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Mandibular ramus shape of *Australopithecus sediba* suggests a single variable species

Terrence B. Ritzman [a, b, c, d, *, 1], Claire E. Terhune [e, 1], Philipp Gunz [f], Chris A. Robinson [g]

[a] Department of Neuroscience, Washington University School of Medicine, 660 S. Euclid Ave., St. Louis, MO, USA
[b] Department of Archaeology, University of Cape Town, Private Bag, Rondebosch, Cape Town, 7701, South Africa
[c] Human Evolution Research Institute, University of Cape Town, Private Bag, Rondebosch, Cape Town, 7701, South Africa
[d] School of Human Evolution, Arizona State University, School of Human Evolution and Social Change Building, P.O. Box 872402, Tempe, AZ, 85287, USA
[e] Department of Anthropology, 330 Old Main, University of Arkansas, Fayetteville, 72701, USA
[f] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig, 04103, Germany
[g] Department of Biological Sciences, Bronx Community College, City University of New York, 2155 University Avenue, Bronx, NY, 10453, USA

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ABSTRACT

The fossils from Malapa cave, South Africa, attributed to *Australopithecus sediba*, include two partial skeletons—MH1, a subadult, and MH2, an adult. Previous research noted differences in the mandibular rami of these individuals. This study tests three hypotheses that could explain these differences. The first two state that the differences are due to ontogenetic variation and sexual dimorphism, respectively. The third hypothesis, which is relevant to arguments suggesting that MH1 belongs in the genus *Australopithecus* and MH2 in *Homo*, is that the differences are due to the two individuals representing more than one taxon. To test these hypotheses, we digitized two-dimensional sliding semilandmarks in samples of *Gorilla*, *Pan*, *Pongo*, and *Homo*, as well as MH1 and MH2. We document large amounts of shape variation within all extant species, which is related neither to ontogeny nor sexual dimorphism. Extant species nevertheless form clusters in shape space, albeit with some overlap. The shape differences in extant taxa between individuals in the relevant age categories are minimal, indicating that it is unlikely that ontogeny explains the differences between MH1 and MH2. Similarly, the pattern of differences between MH1 and MH2 is inconsistent with those found between males and females in the extant sample, suggesting that it is unlikely that sexual dimorphism explains these differences. While the difference between MH1 and MH2 is large relative to within-species comparisons, it does not generally fall outside of the confidence intervals for extant intraspecific variation. However, the MH1-MH2 distance also does not plot outside and below the between-species confidence intervals. Based on these results, as well as the contextual and depositional evidence, we conclude that MH1 and MH2 represent a single species and that the relatively large degree of variation in this species is due to neither ontogeny nor sexual dimorphism.

1. Introduction

The hominins recovered from the paleontological locality of Malapa, South Africa, have provided tantalizing insights into diversity in Plio-Pleistocene australopiths and potentially about the phylogenetic connection between *Australopithecus* and *Homo*. These remains, dated to 1.977 ± 0.002 million years ago (Pickering et al., 2011a), comprise two remarkably complete and well-preserved skeletons representing two individuals: MH1, a subadult purported male, and MH2, an adult purported female (Berger et al., 2010; Berger, 2012, 2013).

The most noteworthy aspect of the Malapa hominins is their intriguing mixture of primitive and derived features (Berger et al., 2010; Spoor, 2011; Berger, 2012, 2013). Specifically, these fossils possess an overall morphological pattern that is very australopith-like, with, for example, relatively small body and brain sizes, primitive features in the facial skeleton and dentition, and relatively long forelimbs bearing large articular surfaces and strongly curved fingers (Berger et al., 2010; Carlson et al., 2011; Kivell et al.,

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* Corresponding author.
E-mail address: terrence.ritzman@uct.ac.za (T.B. Ritzman).
[1] These authors contributed equally to this work.

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2011; Berger, 2012, 2013; Churchill et al., 2013; de Ruiter et al., 2013; Irish et al., 2013). These primitive features are combined with derived features that more closely resemble those of species in the genus *Homo*, such as alterations of the pelvis associated with more energetically efficient locomotion and characteristics of the hands, that may indicate the ability to manufacture and use stone tools (Kibii et al., 2011; Kivell et al., 2011). Based on this unique combination of primitive and derived features (and an adherence to a taxonomic practice that emphasizes grade-based classification), the initial description of the Malapa hominins assigned these remains to a new species, *Australopithecus sediba* (Berger et al., 2010; Berger, 2012, 2013). These authors highlighted its derived, *Homo*-like features in arguing that *A. sediba* is the most likely ancestor to the genus *Homo* (Berger et al., 2010; Berger, 2012, 2013), although this has been contested (Spoor, 2011; Wood and Harrison, 2011; Kimbel, 2013).

Other aspects of the description and analysis of the remains of *A. sediba*—specifically, the degree of variation within the *A. sediba* hypodigm and the distinctiveness of this sample relative to previously known hominin species—have also been questioned (Balter, 2010; Cherry, 2010; Spoor, 2011; Wood and Harrison, 2011; Kimbel, 2013), and the mandibular remains have received particular attention in this regard. Although they did not speculate on possible explanations, the original describers of the Malapa material noted the conspicuous differences in the mandibular rami of MH1 and MH2, the two partial skeletons from the site (Berger et al., 2010; de Ruiter et al., 2013; see also Terhune et al., 2014). Because MH1 is a subadult and a purported male, whereas MH2 is an adult and likely a female, it is possible that the differences between these two specimens are due to ontogenetic variation and/or sexual dimorphism (Terhune et al., 2014). The differences between the MH1 and MH2 rami have also led some authors to question whether the two Malapa individuals represent a single species, with some suggesting that the differences between them indicate that the *A. sediba* hypodigm samples two genera. Specifically, Rak and Been (Been and Rak, 2014; Rak and Been, 2014) argued that the Malapa remains represent a mixture of elements that should be assigned to the genus *Australopithecus* with those that belong in the genus *Homo*. If true, this would challenge the position that *A. sediba* represents a potential link between *Australopithecus* and *Homo*. To address these issues, this study evaluates the morphological differences between the mandibular rami of MH1 and MH2 and tests the hypotheses that ontogenetic shape change and/or sexual dimorphism accounts for these differences. We further test the hypothesis that shape variation represented by these two specimens is consistent with that of a single species.

1.1. *Fossil descriptions and previous research*

The forms of the rami in MH1 and MH2 are quite distinct (de Ruiter et al., 2013; Fig. 1). Despite its younger ontogenetic age and shorter mandibular length, the ramus of MH1 is slightly taller (superoinferiorly) and wider (anteroposteriorly) than that of MH2 in absolute measurements. The anterior and posterior borders of the ramus in MH2 are distinctly non-parallel, with the anterior border exhibiting a marked concavity. In contrast, in MH1, the anterior and posterior borders are relatively vertically oriented and nearly parallel (de Ruiter et al., 2013). Furthermore, MH1 has a posteriorly angled coronoid process and a relatively deep, asymmetrical sigmoid notch (with the deepest point located more posteriorly), while MH2 has a coronoid that, although damaged, does not appear to have a posterior orientation and possesses a shallower, more symmetrical sigmoid notch (with the deepest point located approximately midway between the coronoid process and condyle; de Ruiter et al., 2013; Terhune et al., 2014).

