

Ontogenetic Study of Allometric Variation in *Homo* and *Pan* Mandibles

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ABSTRACT

Investigating ontogenetic variation and allometry in the mandible can provide valuable insight and aid in addressing questions related to the ontogeny of the skull. Here, patterns of ontogenetic shape change and allometric trajectories were examined in the mandible of 187 sub-adult and adult humans, bonobos, and chimpanzees. Procrustes-based geometric morphometrics was employed to quantify and analyze mandibular form. Thirty three-dimensional landmarks were used to capture the overall morphology of the mandible, and the landmarks were analyzed as a whole and subdivided into separate anterior and posterior units. Principal component analyses in Procrustes shape–space and form–space, and multivariate regressions were used to examine patterns of ontogenetic and allometric shape change. Results suggest that humans are distinct from *Pan* both in their mandibular morphology, particularly in the anterior-alveolar region, and direction of allometric trajectory. Chimpanzees and bonobos have parallel ontogenetic trajectories, but also show differences in mandibular shape. Species-specific features and adult mandibular shape are established before or by the eruption of the deciduous dentition. This suggests that developmental processes prior to deciduous teeth eruption have a stronger effect establishing taxa-specific phenotypes than later postnatal effects. This additionally implies that divergent trajectories between *Pan* and *Homo* do not contribute much to the adult mandibular shape after deciduous teeth eruption. Separate analyses of the anterior-alveolar region and ascending ramus show that these regions are semi-independent in their developmental pattern of shape change and allometry. This implies that allometric variation and ontogenetic shape change in the hominoid mandible is decoupled. *Anat Rec*, 297:261–272, 2014. © 2013 Wiley Periodicals, Inc.

Key words: ontogeny; allometry; Procrustes; hominoid; mandible

INTRODUCTION

Investigating the ontogeny and phylogeny of extant apes provides a framework for addressing questions on the development and evolution of closely related hominoid fossil taxa. The majority of research questions that focus on primate morphological evolution rely on the skull to identify taxonomy, reconstruct phylogenies, and map ontogenetic change. Studying the developmental and evolutionary aspects of morphological variation can be particularly challenging with closely related species,

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both extinct and extant. While there have been numerous studies on hominoid growth and development (Schultz, 1924; Giles, 1956; Shea, 1983a; Richtsmeier et al., 1993; Richtsmeier and Walker, 1993; Godfrey and Sutherland, 1994; O'Higgins and Jones, 1998; Bruner and Manzi, 2001; Ponce de Leon and Zollikofer, 2001; Ackermann and Krovitz, 2002; Strand-Viðarsdóttir, 2002; Strand-Viðarsdóttir et al., 2002; Williams et al., 2003; Bastir and Rosas, 2004; Berge and Penin, 2004; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004a, b; Zollikofer and Ponce de Leon, 2004; Mitteroecker et al., 2005; Bulygina et al., 2006; Leigh, 2006; McNulty et al., 2006; O'Higgins et al., 2006; Bastir et al., 2007; Lieberman et al., 2007; Freidline et al., 2012), not many have focused exclusively on mandibular morphology (Johnson et al., 1976; Daegling, 1996; Chen et al., 2000; Taylor and Grooves, 2003; Williams and Krovitz, 2004; Boughner and Dean, 2008; Coquerelle et al., 2010a, b, 2013). The present study examines ontogenetic variation in the mandible of humans, chimpanzees, and bonobos. One of the aims is to compare mandibular development and allometric shape changes to aspects of cranial ontogeny. A second aim is to examine ontogenetic variation in different parts of the mandible, namely the anterior and posterior regions, as defined by Leamy (1993) and Klingenberg et al. (2003). Extensive research done on the mouse mandible suggests that the mammalian mandible is subdivided into different semi-independent units (Moss, 1960, 1968; Atchley and Hall, 1991). It is possible that these semi-independent regions of the mandible have local patterns of growth and development. Separate morphological units within the mandible comprise the ramus, corpus or anterior-alveolar region, gonial angle, condylar, and coronoid processes. Instead of examining all these units separately, two main subdivisions of the mandible were considered: the ramus and anterior-alveolar region. Even though the condylar and coronoid processes and angular region are considered separate morphogenetic units, here the subdivision of the mandible was limited to the anterior-alveolar region that is primarily influenced by dental development and the ramus that is dominated and more influenced by muscle attachments (Leamy, 1993; Klingenberg et al., 2003). Studying the ontogeny of morphological structures provides insight into possible evolutionarily conserved and divergent developmental pathways that give rise to taxon-specific traits. Moreover, examining regions of the mandible separately can provide information on whether or not adult shape differences are achieved through divergent patterns of ontogenetic change in different regions of the mandible, both in an intra- and interspecific context.

Examining ontogenetic variation among taxa includes identifying morphological differences to understand the magnitude and direction of overall morphological change in a phylogenetic context. One approach to study ontogenetic variation among closely related taxa is allometry, which is the association between variation in morphological features (such as shape) and overall size of an organism. Comparing ontogenetic trajectories provides a framework for examining allometric variation through a multidimensional space as dictated by size, shape, and age of the individuals in a species. The aspect of ontogenetic trajectories that allometry encompasses is time, defined as the rate at which morphological traits of an

organism develop (Klingenberg, 1998). This is explicitly different from the concept of heterochrony, which is the change in the rates and timing of development (Gould, 1977; McKinney & McNamara, 1991). While heterochrony is fundamental to understanding the evolution of ontogenies, in this study the main focus is on allometric variation and comparing mandibular ontogenetic trajectories among closely related taxa.

