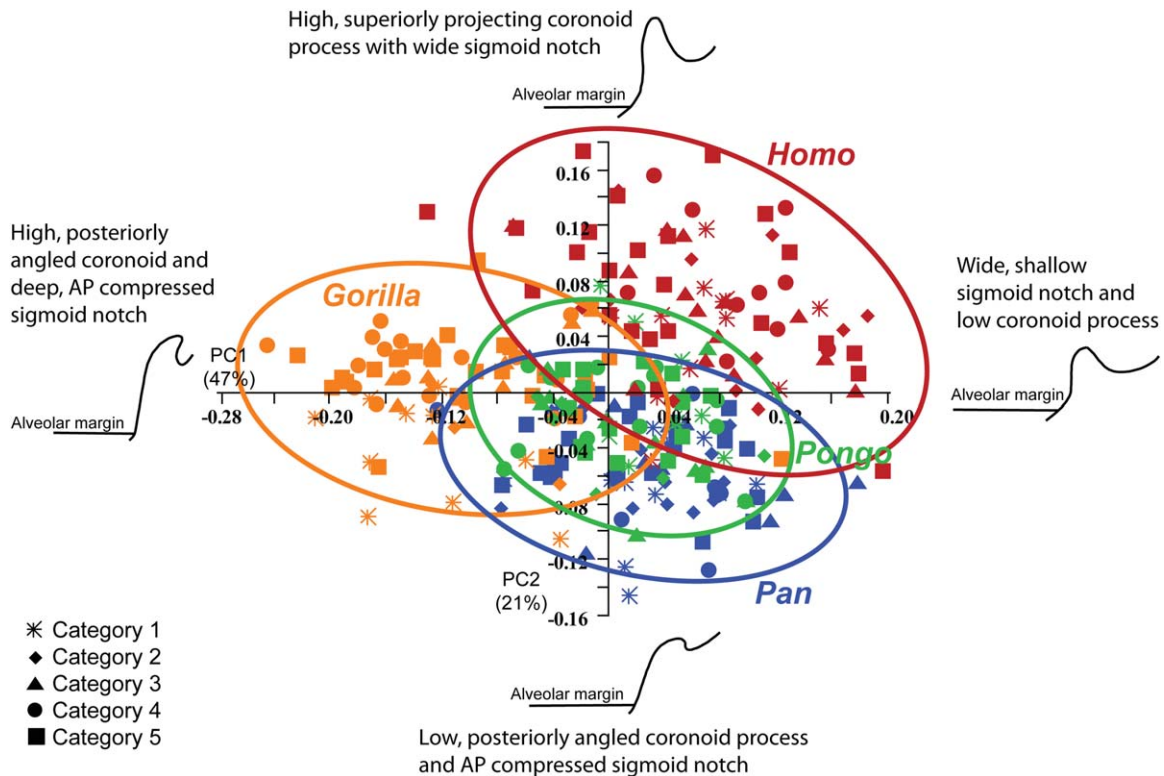


Fig. 2. Bivariate plot of PC axes 1 (x-axis, 47% of sample variance) and 2 (y-axis, 21% of sample variance) with all species and age categories included. Wireframe diagrams represent shape variation at the positive and negative ends of each axis. Circles represent 95% confidence ellipses for each species.

compressed sigmoid notches and relatively lower and more posteriorly angled coronoid processes). Gorillas also appear relatively distinct in this analysis, with very high, posteriorly angled coronoid processes, and a deep and AP compressed sigmoid notch situated close to the mandibular condyle.

Age category 1. Analysis of only the youngest specimens (category 1) for each species (Fig. 3, top) reveals similar morphological differences as observed across the entire sample (i.e., all age categories). Although there is overlap of all taxa on PCs 1 and 2, as there was, to a lesser extent, for the plot of the entire sample, humans load more heavily on the positive end of both axes reflecting their tendency to have wider and uncompressed sigmoid notches. In contrast, gorillas are located on the negative end of PC 1, indicating their tendency to have the most compressed sigmoid notches situated closest to the condyle. Again, the coronoid process and the entire ramus projects more posteriorly in gorillas and less posteriorly in humans. Height of the coronoid process appears to vary less consistently in these young specimens, with *Pan* having slightly lower coronoids, as reflected by their positioning closer to the negative end of PC 2. The angle of the ramus relative to the alveolar margin is more obtuse in subadults of all species,

which may suggest that ramus angle is influenced by mandibular size.

Age category 5. PCA of the adult specimens only suggests some overlap in the ranges of the species on PCs 1 and 2 (Fig. 3, bottom). This distribution and the corresponding shape variation is almost identical to the shape variation observed when the entire sample was analyzed, with humans more clearly separated from the apes compared to both age category 1 and the entire sample.

Thin Plate Spline Analysis

The TPSA (Fig. 4) demonstrates considerable shape change during ontogeny for each species. In all taxa, the ramus of specimens in age category 1 is angled posteriorly, albeit less so in *Pongo*; during ontogeny the ramus gradually becomes more upright, with most of the substantial shape changes occurring by age category 3. In *Gorilla* and *Pongo*, the height of the ramus relative to the length of the alveolar margin increases considerably between age category 1 and 3, with only slight increases in age categories 4 and 5. Figure 4 nicely demonstrates the unique morphology of the ramus in humans relative to the great apes in all age categories. Additionally, this figure illustrates the strong similarities in morphology between *Pan*

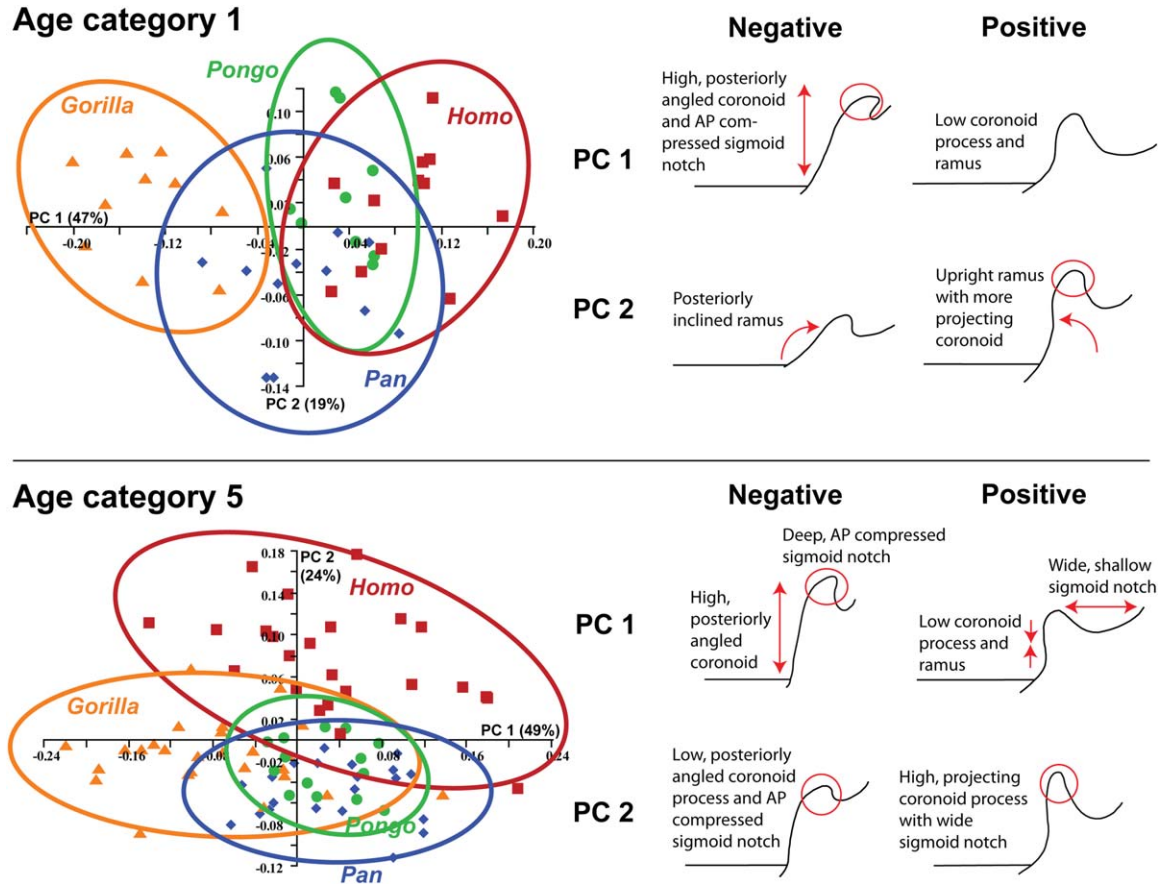


Fig. 3. Principal component plots for category 1 (top) and category 5 (bottom) specimens with corresponding morphological changes shown via wireframes. Circles represent 95% confidence ellipses.