Figure 1. The mandibular rami of MH1 (top) and MH2 (bottom) in lateral view. Both specimens are shown at the same scale and are rotated so that the occlusal plane is approximately horizontal. Note the slight damage to the tip of the coronoid process of MH1 that has occurred since the initial publication of *Australopithecus sediba*; because of this damage, we elected to employ high-quality casts of MH1 and MH2 (made prior to this breakage) in our analysis.

Although the sex of these specimens is not known with absolute certainty, osteometric and dental assessments suggest that MH1 most likely represents a male and MH2 a female (Berger et al., 2010). Other than studies on the robusticity of the mandibular symphysis and corpus (e.g., Weidenreich, 1936; Chamberlain and Wood, 1985; Kimbel and White, 1988; Daegling and Grine, 1991), there are few published data on sexual dimorphism in extant hominid mandibular shape. In general, those that have assessed mandibular shape dimorphism have typically found little or no significant dimorphism in *Pan* and *Homo*, and substantially greater amounts in *Pongo* and *Gorilla* (Wood et al., 1991; Taylor, 2006; Schmittbuhl et al., 2007; Robinson, 2012). By and large, however, sexual dimorphism in the great ape mandible is associated with differences in size rather than shape (Taylor, 2006). Taylor (2006:85) describes *Pan* mandibles as exhibiting "essentially no shape dimorphism," although she did find that condylion-coronion distance (i.e., representing sigmoid notch width) relative to mandible length was dimorphic in *Pongo pygmaeus pygmaeus, Gorilla gorilla gorilla,* and *Pan troglodytes verus*, though not in any other species or subspecies of the great apes. Notably, no analyses have specifically investigated dimorphism in mandibular ramus shape. It is therefore unclear whether the pattern of shape differences between MH1 and MH2 may represent differences due to sexual dimorphism.

Research by Terhune et al. (2014) has shown that differences in ramal morphology among great apes and humans appear early in ontogeny (i.e., prior to M1 eruption), and these differences correspond closely to the differences observed in adults. Terhune et al. (2014) also demonstrated that by M2 eruption specimens are considerably more difficult to classify to age category, suggesting that great ape and human mandibular ramus form changes little during later ontogeny and that adult ramal morphology is achieved prior to the completion of overall craniodental development. That the ramus does not change considerably in form during ontogeny has also been argued to be the case in *Australopithecus afarensis* (Rak et al., 2007). Notably, Terhune et al. (2014) corroborated Rak et al.'s (2007) contention that the morphology of the ramus in *Gorilla* differs greatly from other great ape species and humans and also found general support for Rak et al.'s (2007) specific suite of features distinguishing gorilla rami from *Pongo*, *Pan*, and *Homo sapiens*. However, these authors noted that the clearest distinction was between *Gorilla* and *Homo* (i.e., the former exhibits a high coronoid and a deep, anteroposteriorly compressed sigmoid notch, while the latter exhibits a lower coronoid and a wide and shallow sigmoid notch; see below) and also identified important differences among humans, chimpanzees, and orangutans (i.e., humans possess a somewhat higher coronoid and a wider sigmoid notch, whereas chimpanzees and orangutans possess lower coronoids and anteroposteriorly compressed sigmoid notches). Insofar as it suggests that the form of the mandibular ramus changes relatively little during ontogeny in great apes and humans and indicates that adult differences among these taxa are present at an early age, this work casts some doubt on whether the differences between MH1 and MH2 can be explained by the difference in their ontogenetic ages. However, this position has not been explicitly tested to date.

The argument that MH1 and MH2 cannot be accommodated in a single species and instead represent two distinct hominin genera is based largely on the work of Rak et al. (2007), which focused on the shape of the mandibular ramus in great apes, humans, *Paranthropus robustus*, and *A. afarensis* (see also Rak et al., 2002). Specifically, these authors investigated the shape of the coronoid process and sigmoid notch using two-dimensional (2D) data and demonstrated that ramus shape variation can be used to assign extant specimens to the correct species in roughly 82% of cases. Based on this analysis, Rak et al. (2007) argued that gorillas are distinguished from the other species by a suite of features, including: 1) a coronoid process that is taller than the condyle and possesses a broad base, which causes the deepest point of the sigmoid notch to be located relatively close to the condyle; 2) a posteriorly angled coronoid tip that occasionally overhangs the sigmoid notch; and 3) a deep and anteroposteriorly narrow sigmoid notch. These distinctive features of the gorilla ramus vis-à-vis other great apes and humans were also noted by previous authors (Aitchison, 1965; Humphrey et al., 1999). Rak et al. (2007) further observed these features in rami of *A. afarensis*, *Australopithecus africanus*, and *P. robustus* and therefore posited that coronoid process and sigmoid notch morphology might be profitably used for reconstructing evolutionary relationships among hominids and hominins. Importantly, in the context of Rak et al.'s (2007) work, MH1 can be identified as possessing a morphology that is strikingly gorilla-like, whereas MH2 exhibits the more generalized morphology that Rak et al. (2007) demonstrated is shared by chimpanzees, humans, and orangutans.

The current study quantifies mandibular ramus variation in *A. sediba* and tests three related hypotheses: **Hypothesis 1** states that the differences observed between MH1 and MH2 can be accounted for by ontogeny; **Hypothesis 2** states that the differences observed between MH1 and MH2 can be accounted for by sexual dimorphism; and **Hypothesis 3** states that the variation represented by MH1 and MH2 can be accommodated in a single species. We evaluate these hypotheses by quantifying variation in ramus shape using 2D sliding semilandmark data.

2. Materials and methods

We collected data from ontogenetic samples of four hominid species (*P. pygmaeus*, *G. gorilla*, *P. troglodytes*, and *H. sapiens*) comprising approximately equal numbers of males and females (Table 1; Supplementary Online Material [SOM] Table S1), as well as from the two *A. sediba* ascending rami (MH1 and MH2). The extant sample for the current study was used previously by Terhune et al. (2014), where individuals were assigned to one of four age categories based on dental eruption: Age Category 1—no permanent teeth in occlusion, Age Category 2—M1 erupted and in occlusion, Age Category 3—M1 and M2 erupted and in occlusion, and Age Category 4—M1-M3 erupted and in occlusion. The present sample was restricted to only those individuals assigned to Age Categories 3 and 4 (i.e., the categories to which the two *A. sediba* specimens, MH1 and MH2, were assigned, respectively). In previous work (Terhune et al., 2014), individuals in the last category were separated into those with and without the spheno-occipital synchondrosis (SOS) fused; here, we lump specimens with M3 erupted into a single group since previous analyses suggested no significant differences between individuals with the SOS fused and those without.

Rami were photographed with their lateral aspect parallel to the lens of the camera and with a scale located in the same plane as the ramus. Photographs of high-quality casts of MH1 and MH2 (taken in the same manner as described above) were used to collect data for *A. sediba*; although we examined the originals, we employed casts because of recent damage to the tip of the coronoid process in MH1. For each extant specimen and for both *A. sediba* specimens, tpsDig (Rohlf, 2010) was used to plot 44 2D sliding semilandmarks; the sliding semilandmarks were anchored by three fixed landmarks: (1) the most inferior point on the root of the ramus, (2) coronion, and (3) the point at which the sigmoid crest meets the articular surface of the mandibular condyle (Fig. 2).