Despite there being a number of studies on craniofacial variation and ontogeny in extant and extinct hominoids—both intra- and interspecific—mandibular morphology and ontogeny has received comparatively less attention. There is an ongoing debate on whether ontogenetic trajectories in the cranium are parallel or divergent—parallel trajectories being similar and divergent being different (Bruner and Manzi, 2001; Ackermann and Krovitz, 2002; Williams et al., 2002; Berge and Penin, 2004; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004a, 2005; McNulty et al., 2006; Bastir et al., 2007; Lieberman et al., 2007; Gunz et al., 2010). Understanding whether the trajectories are parallel or divergent between species sheds light on whether species-specific features are achieved through similar or different developmental pathways. Because previous studies have shown hominoids to have *both* parallel and divergent ontogenetic trajectories in the cranium, their conclusions arouse the need to further examine ontogeny of the skull, particularly the mandible. Such studies further provide an important framework for understanding, evaluating, and interpreting the evolutionary, developmental, and functional significance of morphological traits and how they change over time among species. This can further be potentially useful for reconstructing species growth trajectories from isolated mandibles in the fossil record.

Thus, the questions addressed in this study include: (1) is the shape of the mandible achieved via parallel or divergent ontogenetic trajectories in these species; (2) how do patterns of ontogenetic mandibular shape changes compare to those of the cranium in the different species; (3) do chimpanzees, bonobos, and humans have different localized allometric patterns of ontogenetic change in the mandible; (4) are localized ontogenetic changes different in the mandible of each species?

MATERIAL AND METHODS

Sample

This study includes 187 mandibles (Table 1) of modern humans, chimpanzees, and bonobos. The ape taxa are wild-shot individuals. The human sample comprises two populations from Portugal (Lisbon) and Alaska (Point Hope). Each specimen is classified according to respective dental development stages (Table 1). The youngest group, stage 1, consists of individuals with fully erupted deciduous teeth. In four humans, one chimpanzee and one bonobo specimen, the deciduous M_2 s were not fully erupted, but the crowns were completely exposed. These specimens were still included in stage 1 because no shape differences were noted between them and the specimens that had fully erupted M_2 s. The second category, stage 2, comprises individuals with fully erupted M_1 s. Stage 3 includes specimens with fully erupted M_2 s and stage 4 consists of specimens with fully erupted M_3 s

TABLE 1. Specimens and description of dental development stages used in this study

Species	No. of individuals	Source		
<i>Pan troglodytes</i> <i>schweinfurthii</i>	33	Royal Museum of Central Africa, Tervuren		
<i>Pan t. troglodytes</i>	21	Natural History Museum, Berlin		
<i>Pan paniscus</i>	56	Royal Museum of Central Africa, Tervuren		
<i>Homo sapiens</i>	77	Natural History Museum, Lisbon		
Total	187	American Museum of Natural History, New York		
Age groups	Dental developmental stages	Humans	Chimpanzees	Bonobos
Stage 1	All deciduous teeth erupted and no permanent teeth	14	4	6
Stage 2	Permanent M ¹ erupted	4	9	10
Stage 3	Permanent M ² erupted, but basio-spheno synchondrosis still not fused	10	6	6
Stage 4	Permanent M ³ erupted and basio-spheno synchondrosis fully fused	49	35	34
Total		77	54	56

and both partially fused (two specimens) and fully fused basio-spheno synchondrosis.

Thirty three-dimensional coordinates were taken on the entire mandible (Fig. 1) using a MicroScribe G2X, following and extending on collection protocol described elsewhere (Nicholson and Harvati, 2006; Harvati et al., 2011). The mandibular landmarks were analyzed both as a whole and as separate units. The landmarks were subdivided into these two units to examine possible local patterns of ontogenetic shape differences and trajectories. All specimens were measured by one observer (NS). Intra-observer error was estimated by calculating Procrustes distances between the original and repeat measurements. All the specimens included in the study were measured twice to establish reliability of measurements. The largest Procrustes distance between the repeated specimens and their corresponding originals was four to five times smaller than the smallest distance between individuals in the total sample. Individuals with damaged and/or missing landmarks were excluded.

Analytical Methods

Procrustes based geometric morphometrics was used in this study (Bookstein, 1996; Dryden and Mardia, 1998; Rohlf, 1999; Slice, 2007). Generalized Procrustes analysis (GPA) is an effective method, which extracts shape information from two to three-dimensional landmark data by rotating, scaling, and translating specimen landmark configurations and yields a size measure called centroid size (CS). CS is the root sum of squared distances of all landmarks from their mean and is also a measure of how much the landmarks disperse from their centroid; the farther the dispersion of landmarks, the bigger the CS. A principal components analysis (PCA) in shape-space was then conducted on the Procrustes shape coordinates; this was done to explore the overall shape variation in the dataset. Regressions based on PC scores on CS were plotted into the PCA graphs to exam-

ine and compare shape ontogenetic trajectories of the different taxa. A second analysis of PCA in Procrustes form-space was conducted and plots were examined in a similar manner as in shape-space. PCA in form-space uses Procrustes registration, but reintroduces CS into the analysis, including CS as a variable in the PCA. This method has been used in other studies, comparing ontogenetic trajectories in both the cranium and mandible (Bastir et al., 2007; Mitteroecker et al., 2004a). While PCA in shape-space examines ontogenetic shape changes without the effects of isometric size, (i.e., CS), PCA in form-space addresses all aspects of size related shape changes (Mitteroecker et al., 2004a). Including both analyses provides a more comprehensive examination of the ontogenetic shape- and size-related changes in a biological form. The PCA and regression analyses were done in programming software R (R development core team, 2008). The visualizations were done by morphing a hypothetical specimen shape along the PC scores of the chosen PC axes, illustrating the variation along the PCs. Wireframe configurations of landmarks and surface rendered models—triangles used to “fill” the surface between the landmarks in the wireframe configurations—were used to represent shape variation along the PCs.

In addition, Procrustes distances were computed between all age groups in each taxa, respectively, and statistically tested by 10,000 rounds of permutations tests; significance was established at $\alpha \leq 0.05$ (Good, 2000). This was done to test whether the age groups were statistically different from each other. Similarly, to assess for effects of sexual dimorphism in the data, mean shapes were computed for the males and females of the known-sex individuals for each age group in all three taxa. Then the Procrustes distances were calculated between the mean female and the mean male shapes, and the differences were statistically tested by 10,000 rounds of permutation tests.