and *Pongo*, which differ only in the slightly lower height of the coronoid in *Pan* and a slightly more asymmetrical sigmoid notch in age categories 1–3 in *Pongo*. It is also possible to observe the distinctively AP compressed and deep sigmoid notch of gorillas in all age categories.

Regression Analyses

Multivariate regression of the Procrustes residuals onto the natural log of centroid size (Fig. 5, top) reveals that the relationship between shape and size is statistically significant ($P < 0.0001$) but only explains approximately 17% of the variation in the entire sample. It is also worth noting the distribution of specimens in regard to log centroid size; the gorilla sample spans almost the entire range of observed variation in centroid size, and unsurprisingly, adult gorillas reach larger sizes than any other species. In contrast, humans occupy a relatively small portion of the morphospace illustrated by this regression and are relatively restricted in the range of log centroid sizes exhibited, which may be expected based on the

small size of the adult human mandible relative to those of the great apes.

Similarly, the regression of the ramus angle (Table 2) onto the natural log of centroid size demonstrates statistically significant but weak relationships between ramus size and angulation in all taxa (Fig. 5, bottom). Notably, the slope of the regression for *H. sapiens* differs considerably from that of the great apes, suggesting that, in humans, the angle between the ramus and the alveolar margin increases at a faster rate (relative to size) than in the great apes. A box plot of the ramus angle values for each age category within each species (Fig. 6) also demonstrates the relationship between ontogeny and ramus angle. In all taxa, ramus angles are smaller in the youngest specimens. This value gradually increases with age, with an adult ramus angle achieved no later than age category 3 in the apes, and as late as age category 4 in humans. As was evidenced by the TPSA, ramus angles are considerably lower in *Pan* than in any other taxon, particularly after age category 2, and ramus angle changes less in *Pongo* from age category 1–5 than in the other genera.

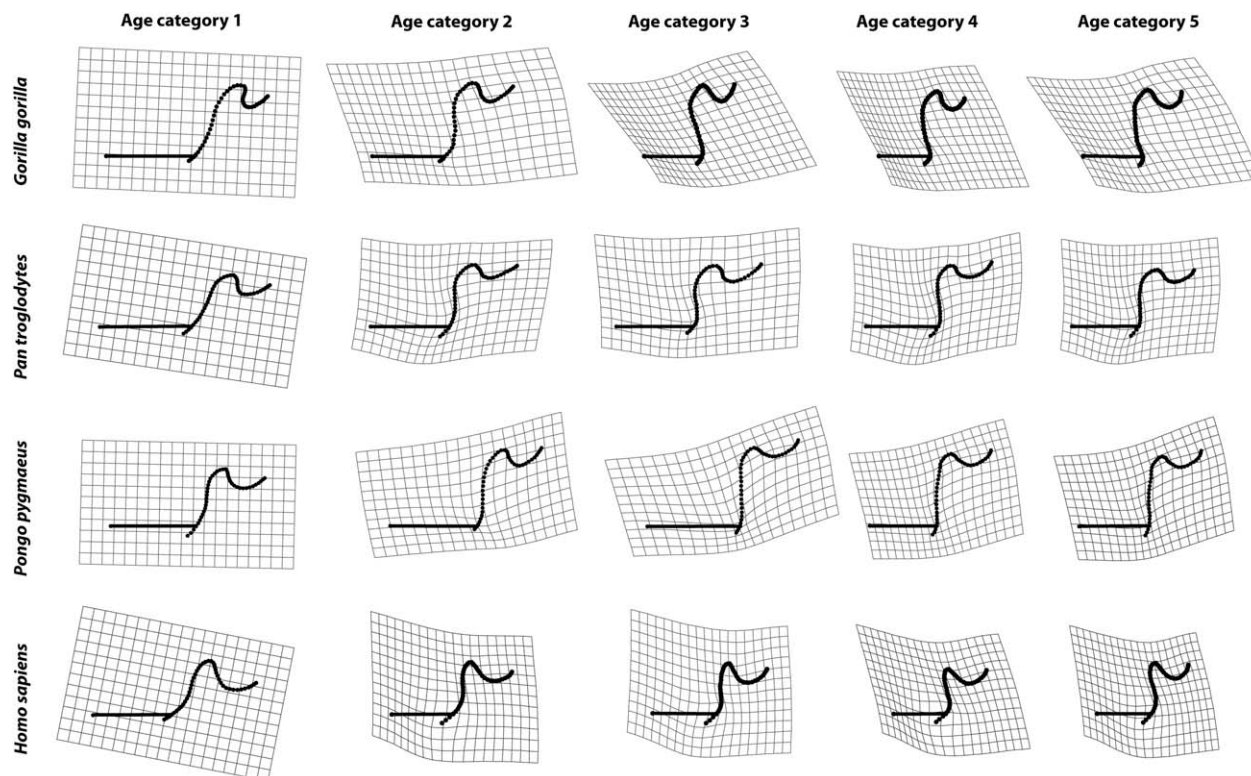


Fig. 4. Thin plate spline analysis showing ontogenetic shape change within each species. All configurations have been rotated so that the occlusal plane is horizontal.

Procrustes Distances and DFA

Among species within each age class. Procrustes distances among taxa (Table 3) were statistically significant in almost all comparisons, suggesting significant shape differences among taxa regardless of age. The only comparisons that were not significantly different were observed in age category 2 (*Pongo pygmaeus* vs. *Pan troglodytes* and *Pongo pygmaeus* vs. *Gorilla gorilla*) and in age category 4 (*Pongo pygmaeus* vs. *Pan troglodytes*). At all ages, the smallest pairwise distances were between *Pan* and *Pongo*.

Similarly, the DFA (Table 4) identified high rates of correct classification to species for all age classes. Classification rates were lowest for specimens in age category 2, although these percentages were still considerably higher than expected based on posterior probability. For the entire sample (i.e., all ages combined), correct classification rates were between 80 and 98%. In all age categories, humans tended to be correctly classified most frequently and except in one instance (a single *P. troglodytes* in category 1) no apes were misclassified as humans. Gorillas also exhibited very high rates of correct classification, with the exception of age category 2; this result is most likely a function of the small sample size ($n = 3$) for *Gorilla* in this age category. Although adult specimens of all species have

high percentages of correct classification (86–96%), there is no clear trend for classification accuracy to increase through development with adults not being classified more accurately compared to other age categories.

Among age classes within each species. Procrustes distances among age classes within each species (Table 5) reveal that, for all species, category 1 specimens could be significantly differentiated from specimens of all other age categories, except in the case of gorillas in age category 2 which, as suggested above, may be an artifact of small sample size. In addition, humans in age category 2 were significantly differentiated from humans in all age categories other than category 4. Similarly, the DFAs performed separately for each species (Table 6) indicate that the youngest and oldest specimens tend to be the most reliably classified to the correct age category in all taxa, with the highest levels of misattribution of specimens generally in age categories 2–4.