We employed two methods to reconstruct the missing portions of MH2 (Gunz et al., 2009). First, we performed a geometric reconstruction, in which we estimated the missing semilandmarks in MH2 using a thin plate spline (TPS) interpolation from the semilandmarks included in MH2 and the complete reference specimen. Separate TPS reconstructions were produced using each extant specimen in Age Category 4 as a reference specimen ($n = 241$), and a reconstruction using MH1 as the reference was also produced (Fig. 3). In addition, we reconstructed the coronoid of MH2 using a multiple multivariate regression approach (Gunz et al., 2009; Gunz and Mitteroecker, 2013; Spoor et al., 2015). To assess the accuracy of the regression-based reconstruction methods, we removed the semilandmarks missing in MH2 from each complete specimen in the extant sample, as well as in MH1, and then

Table 1
Sample sizes for the comparative sample used in this study.[a]

	Category 3			Category 4			
	M1 and M2 erupted and in occlusion			M1-M3 erupted (SOS unfused or fused)			
Species	F	M	U	F	M	U	Totals
Pan troglodytes	4	6	1	14	13	1	39
Gorilla gorilla	4	4	0	17	25	1	51
Pongo pygmaeus	6	4	1	15	13	0	39
Homo sapiens							
Alaskan Inuit	5	1	6	25	25	0	62
Hungarians	3	1	19	25	26	1	75
Nubians	0	0	5	10	10	1	26
SE Asians	1	0	2	9	9	1	22
Totals	23	16	34	115	121	5	315

[a] SOS = Spheno-occipital synchondrosis, F = female, M = male, U = sex unknown.

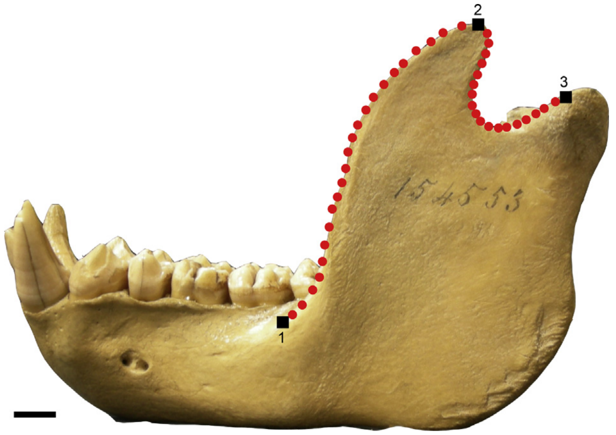

Figure 2. Landmarks and semilandmarks employed in this study as illustrated on the mandible of an adult male gorilla. Black squares are fixed landmarks: (1) the most inferior point on the root of the ramus, (2) coronion, and (3) the point at which the sigmoid crest meets the articular surface of the mandibular condyle. Red dots are sliding semilandmarks. Scale bar is 1 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

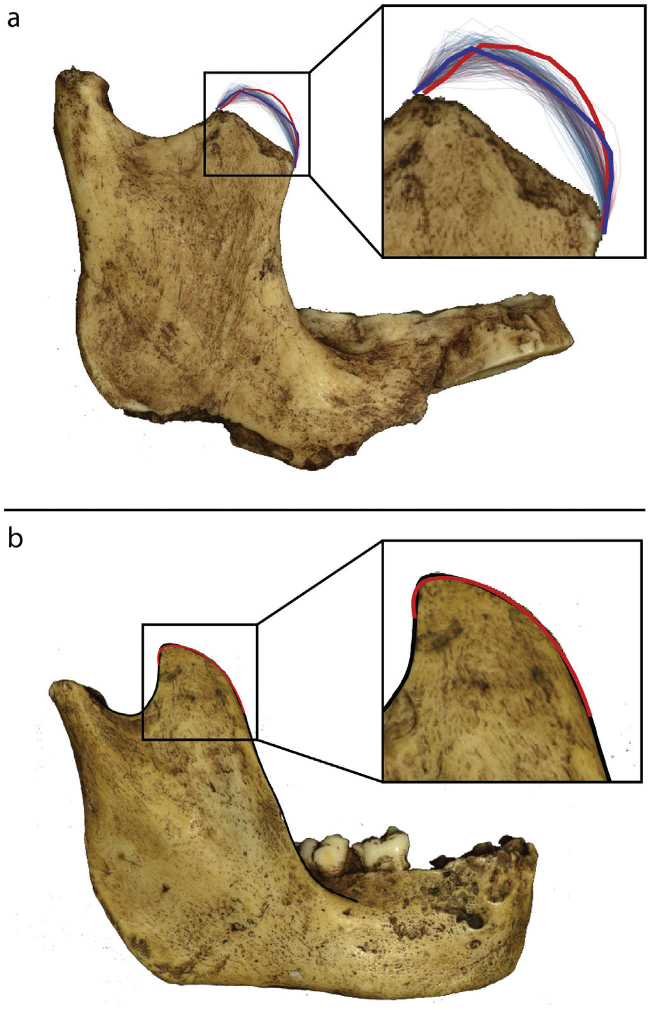

Figure 3. Reconstructions of the MH2 coronoid process as described in the Materials and methods. (a) Thin colored lines indicate reconstructions based on thin plate spline (TPS) models (i.e., geometric reconstruction) for each individual specimen; blue = reconstructions based on *Homo sapiens* specimens, orange = *Pongo pygmaeus*, red = *Pan troglodytes*, and gray = *Gorilla gorilla* specimens. The thick blue curve represents the TPS reconstruction based on MH1, while the thick red curve represents the reconstruction of MH2 based on the multiple multivariate regression technique. (b) MH1 showing a reconstruction of the same landmarks that are missing in MH2 calculated via the regression technique. The close correspondence between the reconstructed curve and the original morphology suggests that the regression technique is well suited for reconstructing the morphology in this region. Specimens not shown to scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reconstructed the “missing” semilandmarks. In all cases, the reconstructed forms closely matched the original form for that specimen (Figs. 3 and 4).

Data were analyzed using geometric morphometric methods. Specimens were registered via Generalized Procrustes Analysis, and semilandmarks were allowed to slide to minimize bending energy (Gunz and Mitteroecker, 2013). Shape variation in the sample was visualized using a between groups principal components analysis (bgPCA; Mitteroecker and Bookstein, 2011) including all individuals from the extant sample (Age Categories 3–4) and the two *A. sediba* specimens. The bgPCA axes were computed based on the covariance matrix of the group means of the extant species; all specimens—including the fossil reconstructions—were projected into that space. The explained variance of these axes was computed by dividing the variance of the respective bgPCA scores by the total variance.

To determine whether ontogenetic shape change explains the pattern of shape differences between MH1 and MH2 (Hypothesis 1), we compared the average shape of individuals in Age Category 3 (the age of MH1) to the average shape of individuals in Age Category 4 (the age of MH2). Separate comparisons were made for each species in the extant sample. Since MH1 is a presumed male and MH2 is a presumed female, we performed an additional analysis that included only males from Age Category 3 and only females from Age Category 4 (but note that sex attribution in Category 3 is limited, particularly for humans). Differences in average shape were visualized using thin plate spline (TPS) analyses. This analysis was included to test for the possible effects of sex (as well as ontogeny) on the difference between MH1 and MH2. To more specifically assess the role of sexual dimorphism in the sample (Hypothesis 2), we calculated mean adult female and male forms for each species, as well as mean female forms for Category 4 only and mean male forms for Category 3 only, and visualized differences between these mean forms using TPS analyses. To test Hypothesis 3 (i.e., that the magnitude of difference between MH1 and MH2 can be accommodated in a single species), we drew all possible pairs of specimens from Age Categories 3 and 4 from each species in the extant sample and calculated the Procrustes distance between the specimens in each pair; the same procedure was followed for all pairs of extant great ape and human species (Spoor et al., 2015). This yielded Procrustes distance distributions within extant taxa, as well as between each pair of extant taxa. These frequency distributions served as a reference for interpreting the Procrustes shape differences between MH1 and MH2, and they encompass both ontogenetic shape differences, as well as differences related to sexual dimorphism (since all possible female and male pairs are included in the distribution).