In order to examine differences among ontogenetic trajectories, angles between species-specific multivariate

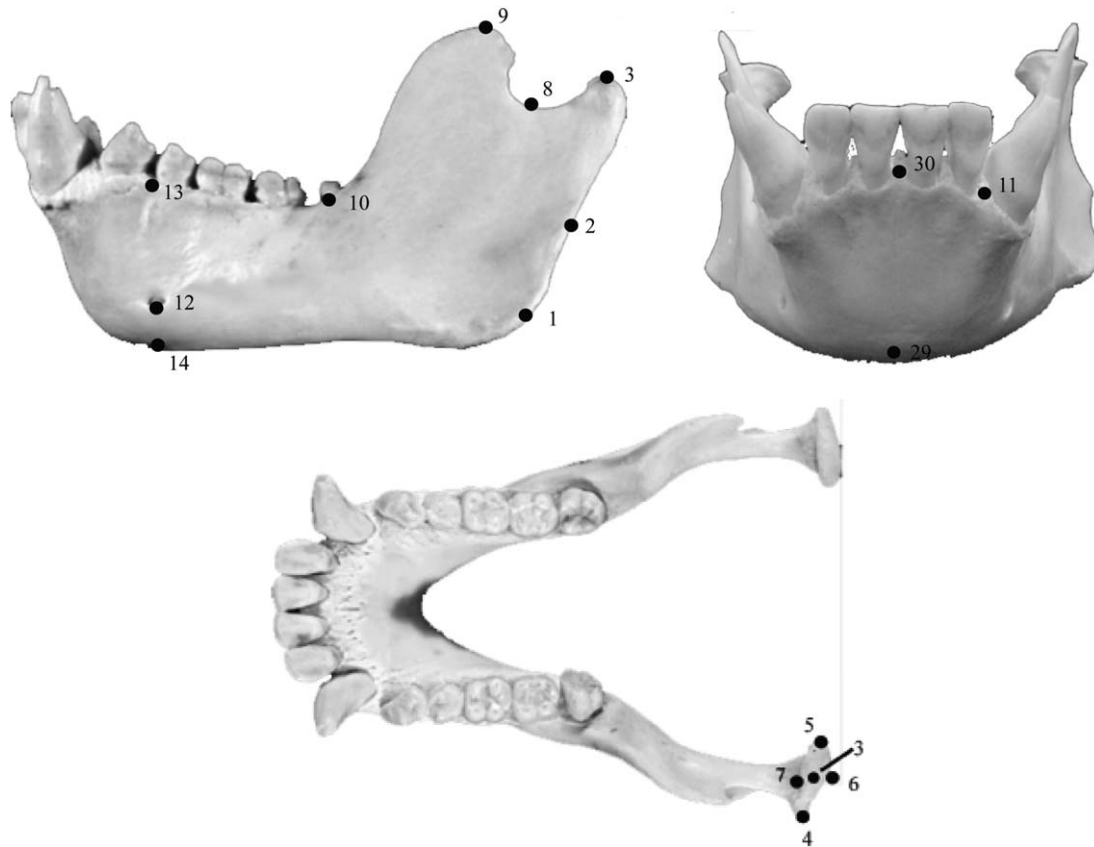


Fig. 1. Mandibular landmarks included in this study; 1. Right gonion, 2. Right posterior ramus, 3. Right condyle, 4. Right condyle lateral, 5. Right condyle medial, 6. Right Condyle Posterior, 7. Right root sigmoid root, 8. Right deepest point on sigmoid notch, 9. Coronoid process, 10. Right inferior anterior ramus; 11. Right 1_2 -canine alveolar septum, 12. Right mental foramen, 13. Right alveolar border of corpus, 14. Right inferior border of corpus; 15–28. are landmarks taken on the left side, 29. Gnathion; and 30. Infradentale.

regression vectors, computed from within-species PC scores (shape) on log-transformed CS were compared (Zelditch et al., 2004)—the null hypothesis being that the angle is zero, indicating parallel trajectories among taxa. The approach used here is outlined in Zelditch et al. (2000) and it basically compares the angle between ontogenetic trajectories of two species to the angles between trajectories obtained from a single taxon. The range of angles computed between trajectories within a taxon is calculated using bootstraps ($n = 2,500$) and this range is then compared with the angles between-species. If the angles between-species exceed the 95% confidence range of the bootstrapped angles computed intraspecifically, then the trajectories are significantly different between taxa. The angles were computed in Integrated Morphometrics Package (Zelditch et al., 2004) and subsequent statistical tests were done in R (R development core team, 2008).

RESULTS

Sexual Dimorphism

Results of the Procrustes distances computed from the mean male and female *shapes* show no significant differences among bonobos, chimpanzees, and humans in

mandibular shape. This is supported by results from previous studies that found male–female differences mainly in the larger apes: gorillas and orangutans (Chamberlain and Wood, 1985; Taylor, 2002; Taylor and Groves, 2003; Schmittbuhl et al., 2007). Therefore, the sexes were pooled in the following analyses.

Mandibular Ontogenetic Trajectories in PCA Shape–Space

The first two principal components account for 72.32% of the total variance in the sample (Fig. 2A). *Homo* and *Pan* are clearly separated along PC 1 (63.7%). One chimpanzee specimen from stage 1 extends the range of variation of that age group into that of stage 1 bonobos. The M_2 crown of this individual has not fully erupted, unlike the other specimens in this group, and is the youngest individual in the chimpanzee sample; this is the same for an individual in the bonobos' age stage 1. The direction of the ontogenetic trajectories between humans and *Pan* is different, but there is overlap between chimpanzees and bonobos, although the chimpanzee trajectory is extended compared with bonobos.