Angles Between Trajectories in Morphospace

Angles between ontogenetic trajectories when shape was regressed on the natural log of centroid size were largest for the *P. pygmaeus* and *G. gorilla* (53°) comparison and for all of the comparisons

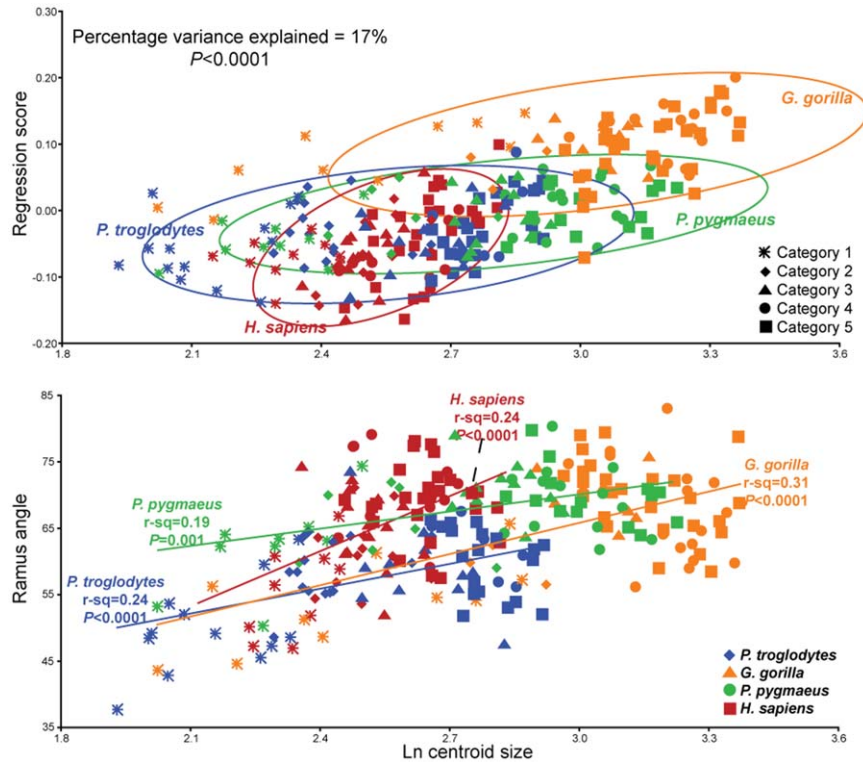


Fig. 5. Multivariate regression of entire sample on the natural log (Ln) of centroid size with 95% confidence ellipses (top), and bivariate plot of angles versus log centroid size with least-squares regression lines (bottom).

between the apes and humans (46–61°; Table 7). However, not all of these angles were statistically significant. When sample sizes for each age category were not held constant, all of the angles

between *H. sapiens* and the apes, and between *P. pygmaeus* and *G. gorilla* were significantly different after Bonferroni correction. However, when sample sizes for each age category were constrained to equal the maximum number of specimens in either

TABLE 2. Means and standard deviations (SD) of ramus angle for each age category, by species

Species	Age category	Ramus angle	
		Mean	SD
<i>G. gorilla</i>	1	53.86	7.02
	2	59.80	3.01
	3	69.87	3.91
	4	67.56	7.46
	5	69.75	5.72
<i>P. troglodytes</i>	1	49.74	6.87
	2	58.72	4.51
	3	58.86	6.52
	4	61.48	4.20
	5	59.93	4.86
<i>P. pygmaeus</i>	1	62.15	6.96
	2	65.61	5.48
	3	71.15	3.82
	4	69.39	5.06
	5	69.87	4.15
<i>H. sapiens</i> *	1	56.28	6.83
	2	61.27	5.43
	3	64.83	6.17
	4	69.81	5.98
	5	69.53	5.28

*The reduced human sample was employed in this analysis.

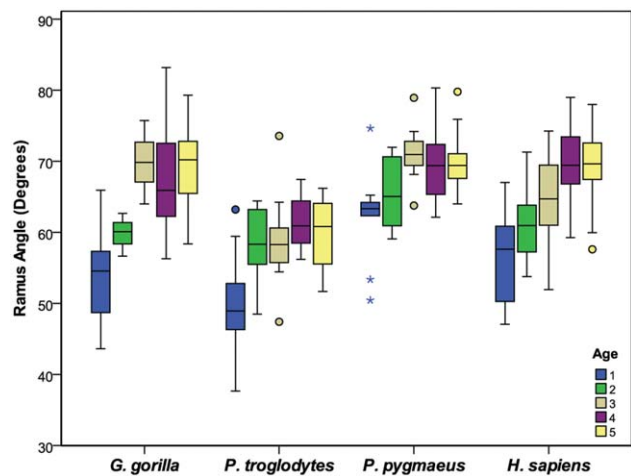


Fig. 6. Box plot of ramus angle (in degrees) for each of the age categories in each species. Darkened bars represent the median value for each group, boxes show the interquartile range (25th to 75th percentile), and the whiskers extend to 1.5 times the interquartile range. Outliers are designated by open circles, and extremes are represented by stars.

TABLE 3. Procrustes distances and permutation test results among species within each age category

	Age Category 1			Age Category 2		
	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>
<i>G. gorilla</i>	0.155 P < 0.0001			<i>G. gorilla</i>	0.1175 P = 0.0071	
<i>P. pygmaeus</i>	0.091 P = 0.0011	0.181 P < 0.0001		<i>P. pygmaeus</i>	0.0494 P = 0.2181	0.1002 P = 0.0595
<i>H. sapiens</i>	0.133 P < 0.0001	0.228 P < 0.0001	0.1 P < 0.0001	<i>H. sapiens</i>	0.1288 P < 0.0001	0.1295 P = 0.0036 P < 0.0001

	Age Category 3			Age Category 4		
	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>
<i>G. gorilla</i>	0.1705 P < 0.0001			<i>G. gorilla</i>	0.1594 P = 0.0018	
<i>P. pygmaeus</i>	0.081 P = 0.0021	0.1395 P < 0.0001		<i>P. pygmaeus</i>	0.0536 P = 0.2937	0.1442 P < 0.0001
<i>H. sapiens</i>	0.1125 P < 0.0001	0.1938 P < 0.0001	0.1188 P < 0.0001	<i>H. sapiens</i>	0.1422 P < 0.0001	0.2348 P < 0.0001 P < 0.0001

	Age Category 5		
	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>
<i>G. gorilla</i>	0.131 P < 0.0001		
<i>P. pygmaeus</i>	0.06 P = 0.002	0.112 P < 0.0001	
<i>H. sapiens</i>	0.132 P < 0.0001	0.155 P < 0.0001	0.107 P < 0.0001

Bold *P*-values are significant after sequential Bonferroni correction. Note that the reduced human sample was employed in this analysis.

TABLE 4. Discriminant function analysis results by age category

	Prior probability	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>	<i>H. sapiens</i> *
All ages	<i>P. troglodytes</i>	26%	80.3	4.5	15.2
	<i>G. gorilla</i>	25%	12.3	86.2	1.5
	<i>P. pygmaeus</i>	21%	12.7	3.6	83.6
	<i>H. sapiens</i>	28%	0	1.4	98.6
Category 1	<i>P. troglodytes</i>	29%	66.7	16.7	8.3
	<i>G. gorilla</i>	24%	0	100.0	0
	<i>P. pygmaeus</i>	21%	22.2	0	77.8
	<i>H. sapiens</i>	26%	0	0	100.0
Category 2	<i>P. troglodytes</i>	41%	53.3	13.3	33.3
	<i>G. gorilla</i>	8%	66.7	33.3	0
	<i>P. pygmaeus</i>	19%	42.9	14.3	42.9
	<i>H. sapiens</i>	32%	8.3	0	83.3
Category 3	<i>P. troglodytes</i>	25%	81.8	0	18.2
	<i>G. gorilla</i>	18%	0	100.0	0
	<i>P. pygmaeus</i>	25%	9.1	0	90.9
	<i>H. sapiens</i>	32%	0	0	100.0
Category 4	<i>P. troglodytes</i>	12%	60.0	20.0	20.0
	<i>G. gorilla</i>	40%	0	94.1	5.9
	<i>P. pygmaeus</i>	26%	9.1	0	90.9
	<i>H. sapiens</i>	23%	0	0	90.0
Category 5	<i>P. troglodytes</i>	25%	95.2	0	4.8
	<i>G. gorilla</i>	31%	0	92.3	7.7
	<i>P. pygmaeus</i>	17%	7.1	7.1	85.7
	<i>H. sapiens</i>	28%	0	0	95.8

*Note that the reduced human sample was employed in this analysis. Bold *P*-values indicate percentages of individuals correctly attributed to each species.