3. Results

Results of the bgPCA are shown in Figure 5. Permutation tests of the Procrustes distances between species average shapes reveal that they differ significantly from one another ($p < 0.003$). The bgPCA highlights the distinctiveness of *H. sapiens* compared to the other species. The contrast between *H. sapiens* is most obvious along bgPC1 (which explains 56.45% of the shape variance), with *H. sapiens* possessing more positive values along this axis and

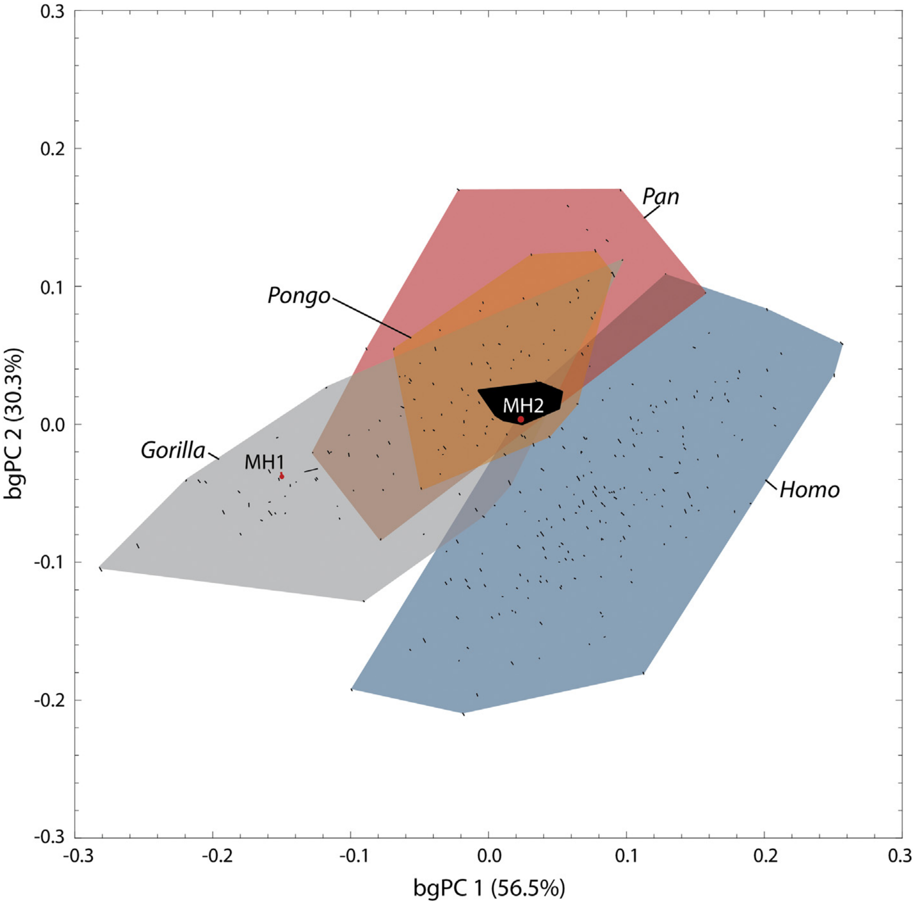

Figure 4. Between-group PCA (bgPCA) illustrating the original and "reconstructed" forms for all specimens employed in this analysis. For each species in the comparative sample, the semilandmarks missing in MH2 were removed and then reconstructed using the geometric technique. Two points, representing the original specimen and the specimen with the semilandmarks reconstructed, are shown for each specimen, and a line connecting these two points is also shown. Note that the lines are very short (and barely discernible) for almost all specimens, which corroborates the utility of our methods for reconstructing the missing portions of MH2. Convex hulls surround the specimens of each species. The convex hull labeled 'MH2' represents the 242 geometric reconstructions of MH2 (i.e., based on each specimen in the comparative sample and a reconstruction based on MH1). The red dot represents the regression-based reconstruction of MH2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

G. gorilla possessing more negative values on average. *H. sapiens* is also separated, albeit to a lesser extent, along bgPC2 (30.3% of the total variance), insofar as this species has somewhat more negative values on average than the other species, particularly *P. troglodytes* and *P. pygmaeus*. These differences are largely related to the relative height of the coronoid process, which is more projecting in *H. sapiens*; this contrast is most apparent when *H. sapiens* is compared to *P. troglodytes* and *P. pygmaeus*. *H. sapiens* also differs from the other species in its possession of a relatively wide sigmoid notch, although this difference is more marked in the comparison of *H. sapiens* and *G. gorilla* than it is in comparisons of *H. sapiens* and *P. troglodytes* and *P. pygmaeus*. *Gorilla gorilla* is also somewhat distinct from the other two non-human species (as well as from *H. sapiens*) along both bgPC axes: gorillas possess a posteriorly angled coronoid process that is somewhat higher than in *P. troglodytes* and *P. pygmaeus* (but lower than in *H. sapiens*) and a deep, anteroposteriorly compressed sigmoid notch. Examination of the distribution of the sexes in morphospace indicates that there is very subtle sexual dimorphism in ramal shape. Although there is substantial overlap in the distributions of male and female specimens within each species, there is a slight tendency for females to fall more positively along bgPCs 1 and 2; this is more evident in gorillas and humans. There is also very little difference between Age Categories 3 and 4, as the individuals assigned to these categories broadly overlap on both bgPCs in all species.

When MH1 and MH2 are projected into the bgPCA space of the extant taxa (Fig. 5), the distance between these specimens is relatively large. The different reconstructions of MH2 cluster tightly in bgPCA space, reflecting the fact that all of the reconstructions are quite similar to each other. Notably, however, all of these reconstructions are located in a portion of the bgPCA space in which all of the extant species overlap. This reflects the fact that the ascending ramus in MH2 has a more generalized morphology. MH1, by contrast, is situated in the portion of the morphospace otherwise occupied exclusively by *G. gorilla*, corroborating Rak and Been's (2014) previous observation that the MH1 ramus is gorilla-like.