Shape changes along PC 1 (Fig. 2A) capture the main interspecific differences between *Pan* and *Homo*

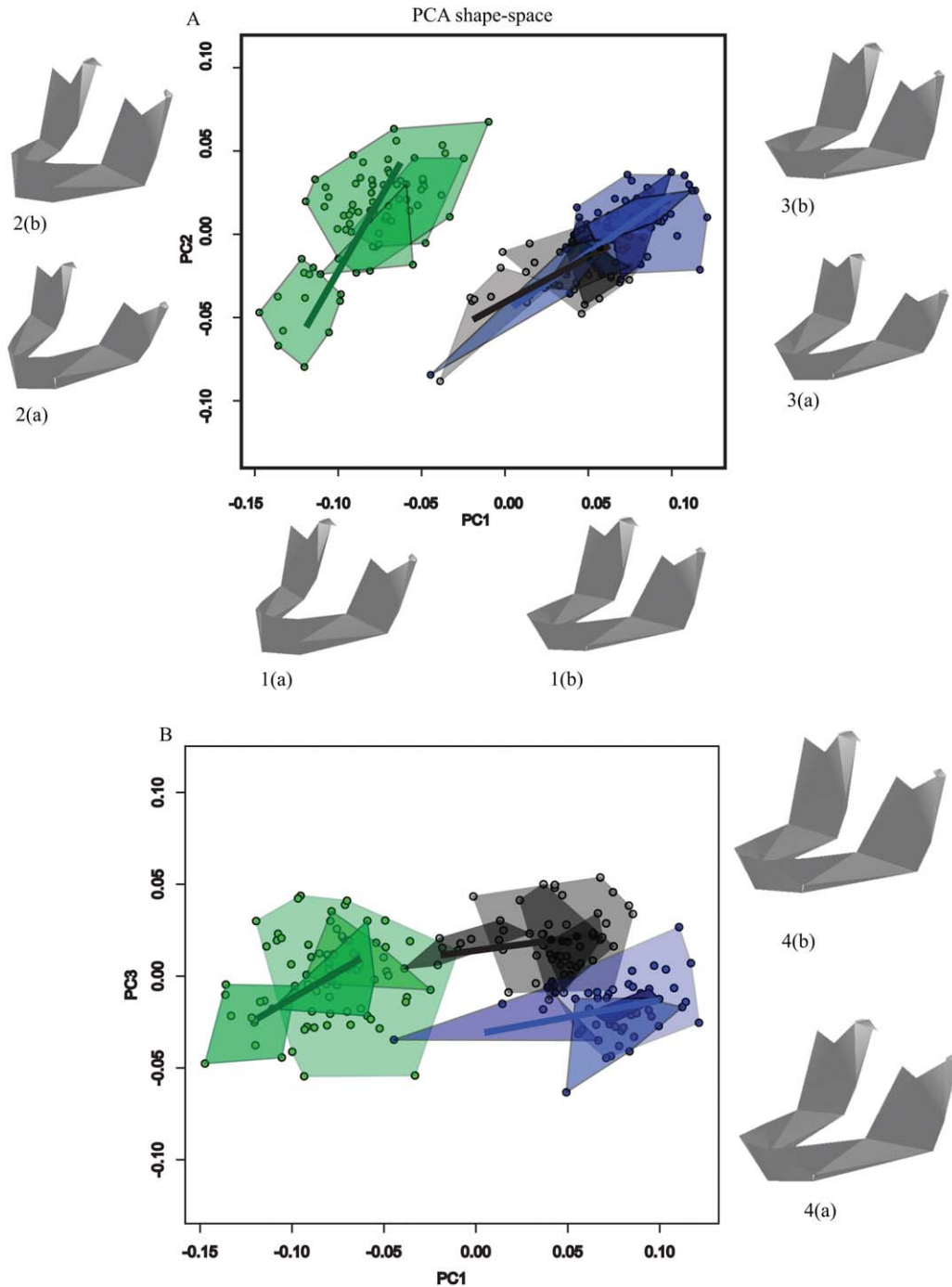


Fig. 2. Ontogenetic changes in the mandible in PCA shape-space. (A) PC1 versus PC2: Humans in green, bonobos in black & chimpanzees in blue. Regression vectors are plotted into the graphs. The surface rendered warps 1a and b represent the shape variation between humans and chimpanzees along PC1 from the negative (1a) to the positive (1b) scores. 2a and b represent ontogenetic shape variation in humans, particularly between age stage 1 (2a) and the other age groups (2b) along PC2. The 3a and b represent ontogenetic shape

variation in *Pan* between stage 1 (3a) and the other age groups (3b). The surface rendered warps (2a, b and 3a, b) illustrate shape variation represented by a combination of PC 1 and PC 2 scores for each taxon, and were constructed by clicking on hypothetical individuals within the scatter of the respective species and their age stages. (B) PC1 versus PC3: The surface rendered warps 4a and b represent shape changes between chimpanzees (4a, negative scores) and bonobos (4b positive scores) along PC3.

mandibles. Modern humans occupy the lower scores on PC 1, which show a parabolic shaped mandible, receding symphyseal region, but marking the presence of a chin

and a deep and symmetric sigmoid notch—features characteristic of modern human mandibles. *Pan* occupies the higher scores along PC 1, and there is considerable