TABLE 5. Procrustes distances and permutation test results among age categories within each species

<i>G. gorilla</i>					<i>H. sapiens*</i>				
	1	2	3	4		1	2	3	4
2	0.076 <i>P</i> = 0.263				2	0.052 <u><i>P</i> < 0.0001</u>			
3	0.11 <u><i>P</i> < 0.0001</u>	0.062 <i>P</i> = 0.237			3	0.086 <u><i>P</i> < 0.0001</u>	0.042 <u><i>P</i> = 0.01</u>		
4	0.11 <u><i>P</i> < 0.0001</u>	0.084 <i>P</i> = 0.093	0.0415 <i>P</i> = 0.217		4	0.104 <u><i>P</i> < 0.0006</u>	0.055 <i>P</i> = 0.069	0.035 <i>P</i> = 0.384	
5	0.12 <u><i>P</i> < 0.0001</u>	0.076 <i>P</i> = 0.182	0.0444 <i>P</i> = 0.293	0.0472 <i>P</i> = 0.083	5	0.0996 <u><i>P</i> < 0.0001</u>	0.051 <u><i>P</i> < 0.0001</u>	0.031 <i>P</i> = 0.055	0.036 <i>P</i> = 0.351
<i>P. pygmaeus</i>					<i>P. troglodytes</i>				
	1	2	3	4		1	2	3	4
2	0.062 <i>P</i> = 0.049				2	0.063 <u><i>P</i> = 0.012</u>			
3	0.073 <u><i>P</i> = 0.0006</u>	0.038 <i>P</i> = 0.379			3	0.0735 <i>P</i> = 0.029	0.023 <i>P</i> = 0.942		
4	0.079 <u><i>P</i> = 0.004</u>	0.046 <i>P</i> = 0.198	0.043 <i>P</i> = 0.13		4	0.08 <i>P</i> = 0.02	0.025 <i>P</i> = 0.934	0.039 <i>P</i> = 0.728	
5	0.073 <u><i>P</i> < 0.0001</u>	0.045 <i>P</i> = 0.067	0.032 <i>P</i> = 0.207	0.019 <i>P</i> = 0.75	5	0.073 <u><i>P</i> < 0.001</u>	0.024 <i>P</i> = 0.64	0.03 <i>P</i> = 0.555	0.025 <i>P</i> = 0.888

*The reduced human sample was employed in this analysis. Bold values are significant at *P*<0.05, bold and underlined values are significant after sequential Bonferroni correction.

species for that age category, only the comparisons *H. sapiens* versus *P. pygmaeus* and *G. gorilla* versus *P. pygmaeus* were significant at *P*<0.05, and only the angle between *G. gorilla* and *P. pygmaeus* was significant after Bonferroni correction.

Similar angular values and levels of significance were obtained when shape was regressed on age category rather than size (Table 8). Notably, the pattern of significance remained comparable to the ontogenetic allometric trajectory angles, with very few significant differences between developmental

trajectories when sample sizes were constrained to be equal to the maximum number of specimens in each age category.

DISCUSSION

Morphological Variation in the Mandibular Ramus of Adult Apes and Humans

The present study suggests that adult ramus form differs significantly among great ape and human species. The strongest shape differences

TABLE 6. Discriminant function analysis results by species

	Prior probability	1	2	3	4	5
<i>P. troglodytes</i>	1	18%	41.7	16.7	0	8.3
	2	23%	13.3	33.3	13.3	6.7
	3	15%	10.0	30.0	10.0	0
	4	11%	0	14.3	0	0
	5	33%	9.1	18.2	13.6	0
<i>G. gorilla</i>	1	15%	50.0	20.0	20.0	10.0
	2	5%	100.0	0.0	0.0	0
	3	12%	0	12.5	50.0	25.0
	4	26%	0	0	5.9	52.9
	5	42%	0	0	0	14.8
<i>P. pygmaeus</i>	1	16%	66.7	22.2	11.1	0
	2	13%	14.3	42.9	28.6	0
	3	20%	0	27.3	45.5	9.1
	4	22%	0	0	8.3	16.7
	5	29%	0	6.3	6.3	37.5
<i>H. sapiens*</i>	1	13%	68.6	31.4	0	0
	2	19%	16.0	56.0	4.0	0
	3	16%	0	26.8	7.3	0
	4	4%	0	30.0	10.0	0
	5	49%	0	3.9	3.9	1.6

*The reduced human sample was employed in this analysis. Bold values indicate percentages of individuals correctly attributed to each age category.

TABLE 7. Angles between ontogenetic allometric trajectories (shape regressed on the natural log of centroid size)

	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>	<i>H. sapiens</i>
<i>P. troglodytes</i>	—	35.30	36.68	47.97
		$P = 0.104$	$P = 0.0905$	$P = 0.0087$
<i>G. gorilla</i>	35.30	—	52.92	45.64
	$P = 0.162$		$P = 0.0026$	$P = 0.0095$
<i>P. pygmaeus</i>	36.68	52.92	—	60.66
	$P = 0.161$	$P = 0.005$		$P = 0.0006$
<i>H. sapiens</i>	47.97	45.64	60.66	—
	$P = 0.112$	$P = 0.1698$	$P = 0.04$	

Upper triangle: permutation test with no sample size constraints; Lower triangle: permutation with sample size constraints (following McNulty et al., 2006). Bold values are significant at $P < 0.05$, bold and underlined values are significant after sequential Bonferroni correction. Note that the full human sample was employed in this analysis.

were found between gorillas and humans with *Pan* and *Pongo* intermediate between these two taxa. These findings are similar to those of Schmittbuhl et al. (2007) who determined that, among great apes and humans, *Pan* and *Pongo* were most similar to each other and humans could be clearly differentiated from great apes. Furthermore, our data indicate that gorillas tend to have high, posteriorly angled coronoid processes with AP compressed sigmoid notches, whereas humans have AP wide sigmoid notches with superiorly oriented coronoid processes. Thus, our results support those of Humphrey et al. (1999) that *Gorilla* has a taller ramus, at least at the coronoid, than other great apes and humans and that the sigmoid notch is AP wider in humans than in great apes. We also find evidence for the traits that Rak et al. (2007) identified as separating gorillas from other great apes and humans, including a posteriorly oriented coronoid and a narrow and deep sigmoid notch positioned closer to the condyle than in the other taxa.