Regarding Hypotheses 1 and 2, our results (Fig. 6) suggest that the pattern of ontogenetic shape change between Age Category 3 and 4 individuals and shape differences between sexes are markedly different from the observed morphological differences between MH1 and MH2. In the comparisons in which all specimens (regardless of sex) were examined, the differences between the average shapes of Age Categories 3 and 4 are very slight in all species (Fig. 6). This result suggests that, in great apes and humans, very little change in mandibular ramus form occurs between Age

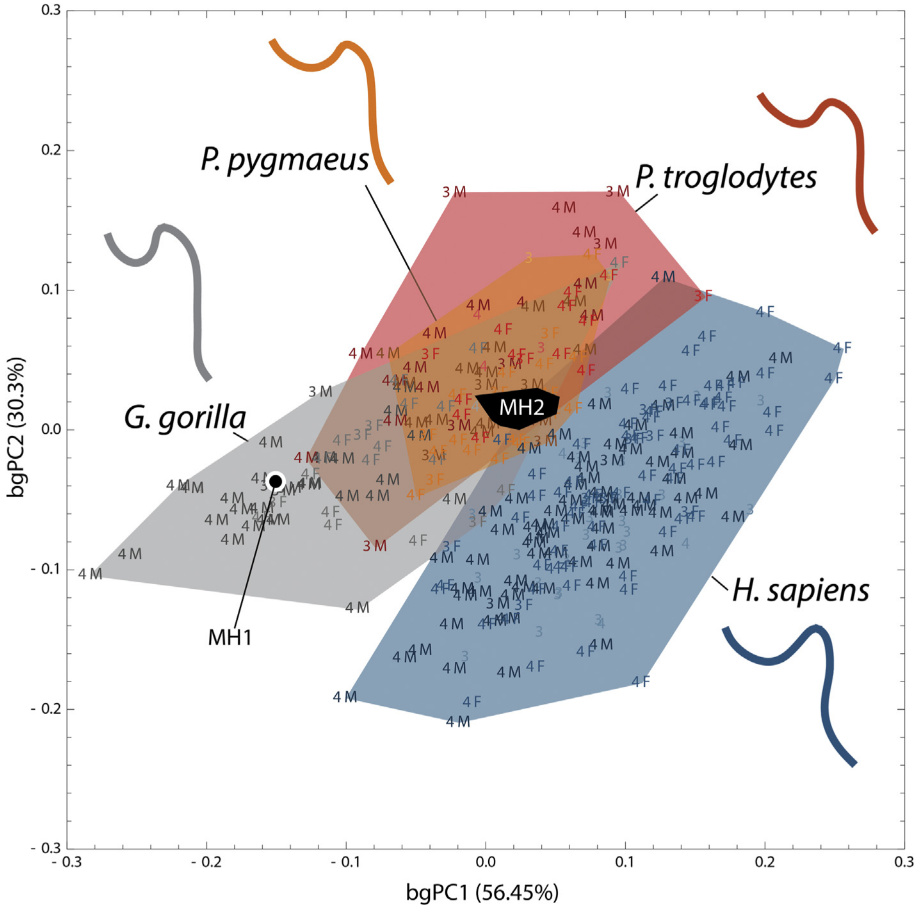

Figure 5. Between-group PCA illustrating shape variation in the extant sample and showing the positions of MH1 and the MH2 reconstructions. Convex hulls surround the specimens in each species. Numbers indicate the age category to which each specimen was assigned and, where known, sex is indicated with M (male) or F (female). Mean shapes for each species are indicated with lines connecting to the corresponding convex hull (colors of the mean shapes correspond to colors of convex hulls). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Categories 3 and 4, as is consistent with our previous work (Terhune et al., 2014). Similarly, shape differences between mean female and male forms for each species are very slight, whether comparing only Age Category 4 individuals or where sex comparisons were restricted to males in Age Category 3 and females in Age Category 4 (i.e., the same sex and age categories suggested for MH1 and MH2; panel on far right of Fig. 6). Notably, males in all taxa exhibit very slightly more superiorly and posteriorly projecting coronoid processes than females on average. Importantly, these average ontogenetic and sex differences are negligible when compared to corresponding TPS analysis plots illustrating differences between MH1 and MH2 (Fig. 6).

Hypothesis 3 was evaluated in two ways. First, the Procrustes distances between MH1 and MH2 were compared to within-species distributions representing all possible pairs of female and male specimens from Age Categories 3 and 4 from each species in the extant sample. Second, the Procrustes distances between MH1 and MH2 were compared to between-species distributions (i.e., distributions created by calculating the Procrustes distances between all possible pairs of female and male specimens from Age Categories 3 and 4 from each pair of species in the extant sample). Comparisons of the Procrustes distances between MH1 and MH2 to the within-species distributions (Fig. 7) suggest that the magnitude of the difference between these two specimens is large. This finding is true regardless of the method used to reconstruct the missing portion of the ramus in MH2 or the reference sample used in the reconstruction. However, the differences between MH1 and MH2 are within the 95% confidence intervals of the within-species distribution for all species except *P. pygmaeus* (in which case all of the distances fall outside of the 95% confidence interval). Some of the distances between MH1 and MH2 (particularly those based on reconstructions of MH2 using the chimpanzee and human reference samples) are outside the 95% confidence interval of the within-species distribution of *P. troglodytes*. However, in this case, the majority of the distances are still within the confidence intervals of this distribution.

In comparisons of the distances between MH1 and MH2 to the between-species distributions (Fig. 7), unlike the within-species distributions (where the MH1-MH2 distances were near the upper tails of the distributions), the distances between MH1 and MH2 are near the center of the between-species distributions. The only exception is the *P. troglodytes*–*P. pygmaeus* distribution, for which the majority of the distances between MH1 and MH2 fall outside and above the 95% confidence intervals. Importantly, however, in no case is the distance between MH1 and MH2 outside and below the 95% confidence intervals of the between-species distributions. This implies that the differences between these two fossil specimens more closely resemble those between two genera than those within a single species. In sum, these results suggest that while the difference between the two fossil mandibular rami is relatively large compared to the within-species Procrustes distance distributions and closer to the mean of the between-species