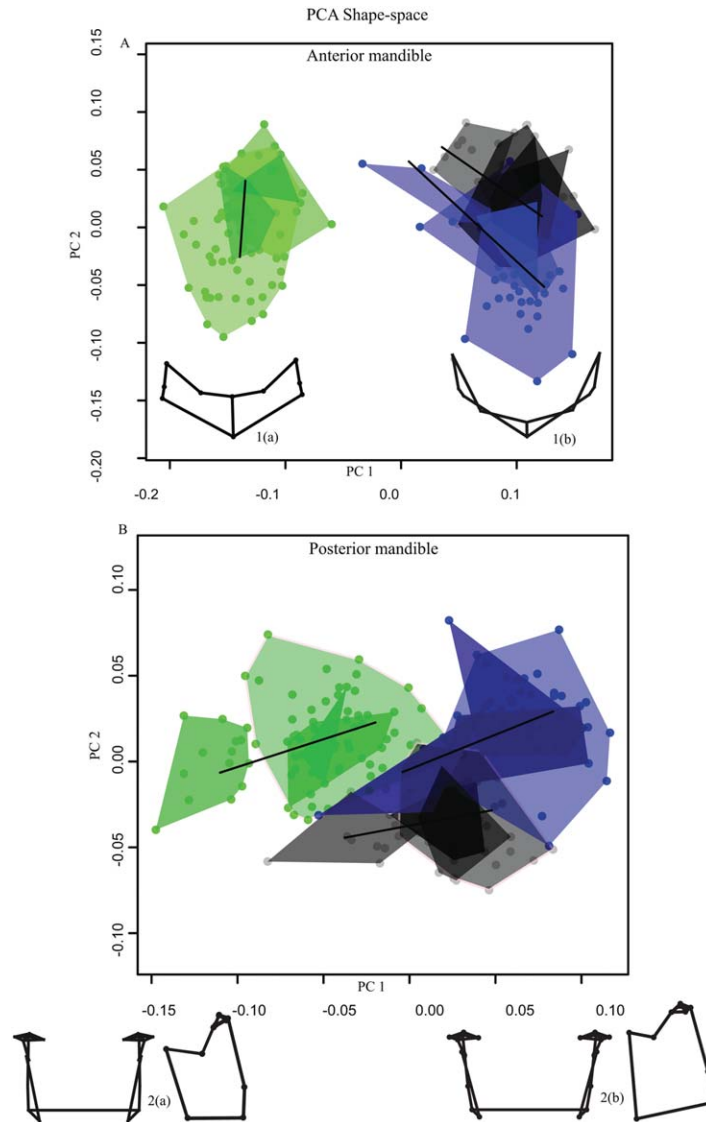


Fig. 3. Ontogenetic changes in the anterior-alveolar region and ramus in PCA shape-space: (A) PC1 versus PC2 of the anterior alveolar region: Humans are represented in *green*, bonobos in *black*, and chimpanzees in *blue*. Regression vectors are plotted in the graphs. Wireframes 1a and b represent shape changes (anterior view of the

anterior-alveolar region) between humans and *Pan* on PC1. (B) PC1 versus PC2 of the ramus: Wireframes 2a and b represent shape changes (anterior and lateral views, respectively) between humans and *Pan* along PC1.

overlap between bonobos and chimpanzees along this axis. The overall *Pan* mandible is more elongated compared with *Homo*. The superior symphyseal region is outwardly projected and posteriorly inclined. The sigmoid notch is shallow and asymmetric relative to humans.

PC 2 (8.62%) accounts for within-group ontogenetic variation in the respective species, particularly separating stage 1 in humans and bonobos from the older age groups (Fig. 2A). Figure 2A shows ontogenetic changes between humans and *Pan*. Stage 1 humans are clearly separated from the other age groups and show a more parabolically shaped mandible and short ramus relative to the corpus, compared with the individuals in the older age stages. In humans, the inferior symphyseal region is projected, possibly marking the presence of a chin even

in stage 1 specimens. In *Pan*, the ontogenetic shape changes in both bonobos and chimpanzees are similar to the humans, with stage 1 being distinct from the other age groups, but the corpus length relative to the ramus is longer in juvenile *Pan* than in *Homo*. PC 3 (Fig. 2B), which accounts for 6.4% of the total variance in the sample, separates bonobos and chimpanzees. PC 1 versus PC 3 also indicates that bonobos and chimpanzees from stage 1 cluster close to human adults. Shape differences between chimpanzees and bonobos along PC 3 are in aspects of the sigmoid notch, which is more asymmetric in chimpanzees (Fig. 2B, 4a) than bonobos (Fig. 2B, 4b), and the inferior aspect of the symphysis (where the gnathion point is placed) is more posteriorly placed in chimpanzees than in bonobos.