In the analysis above, between 86 and 96% of adult great ape and human specimens were allocated to the correct genus using ramal morphology. This accuracy is comparable to other studies that have quantitatively assessed hominid mandibular morphology and provides evidence that contradicts suggestions that the ramus may be less effective for differentiating hominid taxa from one another than the corpus (Robinson, 2012). For example, as noted above, Rak

et al. (2007) correctly identified 82% of their ramal specimens to taxon. Lague et al. (2008), using data from eight linear measurements of the mandibular corpus on specimens from the same four genera analyzed here, were able to classify 80% of their specimens to the correct genus using discriminant analysis. Schmittbuhl et al. (2007), who explored the shape of the entire mandibular outline in the same four ape genera as well as *Hylobates*, had even greater success with 94–98% of specimens correctly identified to genus. This finding suggests that including data from the entire mandible rather than from particular regions may be more effective for discriminating between hominid taxa. These results also provide evidence that intraspecific variation in mandibular morphology is not so extensive as to preclude the use of morphological data from the mandible in taxonomic analyses of fossil hominid specimens. Additional support for this comes from studies of the mandible of *P. paniscus* and *P. troglodytes* in which specimens of these two closely related species were identified to the correct species with high accuracy (Taylor and Groves, 2003; Schmittbuhl et al., 2007; Lague et al., 2008; Robinson, 2012).

Ontogenetic Shape Variation in the Great Ape Mandibular Ramus

Although the youngest specimens in each taxon are morphologically distinct from other age

TABLE 8. Angles between developmental trajectories (shape regressed on age category)

	<i>P. troglodytes</i>	<i>G. gorilla</i>	<i>P. pygmaeus</i>	<i>H. sapiens</i>
<i>P. troglodytes</i>	—	27.88	42.32	43.76
		$P = 0.57$	$P = 0.26$	$P = 0.02$
<i>G. gorilla</i>	27.88	—	57.31	54.46
	$P = 0.66$		$P = 0.0348$	$P = 0.004$
<i>P. pygmaeus</i>	42.32	57.31	—	67.81
	$P = 0.26$	$P = 0.068$		$P = 0.014$
<i>H. sapiens</i>	43.76	54.46	67.81	—
	$P = 0.099$	$P = 0.035$	$P = 0.014$	

Upper triangle: permutation test with no sample size constraints; Lower triangle: permutation test with sample size constraints (following McNulty et al., 2006). Bold values are significant at $P < 0.05$, bold and underlined values are significant after sequential Bonferroni correction. Note that the full human sample was employed in this analysis.

categories, there is otherwise considerable variation among the age groups in each species. This degree of intraspecific variation makes it difficult to determine consistently the age of a specimen from ramal morphology alone, particularly in older specimens. The difficulty of differentiating categories 3, 4, and 5 individuals from each other would seem to suggest that hominids attain their adult ramal morphology prior to the completion of craniodental development. Humans are distinct from apes in that individuals in age category 2 can be significantly differentiated from adults; this may perhaps suggest that changes in ramus shape continue for a longer period of time in humans, albeit only until M2 eruption. This conforms to the findings of Chen et al. (2000) who observed significant shape changes in the position of landmarks on the ramus of modern humans between ages 11 and 15. Although weaning generally occurs in both apes and humans by the eruption of M1, this delay in attainment of fully adult morphology in younger (age category 2) humans could reflect the fact that human children exhibit much slower growth in middle childhood than chimpanzees (Kaplan et al., 2000).

Morphological differences among hominid species in ramus form appear early in ontogeny, as previous researchers have found for the mandible more generally (Williams et al., 2002, 2003; Boughner and Dean, 2008; Coquerelle et al., 2010). Importantly, these morphological differences are established before M1 eruption, and may even be established prenatally (see Coquerelle et al., 2010). The primary shape change that occurs in ramus form during ontogeny is a gradual antero-superior reorientation of the ramus relative to the alveolar margin (i.e., adults have more vertically oriented rami) as Schultz (1969) found, with this shift being less extreme in *Pongo* (rather than in *Pan* as suggested by Schultz). Research using computed tomography (CT) scan data has found that the shift in modern humans to a more vertical ramus begins in the second trimester in utero (Coquerelle et al., 2010) with the ramus then shifting postero-superiorly between birth and the emergence of all of the deciduous dentition (Coquerelle et al., 2013). Contra Aitchison (1963) and Boughner and Dean (2008), we do not find evidence that chimpanzees exhibit a different pattern (i.e., an increasingly posteriorly oriented ramus through development) from other great apes and humans with respect to this character; however, our evidence does suggest that the ramus is oriented more posteriorly in chimpanzees than in the other taxa in all age categories. Similar to the results of Daegling (1996) and Rak et al. (2007), we find that the distinctively deep and narrow sigmoid notch morphology is established early in ontogeny in gorillas.

Our analysis of the angles among the ontogenetic allometric and developmental trajectories

calculated here, as well as our regression analysis of ramus angle versus ramus centroid size, suggests that the primary differences in trajectory orientation are between humans and all other ape taxa as suggested by Humphrey et al. (1999). However, this evidence is equivocal at best, since the angles between the ape and human trajectories are only significant after sequential Bonferroni correction when there are no constraints on the samples employed in the permutation test for significance. It is notable, though, that the angle between the ontogenetic allometric trajectories for *Pongo* and *Gorilla* is significant, regardless of the permutation test employed. Thus, although we are unable to fully reject the hypothesis that great ape ontogenetic allometric trajectories for the mandibular ramus parallel one another in morphospace, our data suggest that there are some important differences in the process through which adult ramal morphologies in *Pongo* and *Gorilla* are achieved relative to size.

These results provide an interesting comparison with previous research examining craniofacial ontogeny in humans, non-human primates, and fossil hominins. Like the present study, this previous work addressed how postnatal changes in ontogenetic trajectory, and thus shape, relate to differences among adults of different hominid species. The results of these studies were split: some researchers (Krovitz, 2000; Ponce de León and Zollikofer, 2001; Ackermann and Krovitz, 2002; Lieberman et al., 2007; Boughner and Dean, 2008) have argued that differences in craniofacial shape between closely related species arise early in ontogeny (perhaps even prenatally), and that ontogenetic trajectories for these species later in ontogeny are parallel. In contrast, other researchers (O'Higgins and Collard, 2002; Strand Viðarsdóttir et al., 2002; Krovitz, 2003; Cobb and O'Higgins, 2004; Strand Viðarsdóttir and Cobb, 2004; Mitteroecker et al., 2004, 2005; Bastir et al., 2007; Terhune et al., 2013) have found that, although shape differences are present very early in ontogeny (i.e., before eruption of the first molar), divergent shape trajectories later in ontogeny further contribute to craniofacial differences between adults of different species, as well as between geographic populations of modern humans (Strand Viðarsdóttir et al., 2002; Strand Viðarsdóttir and O'Higgins, 2003; Strand Viðarsdóttir and Cobb, 2004; Smith et al., 2013). The data presented here are consistent with both of these groups of studies in suggesting the shape differences in the mandible are established relatively early during ontogeny, but we find comparatively less support to suggest that ontogenetic trajectories in morphospace during later stages of development are divergent (at least among all taxa). Given this body of literature, one important conclusion may be that, rather than searching for a single pattern of ontogenetic shape change in hominid taxa, patterns of ontogenetic shape change

may vary depending upon the region or organ system under investigation (e.g., Gould, 1977).

The Influence of Phylogeny and Function on Variation in the Hominid Mandibular Ramus

The finding that significant differences in ramal morphology are established early in ontogeny in these hominid species suggests that the observed differences may be genetically controlled and are less likely to be developmentally plastic. Our results, therefore, appear to support the work of Rak et al. (Rak et al., 2002, 2007), suggesting that this region of the mandible may be informative in phylogenetic analyses of fossil hominins. However, we did not perform a formal phylogenetic analysis that included both fossil and extant taxa. Previous research (Ritzman and Spencer, 2009) has questioned Rak et al.'s (2007) contention that the form of the ramus is not related to function and should therefore be favored over other traits in analyses of early hominin phylogeny. It should be noted, however, that these interpretations are not mutually exclusive; in other words, ramus form may contain a strong functional signal, but it may also be a good indicator of phylogenetic relationships (Lockwood and Fleagle, 1999). Therefore, these data suggest that, whether the morphological differences described here are phylogenetic or epigenetic in nature, they may still be useful in analyses seeking to differentiate among great apes, modern humans, and fossil hominid taxa.