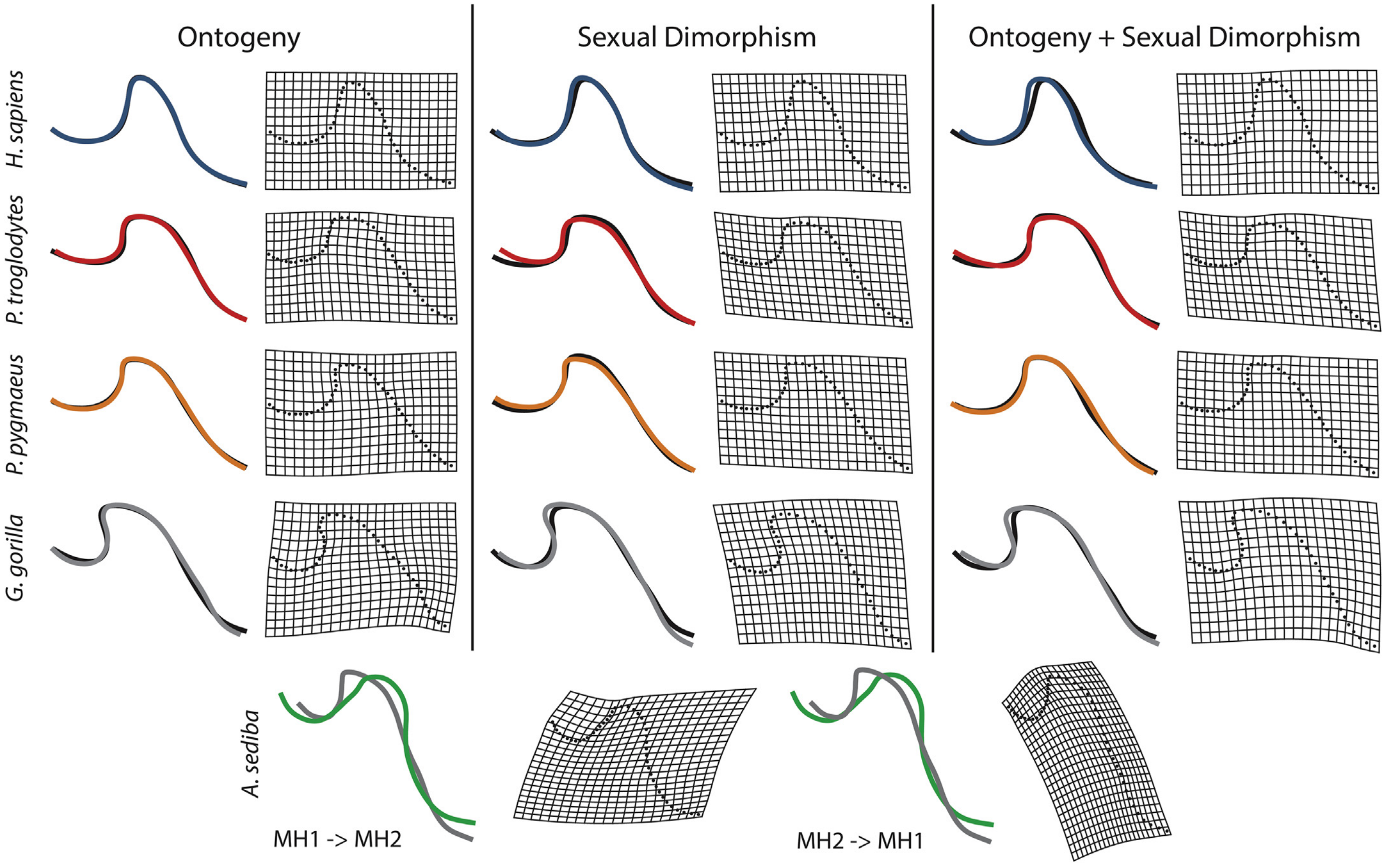

Figure 6. Thin plate spline plots showing average shape differences between individuals from Age Categories 3 (black line) and 4 (colored lines: *Homo sapiens* [blue], *Pan troglodytes* [red], *Pongo pygmaeus* [orange], *Gorilla gorilla* [gray]) with no restrictions on the sex of the specimens (panel named “Ontogeny”), average shape differences between females (black line) and males (colored lines) in each species (panel named “Sexual Dimorphism”), and average shape differences between males of Age Category 3 (black line) and females of Age Category 4 (colored lines) for each species (panel named “Ontogeny + Sexual Dimorphism”). For each panel, curves in the left-hand column represent the reference (black line) and target (colored lines) specimens, and in the right-hand column of each panel the thin plate spline deformations represent the warping from the reference shape to the target shape for that particular comparison. At the bottom, shape differences between MH1 (gray line) and MH2 (green line) are illustrated, with corresponding thin plate spline diagrams shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

distributions, this difference could still be sampled from a single species. Consequently, these results suggest that Hypothesis 3 cannot be rejected.

4. Discussion

Within our sample we document a large within-group variability in mandibular ramus shape that is related to neither sexual dimorphism nor ontogeny. Nonetheless, our results demonstrate that extant groups form distinct clusters in shape space, albeit with some overlap. There are no differences in mean ramus morphology between Age Category 3 and Age Category 4 to the extent observed between MH1 and MH2 in any of the extant species. This finding is echoed in the more extensive ontogenetic analysis of Terhune et al. (2014), which showed that by the eruption of the second molar (Age Category 3), great ape and human mandibular rami become more difficult to classify to age category, indicating that shape changes are negligible later in ontogeny. Thus, the findings here strongly suggest that differences in mandibular ramus shape between MH1 and MH2 are not due to ontogenetic shape change, constituting a rejection of Hypothesis 1. In addition, our results call into question the inference that *A. sediba* exhibits a unique pattern of mandibular ontogeny vis-à-vis other hominin species (de Ruiter et al., 2013). This inference was based on an analysis of the ontogeny of overall mandibular shape that compared *A. sediba* to other fossil hominin species (i.e., *A. africanus* and *Homo erectus*), as well as to *P. troglodytes* and *H. sapiens*. Specifically, de Ruiter et al. (2013) suggested that because the magnitude of mandibular growth and the growth trajectory of *A. sediba* differ greatly from all other species included in the analysis, this species exhibits a unique pattern of mandibular ontogeny. However, in the context of the results presented here, we believe this claim may be premature because the large within-species variability found among great apes and humans in our study makes it unlikely that species-specific ontogenetic patterns can be characterized using only two specimens (see also Kimbel, 2013). It should be noted, however, that de Ruiter et al. (2013) included morphology in the corpus as well as the ramus and, at present, the influence of including these additional regions cannot be evaluated in the context of our results.

The results here also indicate that the differences between MH1 and MH2 are not consistent, in either degree or pattern, with the differences between males and females of species in the extant comparative sample. This finding highlights the fact that the variation in mandibular ramus shape within species is large and largely unrelated to sexual dimorphism or ontogenetic variation. Although our analyses revealed some differences between males and females that were consistent in all of the extant species—i.e., the possession in males of slightly more posteriorly and superiorly projecting coronoid processes—the results also showed that these differences are quite small, particularly when compared to differences among species, and the overwhelming pattern is of only very subtle shape differences between males and females. These results are