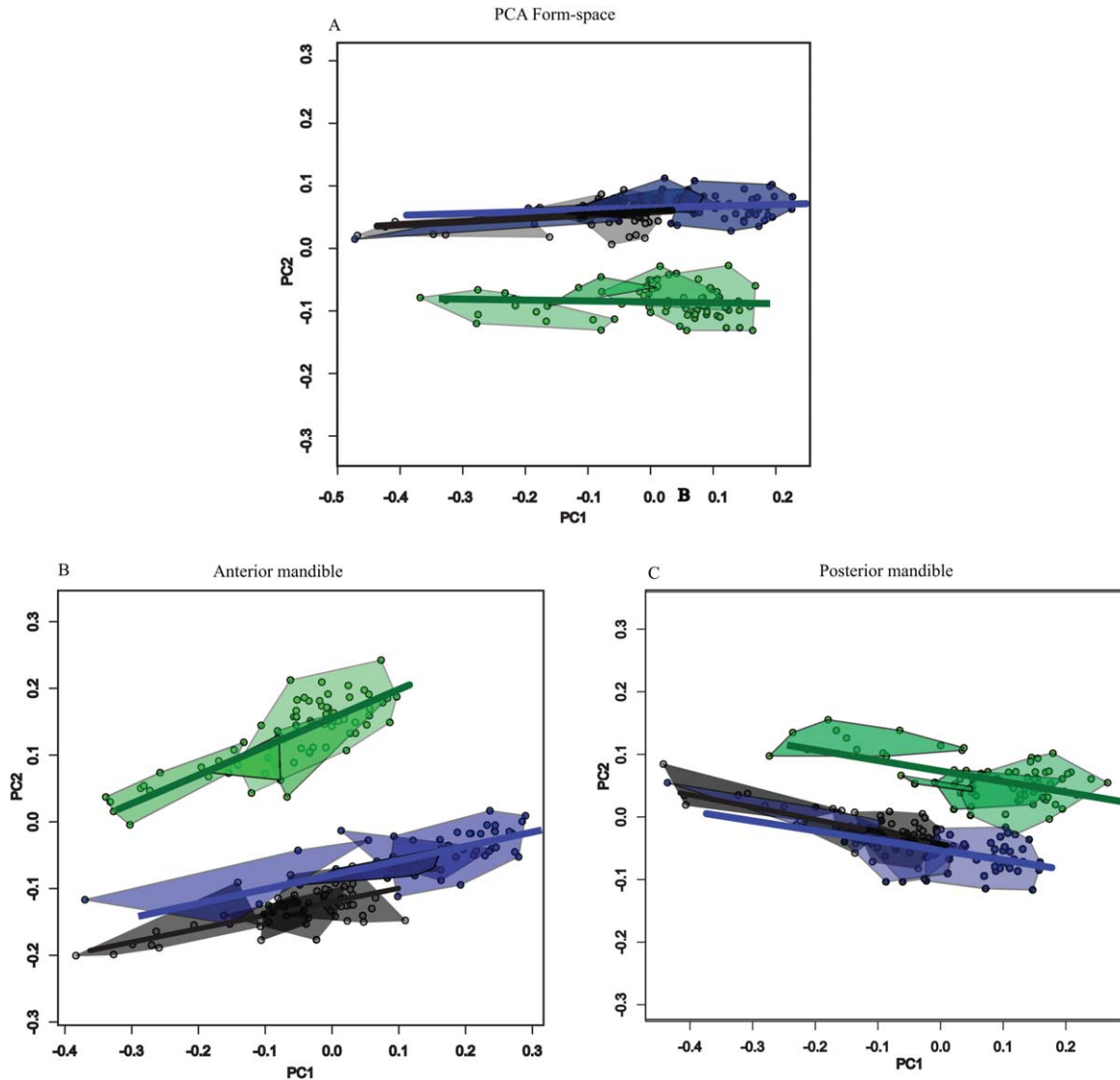


Fig. 4. Ontogenetic shape changes in PCA form-space. Humans are represented in *green*, bonobos in *black*, and chimpanzees in *blue*. Regression vectors are plotted into the graphs. (A) Complete mandibular form; (B) anterior-alveolar region of the mandible; (C) posterior mandible.

PCA in shape-space: anterior-alveolar and posterior mandibular region.

In the anterior-alveolar region, the first two PCs account for 74.6% and 10.2%, respectively, of the total variance in the sample. PC 1 (Fig. 3A) accounts for interspecific differences between *Homo* and *Pan* and PC 2 captures subtle differences between bonobos and common chimpanzees. There is considerable overlap among all the age groups in each of the species along these two dimensions. No differentiation among the age groups in shape-space indicates that shape of the anterior mandible is achieved before stage 1 for humans, chimpanzees, and bonobos. The direction of the human growth trajectory is clearly different from chimpanzees and bonobos, which have more parallel trajectories. The main shape distinction between *Homo* and *Pan* is in the outline of the dental arcade and symphysis (Fig.

3A). The shape of the dental arcade is more parabolic and the inferior aspect of the anterior mandible is projected forward and downward in humans relative to *Pan*.

Unlike the anterior mandible, the posterior mandible (Fig. 3B) separates the age groups in all three taxa much better along PC 1 (48.5%). PC 2 (14.6%) captures the differences among chimpanzees and bonobos and also shows some overlap between the younger age groups of chimpanzees and adult bonobos. The direction of ontogenetic shape change between the taxa seems to be more similar in the ramus than in the anterior-alveolar region. The main shape differences are in the width of the mandible, the inclination of the ascending ramus, and aspects of the gonion region (Fig. 3B). The sigmoid notch is deep and symmetrical in humans compared with *Pan*.

Mandibular Ontogenetic Trajectories in PCA Form-Space

PC 1 accounts for 68% of the total variance in the sample, and primarily accounts for size differences among the age groups; PC 2 accounts for 20% of the total variance in the sample and separates *Pan* and *Homo* (Fig. 4A). Ontogenetic variation along PC 1 is similar in all three taxa, with the youngest age stage separating out. However, there is considerable overlap between the younger age stages of the chimpanzees and adult bonobos. The direction of ontogenetic shape change is similar among the taxa, and size-related shape changes among the age groups (in all three species) are more apparent in form-space than in space-space.

PCA in Procrustes form-space: anterior and posterior mandibular region. Unlike the results of the anterior-alveolar region in shape-space, form-space shows a better separation of the age groups. Stage 1 separates out from the other groups, which show some overlap along PC 1 (50.7%) (Fig. 4B). PC 2 (35.9%) mainly accounts for inter-specific differences between humans, chimpanzees, and bonobos. The ontogenetic trajectories are divergent between humans and *Pan*, but not chimpanzees and bonobos, and the chimpanzee trajectory is extended compared with bonobos. It is important to note here that even though shape changes along PC 2 separate chimpanzees and bonobos, the direction of their respective ontogenetic trajectories is similar. The posterior mandible (Fig. 4C) also shows a better separation of the age groups along PC 1 (72%) than in shape-space (Fig. 3B). As in shape-space, stage 1 humans are separate from the other age groups. PC 2 (13.4%) captures the differences between humans and *Pan* (Fig. 4C). The direction of interspecific shape change in bonobos and chimpanzees, as indicated by the ontogenetic trajectories, is more similar in the ramus than the anterior-alveolar region. Humans are more similar to *Pan* in their pattern of ontogenetic size-shape change in the ramus than in the corpus.

In addition to the PCA analyses, Procrustes distances were calculated among the age stages in each species; this was done for the entire mandible as well as the anterior alveolar region and ramus, respectively. Results computed from the mean of each age stage in each species only showed a significant difference between age stage 1 and the other age groups. The significance between the means was statistically tested by 10,000 rounds of permutation tests and significance was established at $\alpha \leq 0.05$: the average *P*-value between age stage 1 and other age stages in humans and bonobos was $\alpha < 0.0001$ and chimpanzees $\alpha < 0.0003$.