Schmittbuhl et al. (2007) argue that the substantial differences between the mandibular morphologies of *Pan* and *Homo* and strong similarities between the shape of the mandible in *Pan* and *Pongo* found in their study (and this one) are evidence that the species that are most similar to one another in shape do not conform to predictions based on phylogenetic relatedness. Based on this observation, the results of the present study suggest that, while the mandible may be useful in taxonomic analyses, it may not be as profitable for phylogenetic analyses. However, if *Pan* and *Pongo* share the ancestral mandibular great ape/human morphotype, as suggested by Rak et al. (2007), and the morphologies of *Homo* and *Gorilla* are derived from this morphotype, then the results of this study are not incompatible with the currently well-supported extant hominid phylogenetic relationships.

The shape of the mandibular ramus undoubtedly contains information related to masticatory function and temporalis muscle form. Experimental work in which the temporalis was partly or entirely excised has demonstrated that, in the absence of muscle force, the coronoid process either changed orientation [in the case of partial excision of the temporalis in cats (Avis, 1959)] or was almost entirely resorbed [when the temporalis

was entirely removed in rats (Washburn, 1947)]. Further, experimentally induced hypomobility of the juvenile macaque mandible was shown to result in elongation of the coronoid process (Isberg et al., 1990). These studies demonstrate clear departures from the normal range of variation in the masticatory apparatus in animals whose behaviors were manipulated experimentally during development, but evidence for experimentally induced changes in the external morphology of the mandibular ramus among adults is equivocal or absent. Thus, these data would seem to suggest that the form of the coronoid process and mandibular ramus is most labile during ontogeny.

A comparative analysis of coronoid form in relation to bony markers of the temporalis in anthropoid primates (Ritzman and Spencer, 2009) further suggests that height and width of the coronoid process are related to the orientation of the temporalis muscle in interspecific comparisons. In addition to interspecific differences in the position and angulation of the coronoid process, work by Carlson et al. (1978) identified changes in the orientation of the temporalis muscle during ontogeny as the anterior component of the macaque temporalis becomes relatively better developed with increasing age. These findings accord well with our data indicating that the mandibular ramus becomes more vertically oriented during ontogeny, and that the coronoid process tends to increase in projection with age. This reorientation of the temporalis muscle and its attachments may have important impacts on the length of the temporalis moment arm and the lever-to-load arm ratio, and thus may suggest important differences in relative bite force during ontogeny.

Mandibular Ramus Shape in Fossil Hominins

The data presented here have important implications for analyses of fossil hominin mandibular variation, and can help pave the way for future analyses of this morphological region in hominins. For example, in their study of the morphology of the mandibular ramus of humans and great apes, Rak et al. (2007) grouped *H. sapiens*, *P. troglodytes*, and *P. pygmaeus* as having a similar morphology that was distinct from that possessed by *G. gorilla*, *Au. afarensis*, and *P. robustus*. This evidence was used to suggest that *Australopithecus* and *Paranthropus* shared a derived morphology that evolved independently from gorillas. However, this interpretation was partly based on their finding that modern humans have a similar morphology to chimpanzees. If, as the results of the present study suggest, humans have a uniquely derived mandibular morphology compared to the great apes (including *Pan*), one could alternatively argue that the ancestral hominin morphotype was inherited by *Australopithecus* and *Paranthropus*

from *Gorilla* and that *P. troglodytes* and *P. pygmaeus* have independently evolved similar ramal morphologies. However, Rak et al. (2007) contend that *Ardipithecus* is similar to *Pan* in its ramal morphology, which may suggest that the ancestral hominin morphotype was more similar to *Pan*, although this interpretation is complicated by debate over whether *Ardipithecus* is indeed ancestral to later hominins (e.g., Wood and Harrison, 2011; but see Kimbel et al., 2014). Given the importance of these characters for Rak and colleagues' suggestion that *Australopithecus* and *Paranthropus* form a clade that is separate from that of the genus *Homo* and, consequently, that *Australopithecus* is not ancestral to modern humans, it will be important to resolve this issue through a more extensive analysis of the morphology of the mandibular ramus that includes fossil hominin specimens. One particularly important fossil specimen to be included in future analyses will be KNM-ER 60000, an early *Homo* mandible from Ileret, Kenya (Leakey et al., 2012). This specimen, which preserves a largely intact mandibular ramus (albeit with some damage to the sigmoid notch and mandibular condyle), shares features of both the *Gorilla* and human morphotypes identified in the present study, with an anterior concavity of the ramus that is human-like but a more posteriorly facing coronoid process as found in *Gorilla*. Clearly, further analyses are warranted to place these morphologies in a phylogenetic context and to polarize these character traits in the hominin lineage.

Given how rarely rami are found in the hominin fossil record it is important to glean as much information as possible from the few specimens available. Fortunately, our findings, like those of Rak et al. (2007), suggest that adult ramal morphology

is established early in ontogeny in great apes and humans. If so, we should be able to include juvenile mandibular specimens to increase the sample size of fossil hominins in comparative analyses of ramal morphology. Unfortunately, only a handful of subadult early hominin specimens with intact rami have been recovered. These specimens include A.L. 333-43b, A.L. 333n-1, and DIK-1-1 (*Au. afarensis*), and most recently MH 1, a juvenile attributed to the species *Australopithecus sediba*. This latter specimen exhibits a relatively vertically oriented and tall ramus with an anterior margin that is directed superiorly and slightly posteriorly, a posteriorly angled coronoid process, and a deep and asymmetric sigmoid notch (Fig. 7; Berger et al., 2010). In general, this morphology appears very ape-like, and the slight posterior tilt to the ramus is consistent with the estimated developmental age of this specimen. Interestingly, a presumed adult female of this same species (MH 2) contains a largely intact mandibular ramus, although the coronoid process is damaged. Despite this damage, the ramus is markedly different in these two *Au. sediba* specimens, with the purported adult female exhibiting a concave profile to the anterior margin of the ramus, a deep and symmetric sigmoid notch, and a coronoid process that does not appear to have been posteriorly angled (Fig. 7; Berger et al., 2010). These qualitative descriptions are consistent with a recent ontogenetic analysis (that did not incorporate ramus shape) by de Ruiter et al. (2013), which revealed that the pattern and magnitude of mandibular change in *Au. sediba* is largely inconsistent with and exceeds the pattern and magnitude of mandibular change in extant chimpanzees and humans and in *Au. africanus*, although the observed pattern of ontogenetic shape change was similar to that of *H. erectus*.

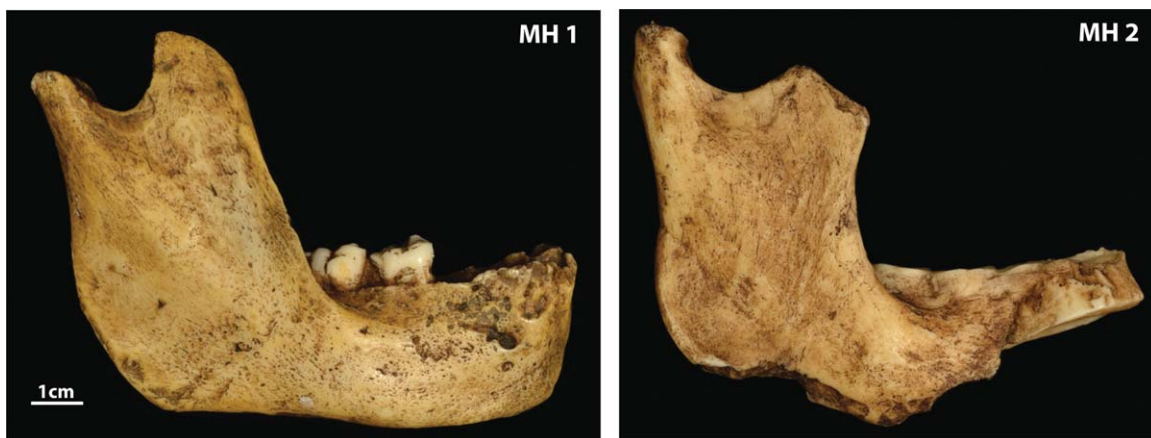


Fig. 7. Lateral view photographs of high quality casts of the *Au. sediba* mandibles (MH1 and MH2) showing the differences in ramal morphology discussed in the text. Both photos are shown at the same scale. Casts are housed at Ditsong National Museum of Natural History.