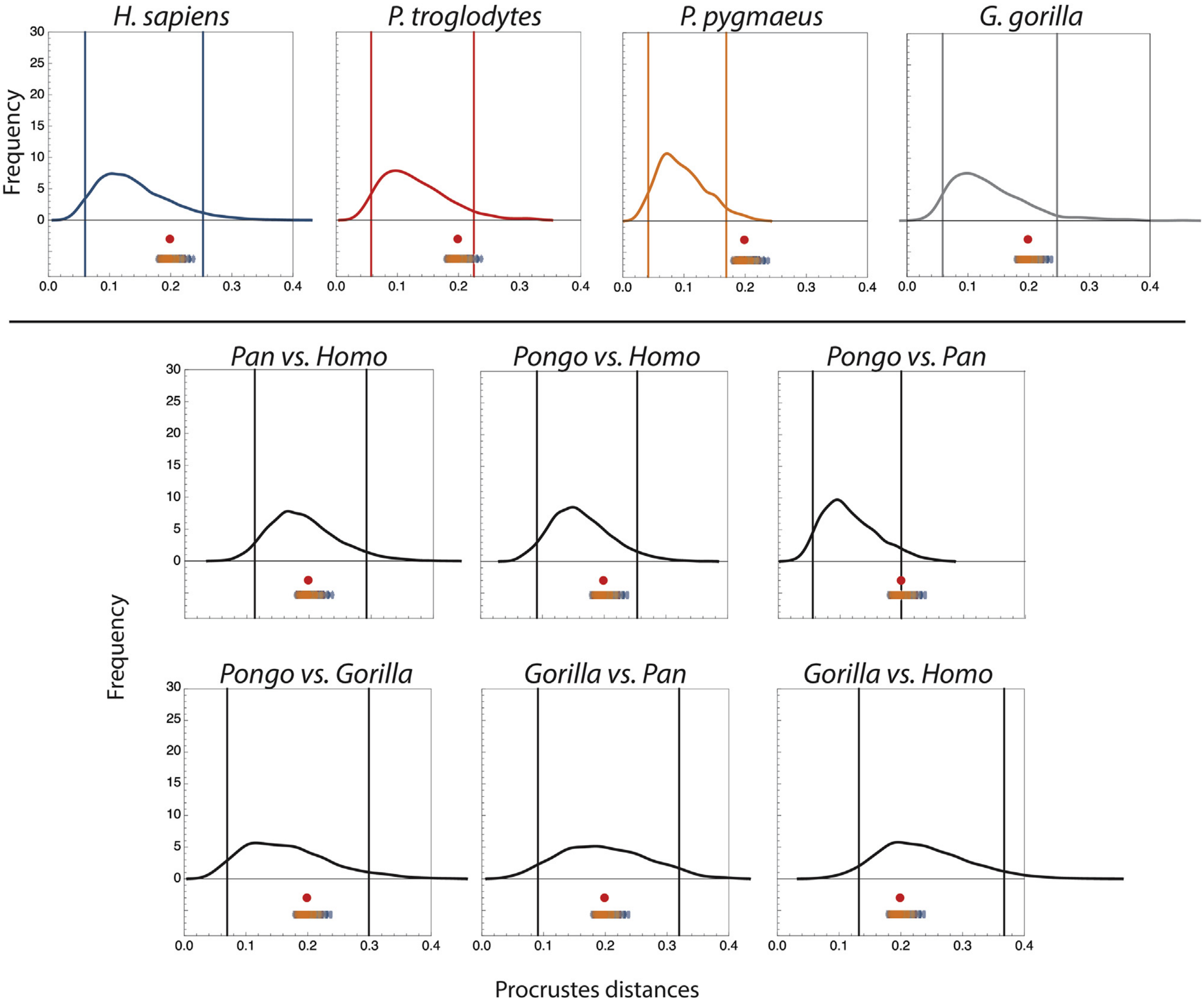

Figure 7. Within-species (top) and between species (bottom) Procrustes distance distributions between Age Categories 3 and 4 individuals for the extant samples, showing the 95% confidence intervals (vertical bars) and the Procrustes distances between MH1 and MH2. For each plot, the red dot represents the distance between MH1 and MH2 when the multiple multivariate regression technique was used to reconstruct the missing portions of MH2. The colored dots (which, due to their proximity, appear as multi-colored horizontal bars below the red dots) represent the distances between MH1 and the 312 reconstructions of MH2 using the thin plate spline method. The colors of these dots correspond to the species used as a reference for the reconstruction (blue = *H. sapiens*, red = *P. troglodytes*, gray = *G. gorilla*, orange = *P. pygmaeus*). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

consistent with previous research by Rak et al. (2007), who noted an absence of differences in ramal shape between male and female gorillas, as well as work by Taylor (2006) who found no significant differences in scaled measures describing the morphology of the ramus in great apes more generally. The differences between MH1, a presumed male, and MH2, a presumed female, are much more pronounced than the average differences demonstrated here between males and females in the extant samples. The slight differences noted above between males and females that are seen in all the species in the extant sample—i.e., a slightly taller, more posteriorly projecting coronoid—also exist between MH1 and MH2. However, the differences between MH1 and MH2 are much more marked than the average difference between males and females in any of the species in the comparative sample. Additionally, these two specimens differ in features that do not differ between males and females in any of the extant species, including, most notably, differences in the shape of the sigmoid notch (see above), which clearly distinguish the mandibular rami of MH1 and MH2. Although these results could be interpreted as evidence that the differences between MH1 and MH2 are due to sexual dimorphism, but that the degree and pattern of dimorphism in *A. sediba* differs from that of great apes and humans, we argue that it is more parsimonious to interpret the findings as an indication that sexual dimorphism does not explain these differences, and we therefore conclude that our results constitute a rejection of Hypothesis 2.

The present study cannot refute the hypothesis that MH1 and MH2 belong to a single species. Although the magnitude of differences between these two specimens is large relative to the within-species variation of extant hominids, it is not unusually large for most great ape and human species and could be sampled from a single great ape or human species, with *P. pygmaeus* being the single, notable exception. Interestingly, however, our results also suggest that it would not be unusual to observe the difference between MH1 and MH2 in a sample comprising two great ape and/or human taxa. In particular, the magnitude of the shape differences between MH1 and MH2 does not fall below the 95% confidence intervals of the between-species comparisons. Moreover, the difference between the two *A. sediba* specimens is more typical of between-species comparisons than it is of within-species comparisons. It should be noted, however, that, as can be seen in Figure 7, some intraspecific pairwise differences would not fall below the 95% confidence intervals of the between-species comparisons; moreover, some of the intraspecific differences would be closer to the mean of the intergeneric differences than to the mean of the distributions of the taxon from which they were drawn. Taken together, the results relating to the conspecificity of MH1 and MH2 suggest that it is more likely that, based on the shape of the mandibular ramus, the hypodigm of *A. sediba* represents a single, highly variable species. That being said, the possibility that it samples two taxa cannot be completely refuted.

Our results demonstrate that the shape of the ascending ramus in MH1 closely resembles that of *G. gorilla* (see Fig. 5). This resemblance is evident in this specimen's possession of a ramus with a posteriorly angled coronoid process and a narrow, asymmetrical sigmoid notch; it is important to note, however, that the posterior angulation of the coronoid process is also a feature possessed by males compared to females (see above) and, therefore, may also be due to MH1's presumed sex. Notably, the morphological pattern of the ramus possessed by *G. gorilla* has also been argued to characterize *Australopithecus* (Rak et al., 2007). Thus, to the extent that they establish a close similarity between the MH1 and an *Australopithecus*-like ramus shape, our analyses corroborate Rak and Been's (2014) argument. However, our study also shows that MH2 plots in a portion of morphospace in which all four great ape and human species overlap. The morphology of MH2 is therefore not specifically *Homo*-like, but rather is relatively generalized and could be found in individuals in any of the four species, including *Gorilla*. Based on our analyses, we cannot reject that two hominin taxa are present at Malapa, as they show that the shape differences between the MH1 and MH2 mandibles can be accommodated within most extant groups. The patterns of shape variation in the comparative sample may explain the somewhat equivocal results of our study. In particular, as can be seen in Figure 5, in which the convex hulls representing the extant species overlap considerably, ramus morphology in the four extant species is quite similar and the degree of within-species variation in ramus form is not substantially larger than the between-species variation. This limited degree of between-species variation in the mandibular ramus is also evident in a comparison of the 95% confidence intervals of the within-species distribution for *P. troglodytes* and the between-species distribution between *Pan* and *Pongo*. Specifically, the upper limit of the confidence interval of the *Pan*–*Pongo* distribution is less than the upper limit of the confidence interval for the within-species distribution of *P. troglodytes*, indicating that there would be a relatively high probability of failing to reject a hypothesis of conspecificity for two specimens drawn from *Pan* and *Pongo*, respectively. If this pattern of limited between-species variation also holds for hominin species, our ability to rule out the hypothesis that the Malapa mandibles come from a single species may be somewhat limited—i.e., because specimens from different species may be closer in shape to one another than they are to specimens belonging to their same species.