Results from the analysis of angles within and between species' ontogenetic trajectories indicate that angles between humans and bonobos or chimpanzees (Table 2) are higher than the range of angles within-species. Chimpanzees and bonobos are similar in their direction of shape change, showing either overlapping or parallel trajectories in both space-space and form-space (Figs. 2–4). Statistically significant differences between bonobo and chimpanzee trajectories cannot be established given the available dataset, however, this does not imply that the angle (Table 2) between the two popu-

TABLE 2. Angles computed between species' ontogenetic trajectories

	<i>Homo sapiens</i>	<i>Pan paniscus</i>
<i>Pan paniscus</i>	40.1°	
<i>Pan troglodytes</i>	40.9°	21.4°
Anterior-alveolar region		
	<i>Homo sapiens</i>	<i>Pan paniscus</i>
<i>Pan paniscus</i>	60.2°	
<i>Pan troglodytes</i>	57°	20.7°
Ramus		
	<i>Homo sapiens</i>	<i>Pan paniscus</i>
<i>Pan paniscus</i>	40.7°	
<i>Pan troglodytes</i>	43.7°	27.6°

lations is the same, but rather that a null hypothesis of parallel or similar trajectories cannot be rejected.

DISCUSSION

In the present study the primary aim was to explore different patterns of ontogenetic shape changes in the mandible of chimpanzees, bonobos and humans. The results suggest the following: (1) as in the cranium, humans are distinct in their mandibular morphology from chimpanzees and bonobos both in aspects of shape and ontogenetic trajectory; (2) ontogenetic trajectories in the mandible are divergent between *Homo* and *Pan*, but not chimpanzees and bonobos. However, humans are most distinct from *Pan* in their direction of ontogenetic shape change in the anterior-alveolar region; (3) overall adult shape of the mandible is achieved by M₁ eruption; (4) the anterior and posterior aspects of the mandible follow different patterns of ontogenetic shape change prior to M₁ eruption.

Humans are already morphologically distinct at stage 1 from the other taxa, and this distinction in mandibular shape is possibly established at an earlier ontogenetic stage than the ones included in this study, perhaps even prenatally (Coquerelle et al., 2010a, 2013). A characteristic difference between chimpanzees and humans noted during fetal development and pre-deciduous teeth eruption is in the inclination of the symphysis region, which shifts from an anterior to a vertical inclination in chimpanzees, but always remains vertical in humans (Coquerelle et al., 2010a). Humans and chimpanzees also share a combination of early developmental changes, although, occurring at different times in the respective species during early ontogeny. These changes occur in the basal symphysis region, anterior buccal groves, and in the reorientation of the incisors prior to eruption (Coquerelle et al., 2010a). Developmental shifts in morphology reported by Coquerelle et al. (2010a) help to better understand how chimpanzees and humans diverge during early ontogeny. In corroboration, results from this study suggest that humans are most distinct in their direction of shape and size change in the anterior-alveolar region. This change can largely be attributed to the symphysis region, the species-specific shape and inclination of which is established during fetal developmental and early infancy.

The results additionally show that postnatal ontogenetic trajectories between *Pan* and *Homo* are divergent.

The relative contribution of pre- versus postnatal trajectories to overall phenotypic divergence and whether growth trajectories are parallel or divergent among taxa, is still under debate. However, the majority of these studies were on the cranium and not the whole skull (Shea, 1983a, b; Richtsmeier et al., 1993; Richtsmeier and Walker, 1993; Lieberman and McCarthy, 1999; Bruner and Manzi, 2001; Ponce de Leon and Zollikofer, 2001; Ackermann and Krovitz, 2002; Penin et al., 2002; Strand-Viðarsdóttir, 2002; Strand-Viðarsdóttir et al., 2002; Bastir and Rosas, 2004; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004a; Zollikofer and Ponce de Leon, 2004; Mitteroecker et al., 2005; Lieberman et al., 2007; Gunz et al., 2010). Earlier studies on cranial development by Schultz (1924) found that the majority of specialized features in humans, other apes, and monkeys manifested and diverged post-infancy in the developmental process. This finding was corroborated by a number of studies on different primate taxa, both extant and extinct (Richtsmeier et al. 1993; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004a; McNulty et al. 2006). Richtsmeier et al. (1993) found that facial morphology of macaques, vervet, and capuchin monkeys were predominantly influenced by postnatal ontogeny, and not simply extensions of features established prenatally. They concluded that while species-specific characteristics may emerge prenatally, they continue to develop and possibly diverge between taxa later in ontogeny. Cobb and O'Higgins (2004) reached a similar conclusion with hominins, showing that species-specific features established prenatally were further accentuated, but via diverging postnatal growth trajectories in the face. Mitteroecker et al. (2004a, 2005), found humans to have the most distinct and divergent postnatal morphology and ontogenetic trajectory relative to the other apes. A slightly different conclusion was reached by McNulty et al. (2006), where they showed that despite the divergent pattern of cranial development among African apes and modern humans, diverging trajectories did not greatly impact the adult morphology. Given that the present sample does not comprise neonates or older infants, the relative contribution of pre- versus postnatal trajectories on mandibular development cannot be examined. However, the mandibular data and age ranges included in this study support some of the conclusions of the above-mentioned studies on cranial development. McNulty et al.'s (2006) findings, showing that species-specific craniofacial morphology established by the occlusion of M_1 is indicative of the adult form, is also true for the mandible in chimpanzees, bonobos, and humans. This suggests that developmental processes at birth or even prenatally possibly have a stronger effect establishing taxa-specific phenotypes than postnatal effects, particularly after the eruption of M_1 . This additionally implies that divergent trajectories between *Pan* and *Homo* do not contribute much to the adult mandibular shape past stage 1. However, not all studies on cranial ontogeny show extant hominoids to have divergent developmental pathways in the cranium (Bruner and Manzi, 2001; Ponce de Leon and Zollikofer, 2001; Ackermann and Krovitz, 2002; Williams et al., 2002; Zollikofer and Ponce de Leon, 2004). The latter is true for mandibular development in chimpanzees and bonobos. The general direction of shape changes and trajectories is similar among chimpanzees and bonobos. There is also some overlap between adult bonobos and subadult chimpanzees, indicating that the bonobo devel-

opmental pathway is truncated compared with chimpanzees (Shea, 1983a, b; Lieberman et al., 2007) in addition to being parallel (Boughner and Dean, 2008).