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LITERATURE CITED

- Ackermann RR, Krovitz GE. 2002. Common patterns of facial ontogeny in the hominid lineage. *Anat Rec B* 269:142–147.
- Adams DC, Collyer ML. 2009. A general framework for the analysis of phenotypic trajectories in evolutionary studies. *Evolution* 63:1143–1154.
- Adams DC, Otárola-Castillo E. 2012. Package ‘geomorph’: Geometric morphometric analysis of 2d/3d landmark data. R package version 1.0.
- Adams DC, Otárola-Castillo E. 2013. Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol Evol* 4:393–399.
- Aitchison J. 1963. Comparison of chimpanzee skulls, jaws and teeth with those of modern hominids. *Aust Dent J* 8:477–482.
- Aitchison J. 1965. Contrasts in the mandibles and mandibular teeth of the chimpanzee, orangutan and gorilla. *Dent Mag Oral Top* 81:105–108.
- AlQahtani SJ, Hector MP, Liversidge HM. 2010. Brief communication: The London atlas of human tooth development and eruption. *Am J Phys Anthropol* 142:481–490.
- Anderson MJ, Ter Braak CJF. 2003. Permutation tests for multi-factorial analysis of variance. *J Stat Comput Simul* 73: 85–113.
- Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999. Cladistics and early hominid phylogeny: Response. *Science* 285:1209–1212.
- Avis V. 1959. The relation of the temporal muscle to the form of the coronoid process. *Am J Phys Anthropol* 17:99–104.
- Bastir M, O’Higgins P, Rosas A. 2007. Facial ontogeny in Neanderthals and modern humans. *Proc R Soc B* 274:1125–1132.
- Begun DR. 1994. The significance of *Otavipithecus namibiensis* to interpretations of hominoid evolution. *J Hum Evol* 27:385–394.
- Berger LR, de Ruiter DJ, Churchill SE, Schmid P, Carlson KJ, Dirks PHGM, Kibii JM. 2010. *Australopithecus sediba*: A new species of *Homo*-like australopithecine from South Africa. *Science* 328:195–204.
- Bookstein FL. 1991. *Morphometric Tools for Landmark Data*. Cambridge: Cambridge University Press.
- Boughner J, Dean MC. 2008. Mandibular shape, ontogeny and dental development in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). *Evol Biol* 35:296–308.
- Carlson DS, McNamara JA Jr, Jaul DH. 1978. Histological analysis of the growth of the mandibular condyle in the rhesus monkey (*Macaca mulatta*). *Am J Anat* 151:103–118.
- Chen SYY, Lestrel PE, Kerr WJS, McColl JH. 2000. Describing shape changes in the human mandible using elliptical Fourier functions. *Eur J Orthod* 22:205–216.
- Cobb SN, O’Higgins P. 2004. Hominins do not share a common postnatal facial ontogenetic shape trajectory. *J Exp Zool* 302B:302–321.
- Collard M, Lycett SJ. 2009. An assessment of the likely impact of strain-related phenotypic plasticity on hominin fossil species identification. *S Afr J Sci* 105:312–316.
- Collard M, Wood B. 2001. Homoplasy and the early hominid masticatory system: Inferences from analyses of extant hominoids and papionins. *J Hum Evol* 41:167–194.
- Collyer ML, Adams DC. 2007. Analysis of two-state multivariate phenotypic change in ecological studies. *Ecology* 88:683–692.
- Coquerelle M, Bookstein FL, Braga J, Halazonetis DJ, Weber GW. 2010. Fetal and infant growth patterns of the mandibular symphysis in modern humans and chimpanzees. *J Anat* 217:507–520.
- Coquerelle M, Prados-Frutos JC, Benazzi S, Bookstein FL, Senck S, Mitteroecker P, Weber GW. 2013. Infant growth patterns of the mandible in modern humans: A closer exploration of the developmental interactions between the symphyseal bone, the teeth, and the suprahyoid and tongue muscle insertion sites. *J Anat* 222:178–192.
- Daegling DJ. 1996. Growth in the mandibles of African apes. *J Hum Evol* 30:315–341.
- de Ruiter DJ, DeWitt TJ, Carlson KB, Brophy JK, Schroeder L, Ackermann RR, Churchill SE, Berger LR. 2013. Mandibular remains support taxonomic validity of *Australopithecus sediba*. *Science* 340:1232997-1-4.
- Godfrey LR, Samonds KE, Jungers WL, Sutherland MR. 2001. Teeth brains, and primate life histories. *Am J Phys Anthropol* 114:192–214.
- Gould SJ. 1977. *Ontogeny and Phylogeny*. Cambridge: Harvard University Press.
- Groves C. 2001. *Primate Taxonomy*. Primate Taxonomy. Washington DC: Smithsonian Institution Press.
- Harvati K, Singh N, Lopez EN. 2011. A three-dimensional look at the Neanderthal mandible. In: Condemi S, Weniger G-C, editors. *Continuity and Discontinuity in the People of Europe: One Hundred Fifty Years of Neanderthal Study*. New York: Springer. pp 179–192.
- Hrdlicka A. 1940a. Mandibular and maxillary hyperostosis. *Am J Phys Anthropol* 27:1–55.
- Hrdlicka A. 1940b. Lower jaw. *Am J Phys Anthropol* 27:281–308.
- Hrdlicka A. 1940c. Lower jaw further studies. *Am J Phys Anthropol* 27:383–467.
- Humphrey LT, Dean MC, Stringer CB. 1999. Morphological variation in great ape and modern human mandibles. *J Anat* 195:491–513.
- IBM Corp. 2012. *IBM SPSS Statistics for Windows, Version 21.0*. Armonk, NY: IBM Corp.
- Isberg AM, McNamara JA, Carlson DS, Isacson G. 1990. Coronoid process elongation in rhesus monkeys (*Macaca mulatta*) after experimentally induced mandibular hypomobility. *Oral Surg Oral Med Oral Pathol* 70:704–710.
- Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: Diet, intelligence, and longevity. *Evol Anthropol* 9:156–185.
- Kelley J, Schwartz GT. 2010. Dental development and life history in living African and Asian apes. *Proc Natl Acad Sci USA* 107:1035–1040.
- Kimbel WH, Suwa G, Asfaw B, Rak Y, White TD. 2014. *Ardipithecus ramidus* and the evolution of the human cranial base. *Proc Natl Acad Sci* doi: 10.1073/pnas.1322639111.
- Klingenberg CP. 2011. MorphoJ: An integrated software package for geometric morphometrics. *Mol Ecol Resour* 11:353–357.
- Krovitz G. 2000. Three dimensional comparisons of craniofacial morphology and growth patterns in Neanderthals and modern humans. PhD dissertation. John Hopkins University, Baltimore, Maryland.
- Krovitz G. 2003. Shape and growth and differences between Neanderthals and modern humans: Grounds for a species level distinction? In: Thompson JL, Krovitz GE, Nelson AJ, editors. *Patterns of Growth and Development in the Genus Homo*. Cambridge: Cambridge University Press. pp 320–342.
- Lague MR, Collard NJ, Richmond BG, Wood BA. 2008. Hominid mandibular corpus shape variation and its utility for recognizing species diversity within fossil *Homo*. *J Anat* 213: 670–685.