Some of the intraspecific variation observed here is most likely a result of morphological plasticity and/or functional variation in ramus and coronoid form. As the insertion site for the temporalis muscle, ramus form is definitely linked to masticatory function. Experimental studies have demonstrated that coronoid process shape and orientation can be altered by either partial or complete excision of the temporalis muscle (e.g., Washburn, 1947; Avis, 1959), often quite radically, or when mandibular hypomobility is induced experimentally (Isberg et al., 1990). Moreover, comparative analysis of coronoid and temporalis form found a correlation between the height and width of the coronoid process and temporalis orientation (Ritzman and Spencer, 2009) in an interspecific analysis of anthropoid primates. Thus, it is highly likely that individual variation in the position and architecture of the temporalis muscle influences coronoid form, and this prior experimental work suggests that coronoid process form is labile during ontogeny. However, it is also notable that previous work (Terhune et al., 2014) found that significant differences in ramal morphology are established early in ontogeny in the great apes and humans, even before eruption of the first molars. Therefore, while this region of the mandible may be somewhat plastic insofar as the experimental results suggest that radical alteration of the temporalis affects the morphology of the coronoid, other important aspects of this region do not change greatly during ontogeny, even as the masticatory apparatus changes its configuration. Therefore, we do not believe that possible morphological plasticity of the mandibular ramus has a large effect on the results of this study, nor do we believe that plasticity specifically explains the somewhat equivocal nature of these results.

We recognize that our study is limited insofar as it bases interpretations about the conspecificity of MH1 and MH2 on a single anatomical region. Certainly, given the relative completeness of the two *A. sediba* individuals, information from other anatomical regions is germane to the question of whether or not these specimens represent a single taxon. However, with this in mind, it is important to consider which skeletal elements are present in both MH1 and MH2—i.e., which parts of the skeleton can be used to address the question of conspecificity of these specimens. In addition to the mandible, the skeletal elements that are repeated in MH1 and MH2 derive primarily from the upper limb and pectoral girdle, and, in these regions, the morphologies of MH1 and MH2 are strikingly similar (Churchill et al., 2013). Moreover, the morphology of the upper limb and pectoral girdle in some australopith taxa may possess some derived, *Homo*-like features (Asfaw et al., 1999), and others have suggested a high degree of intraspecific variation in this region (Alemseged et al., 2006; Haile-Selassie et al., 2010; Green and Alemseged, 2012). Therefore, the phylogenetic valence of the morphology in the shoulder may not be sufficient (or not sufficiently resolved) for it to be used to address questions of conspecificity in the hominin fossil record. The describers of the axial skeleton, pelvic girdle, and lower limb in MH1 and MH2 do not note any differences between MH1 and MH2 with respect to elements that are repeated in the two specimens, including thoracic vertebrae, ribs, portions of the ilium, proximal femur, and calcaneus (Kibii et al., 2011; Zipfel et al., 2011; DeSilva et al., 2013; Schmid et al., 2013; Williams et al., 2013). The first rib, which is preserved in MH1 and MH2, is particularly instructive here due to the similarity between the first ribs in the two specimens and because, in both specimens, the curvature of the first rib indicates an ape-like, mediolaterally narrow upper thoracic shape that differs from the broader upper thoracic region exhibited by *Homo* (Schmid et al., 2013). The portions of the os coxa that are repeated in both specimens are also very similar and suggest a morphology with a mosaic of primitive (australopith-like) and derived (*Homo*-like) features, with some features that are intermediate between the conditions seen in *Australopithecus* and *Homo* (Kibii et al., 2011). In the lower limb, the proximal femora of both MH1 and MH2 display features (such as a long, anteroposteriorly compressed femoral neck) that are shared with *Australopithecus* and other, more human-like traits (such as a long femoral head [in MH2] and a well-developed hypertrochanteric fossa [in MH2]; DeSilva et al., 2013). Lastly, the calcaneal tuberosities in MH1 and MH2 are very similar and suggest an ape-like form, resembling neither *Australopithecus* nor *Homo* (Zipfel et al., 2011). Taken together, the available evidence from the entire skeletons of MH1 and MH2 do not present compelling evidence that MH1 and MH2 should be attributed to different species.

The geologic context of the Malapa fossils may also argue against the contention that they sample two hominin taxa. Specifically, the two partial skeletons come from a single, well-dated facies and this stratum is thought to have accumulated in a single, rapid depositional event (Dirks et al., 2010; Pickering et al., 2011a; Berger, 2012). This fact suggests, at least, that these two individuals occupied a similar habitat when they were deposited into the cave system. These facts, of course, do not entirely exclude the possibility that MH1 and MH2 represent different hominin taxa, particularly given the fact that fossil-bearing members at other geographically proximate and roughly contemporaneous sites (e.g., Swartkrans Member 1 [Lower Bank deposit] and Kromdraai B) have yielded fossils argued to belong in the genus *Paranthropus* and others placed in the genus *Homo* (Clarke and Howell, 1972; Hughes and Tobias, 1977; Olson, 1978; Clarke, 1985, 1994; Grine et al., 1993; Susman et al., 2001; Braga and Thackeray, 2003; Grine, 2005; Curnoe and Tobias, 2006; Smith and Grine, 2008; Pickering et al., 2011b; Rak and Been, 2014).

We believe that our analyses clearly demonstrate that the differences between the two Malapa mandibular rami are not due to ontogenetic variation or sexual dimorphism. Furthermore, we contend that, despite the fact that our results regarding the conspecificity of MH1 and MH2 are somewhat equivocal, the contention that MH1 and MH2 belong to a single hominin species cannot be refuted based on the results presented here. Taken together, these results do not provide a definitive explanation for the morphological diversity found in the *A. sediba* remains. However, in the context of the hypothesis of some researchers that *A. sediba* represents a potential ancestor for the genus *Homo* (Berger et al., 2010; Berger, 2012, 2013; but see Spoor, 2011; Wood and Harrison, 2011; Kimbel, 2013), the relatively high degree of morphological variation in the ramus of this species, which has been documented here, warrants discussion. To the extent that the high degree of morphological variation in the mandibular ramus of *A. sediba* as represented by MH1 and MH2 suggests a large degree of overall skeletal variation, our results indicate that if indeed *A. sediba* is ancestral to the genus *Homo* (an interpretation that was favored by the discoverers but not tested here and that has been challenged by others [see above]), this species was strongly morphologically variable relative to extant great apes (and particularly *P. pygmaeus*). This fact, in turn, may indicate that if *A. sediba* represents the ancestor of the genus *Homo*, our genus emerged from a highly variable anatomical milieu, of which many unique combinations of primitive, australopith-like features and derived, *Homo*-like traits were possessed in concert in individual hominin lineages.

In conclusion, our study indicates that the hypotheses that the differences between MH1 and MH2 in mandibular ramus form are due to ontogeny or sexual dimorphism can be rejected, but it cannot refute the hypothesis that MH1 and MH2 sample a single species. However, we believe that these results may suggest that *A. sediba* was an unusually variable species, at least in regard to mandibular ramus morphology, and that this fact has important implications for diversity in the genus *Australopithecus* and perhaps for the origin of the genus *Homo*. Additional research, particularly work that examines patterns of shape differences and incorporates non-metric data, is needed to probe the more nuanced differences between MH1 and MH2 and further evaluate the morphological variability found in *A. sediba*.

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Supplementary Online Material

Supplementary online material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2016.09.002.

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