The stark difference between *Homo* and *Pan* obscures the shape differences between bonobos and chimpanzees. In a study on global and local shape changes in the cranium, Mitteroecker et al. (2005) noted that bonobos and chimpanzees had different growth vectors associated with different regions of the face. Despite the attention given to the cranium, only a select few studies have focused on chimpanzee and bonobo mandibular morphology (Daegling, 1996; Humphrey et al., 1999; Taylor, 2002; Taylor and Groves, 2003; Rak et al., 2007; Schmittbuhl et al., 2007; Boughner and Dean, 2008; Guy et al., 2008; Lague et al., 2008; Zihlman et al., 2008; Robinson and Williams, 2010; Robinson, 2012). Boughner and Dean (2008) found that despite having parallel ontogenetic trajectories, chimpanzees and bonobos were significantly different in their species' mean mandibular shapes. They also found less overlap among the older age groups in chimpanzees than in bonobos. These results are largely similar to Boughner and Dean's (2008), with the exception that there is overlap between older age stages in both species. One of the main shape differences found between chimpanzees and bonobos was in the symphyseal region, the symphysis being more posteriorly inclined in the former than in the latter (Robinson, 2012). The shape of the symphysis is considered useful for indicating taxonomic affinity among hominoids, and in some cases also between chimpanzee subspecies (Taylor and Groves, 2003; Lague et al., 2008).

Another important aspect of this study was to examine whether different regions of the mandible, namely the anterior-alveolar region and ramus, have different ontogenetic patterns of shape change in chimpanzees, bonobos, and modern humans. Differential growth and developmental patterns in the mandible have been widely studied using mouse models (Moss, 1960, 1968; Atchley & Hall, 1991; Atchley, 1993). By analyzing the anterior and posterior mandible separately, the local patterns of allometric shape change in the mandible were more apparent. In aspects of the anterior-alveolar region, the human growth trajectory is clearly distinct from chimpanzees and bonobos, which have more parallel trajectories. Shape-space (Fig. 3A) shows considerable overlap among all the age groups in each taxon, suggesting that shape of the anterior-alveolar region is already fixed before M_1 eruption. However, while the shape of the anterior region is established by stage 1, size of stage 1 individuals is distinct from the other age groups as shown in form-space (Fig. 4). That is, stage 1 individuals in *Pan* and *Homo* do not overlap in size with the other age groups in their respective species despite overlapping in shape. The overlap among the age groups in shape-space, but not in size suggests isometric growth in the alveolar region. In addition, it reflects that the developing dentition, post-deciduous teeth eruption, does not have much effect on the shape of the alveolar region. The finding that all species show an overlap among the older age groups also suggests that the relative size of the permanent dentition does not play a role in determining alveolar shape.

In contrast, shape changes in the ramus show differences among the age groups in each species, particularly separating stage 1 individuals from the rest (Fig. 3B). The

shape distinctions among the age groups in shape–space, suggest a slightly different developmental pattern in the ramus than in the anterior-alveolar region: the shape of the anterior mandibular region is established before or at the latest by the eruption of all the deciduous teeth, whereas the ramus changes until the eruption of M_1 . The direction of ontogenetic shape change seems to be similar in all three taxa, more so than in the alveolar region. Because the anterior-alveolar region houses the developing dentition, the morphology of this region is more influenced by dental development—at least before or until age stage 1—than the ramus, which maybe more affected by different types of functional demands such as the development and activity of muscles. For example, the insertion areas for the masseter and medial pterygoid muscles are no doubt affected by the level of activity of these muscles (Daegling, 1996). These aspects of the mandible warrant further investigation with age stages younger than ones included in this study, possibly including individuals with no deciduous teeth. However, both the anterior region and ramus exhibit similar shape development in stages post M_1 eruption, as indicated by the overlap among stages 2–4 in shape–space.

CONCLUSION

Five main conclusions can be drawn from this study. First, species-specific features in the mandible are established early in ontogeny, and possibly before the youngest age stage included in this study. Morphological distinctiveness between *Homo* and *Pan*, and also between bonobos and chimpanzees makes the mandible a good candidate for taxonomic evaluation. Second, the adult mandibular shape in *Pan* and *Homo* is established by M_1 eruption. Third, ontogenetic trajectories between *Homo* and *Pan* are divergent. Divergent ontogenetic trajectories between *Homo* and *Pan* imply that the evolutionary/developmental processes that influence mandibular morphology are different. However, parallel trajectories in chimpanzees and bonobos imply that patterns of shape change influenced by functional/biomechanical and/or developmental processes are conserved among taxa. Fourth, results from this study closely corroborate findings of studies on cranial ontogeny that suggest divergent ontogenetic trajectories between *Pan* and *Homo*. Taxon-specific features in the cranium and mandible are established at least by deciduous teeth eruption; however, the subsequent contribution of pre- versus postnatal trajectories is still under debate. Nonetheless, given that the older age stages overlap considerably and that species-specific shapes are already established by deciduous teeth eruption, prenatal ontogenetic processes, and trajectories may be more influential in establishing species' shape than postnatal trajectories. Fifth, the hominoid mandible consists of semi-independent growth regions and further analysis of integration and modularity are essential to fully understand mandibular ontogeny in primates. Even though in this study an integrative approach was not applied to address interspecific differences in mandibular morphology, this study demonstrates that different parts of the mandible, such as the corpus and ramus, are semi-independent. Further investigation of the patterns of integration not just between the corpus and ramus, but among other elements such as the coronoid and condylar

processes, will shed light on possible factors that contribute to species-specific morphological change.

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