- Leakey MG, Spoor F, Dean MC, Feibel CS, Antón SC, Kiarie C, Leakey LN. 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. *Nature* 488:201–204.
- Lieberman DE, Wood BA, Pilbeam DR. 1996. Homoplasy and early *Homo*: Analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis*. *J Hum Evol* 30:97–120.
- Lieberman DE, Carlo J, Ponce de Leon M, Zollikofer CPE. 2007. A geometric morphometric analysis of heterochrony in the cranium of chimpanzees and bonobos. *J Hum Evol* 52: 647–662.
- Lockwood CA, Fleagle JG. 1999. The recognition and evaluation of homoplasy in primate and human evolution. *Yearb Phys Anthropol* 42:189–232.
- McHenry HM. 1994. Tempo and mode in human evolution. *Proc Natl Acad Sci USA* 91:6780–6786.
- McNulty KP. 2012. Evolutionary development in *Australopithecus africanus*. *Evol Biol* 39:488–498.
- McNulty KP, Frost SR, Strait DS. 2006. Examining affinities of the Taung child by developmental simulation. *J Hum Evol* 51:274–296.
- Mitteroecker P, Gunz PG, Bernhard M, Schaefer K, Bookstein FL. 2004. Comparison of cranial ontogenetic trajectories among great apes and humans. *J Hum Evol* 46:679–698.
- Mitteroecker P, Gunz P, Bookstein FL. 2005. Heterochrony and geometric morphometrics: A comparison of cranial growth in *Pan paniscus* versus *Pan troglodytes*. *Evol Dev* 7:244–258.
- Nicholson E, Harvati K. 2006. Quantitative analysis of human mandibular shape using three dimensional geometric morphometrics. *Am J Phys Anthropol* 131:368–383.
- O'Higgins P, Collard M. 2002. Sexual dimorphism and facial growth in papionin monkeys. *J Zool* 257:255–272.
- O'Higgins P, Jones N. 1998. Facial growth in *Cercocebus torquatus*: An application of three-dimensional geometric morphometric techniques to the study of morphological variation. *J Anat* 193:251–272.
- O'Higgins P, Chadfield P, Jones N. 2001. Facial growth and the ontogeny of morphological variation within and between the primates *Cebus apella* and *Cercocebus torquatus*. *J Zool* 254: 255–272.
- Piras P, Colangelo P, Adams DC, Buscalioni A, Cubo J, Kotsakis T, Meloro C, Raia P. 2010. The Gavialis-Tomistoma debate: The contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships. *Evol Dev* 12:568–579.
- Ponce de León M, Zollikofer C. 2001. Neanderthal cranial ontogeny and its implication for late hominid diversity. *Nature* 412:534–538.
- R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.
- Rak Y, Ginzburg A, Geffen E. 2002. Does *Homo neanderthalensis* play a role in modern human ancestry? The mandibular evidence. *Am J Phys Anthropol* 119:199–204.
- Rak Y, Ginzburg A, Geffen E. 2007. Gorilla-like anatomy on *Australopithecus afarensis* mandibles suggests *Au. Afarensis* link to robust australopithecines. *Proc Natl Acad Sci USA* 104: 6568–6572.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Ritzman TB, Spencer MA. 2009. Coronoid process morphology and function in anthropoid primates. *Am J Phys Anthropol* 104:221.
- Robinson CA. 2012. Analysis of three-dimensional mandibular shape in *Pan*. *J Hum Evol* 63:191–204.
- Rohlf FJ. 2010a. tpsDig, Version 2.16. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Rohlf FJ. 2010b. tpsRelw, Relative Warps Analysis, Version 1.49. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Schmittbuhl M, Rieger J, LeMinor J-M, Schaaf A, Guy F. 2007. Variations of the mandibular shape in extant hominoids: Generic, specific and subspecific quantification using elliptical Fourier analysis in lateral view. *Am J Phys Anthropol* 132:119–131.
- Schultz AH. 1969. The skeleton of the chimpanzee. In: Bourne GH, editor. *Anatomy, Behavior, and Diseases of Chimpanzees*. Basel: S. Karger AG. pp 50–103.
- Singleton M. 2012. Postnatal cranial development in papionin primates: An alternative model for hominin evolutionary development. *Evol Biol* 39:499–520.
- Skelton RR, McHenry HM. 1992. Evolutionary relationships among early hominids. *J Hum Evol* 23:309–349.
- Smith BH. 1991. Dental development and the evolution of life history in Hominidae. *Am J Phys Anthropol* 86:157–174.
- Smith BH. 1994. Patterns of dental development in *Homo*, *Australopithecus*, *Pan*, and *Gorilla*. *Am J Phys Anthropol* 94: 307–325.
- Smith BH, Crummett TL, Brandt KL. 1994. Ages of eruption of primate teeth: A compendium for aging individuals and comparing life histories. *Yearb Phys Anthropol* 37:177–231.
- Smith HF, Ritzman T, Otárola-Castillo E, Terhune CE. 2013. A 3-D geometric morphometric study of intraspecific variation in the ontogeny of the temporal bone in modern *Homo sapiens*. *J Hum Evol* 65:479–489.
- Strand Viðarsdóttir U, Cobb S. 2004. Inter- and intra-specific variation in the ontogeny of the hominoid facial skeleton: Testing assumptions of ontogenetic variability. *Ann Anat* 186: 423–428.
- Strand Viðarsdóttir U, O'Higgins P. 2003. Variation in the facial skeleton of *Homo sapiens*. In: Thompson JL, Krovitz GE, Nelson AJ, editors. *Patterns of Growth and Development in the Genus Homo*. Cambridge: Cambridge University Press. pp 114–143.
- Strand Viðarsdóttir U, O'Higgins P, Stringer CB. 2002. A geometric morphometric study of regional differences in the growth of the modern human facial skeleton. *J Anat* 201:211–229.
- Taylor AB. 2002. Masticatory form and function in the African apes. *Am J Phys Anthropol* 117:133–156.
- Taylor AB, Groves CP. 2003. Patterns of mandibular variation in *Pan* and *Gorilla* and implications for African ape taxonomy. *J Hum Evol* 44:529–561.
- Terhune CE, Kimbel WH, Lockwood CA. 2013. Postnatal temporal bone ontogeny in *Pan*, *Gorilla*, and *Homo*, and the implication for temporal bone ontogeny in *Australopithecus afarensis*. *Am J Phys Anthropol* 151:630–642.
- Turner A, Wood B. 1993. Comparative palaeontological context for the evolution of the early hominid masticatory system. *J Hum Evol* 24:301–318.
- Ubelaker DH. 1989. *Human Skeletal Remains: Excavation, Analysis, Interpretation*, 2nd ed. Washington, DC: Taraxacum.
- Washburn SL. 1947. The relation of the temporal muscle to the form of the skull. *Anat Rec* 99:239–248.
- White T. 2000. *Human Osteology*. San Diego: Academic Press.
- Williams FL, Godfrey LR, Sutherland MR. 2002. Heterochrony and the evolution of neandertal and modern human craniofacial form. In: Minugh-Purvis N, McNamara K, editors. *Human Evolution through Developmental Change*. Baltimore: Johns Hopkins University Press. pp 405–441.
- Williams FL, Godfrey LR, Sutherland MR. 2003. Diagnosing heterochronic perturbations in the craniofacial evolution of *Homo* (Neandertals and modern humans) and *Pan* (*P. troglodytes* and *P. paniscus*). In: Thompson J, Krovitz G, Nelson A, editors. *Patterns of Growth and Development in the Genus Homo* (Cambridge Studies in Biological and Evolutionary Anthropology). Cambridge, UK: Cambridge University Press. pp 295–319.
- Wood B, Harrison T. 2011. The evolutionary context of the first hominins. *Nature* 470:347–352.
- Wood BA, Lieberman DE. 2001. Craniodental variation in *Paranthropus boisei*: A developmental and functional perspective. *Am J Phys Anthropol* 116:13–25.