Geometric morphometric analysis of mandibular shape diversity in Pan

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A B S T R A C T

The aim of this research is to determine whether geometric morphometric (GM) techniques can provide insights into how the shape of the mandibular corpus differs between bonobos and chimpanzees and to explore the potential implications of those results for our understanding of hominin evolution. We focused on this region of the mandible because of the relative frequency with which it has been recovered in the hominin fossil record. In addition, no previous study had explored in-depth three-dimensional (3D) mandibular corpus shape differences between adults of the two Pan species using geometric morphometrics. GM methods enable researchers to quantitatively analyze and visualize 3D shape changes in skeletal elements and provide an important compliment to traditional two-dimensional analyses.

Eighteen mandibular landmarks were collected using a Microscribe 3DX portable digitizer. Specimen configurations were superimposed using Generalized Procrustes analysis and the projections of the fitted coordinates to tangent space were analyzed using multivariate statistics. The size-adjusted corpus shapes of Pan paniscus and Pan troglodytes could be assigned to species with approximately 93% accuracy and the Procrustes distance between the two species was significant. Analyses of the residuals from a multivariate linear regression of the data on centroid size suggested that much of the shape difference between the species is size-related. Chimpanzee subspecies and a small sample of Australopithecus specimens could be correctly identified to taxon, at best, only 75% of the time, although the Procrustes distances between these taxa were significant. The shape of the mandibular symphysis was identified as especially useful in differentiating Pan species from one another. This suggests that this region of the mandible has the potential to be informative for taxonomic analyses of fossil hominoids, including hominins. The results also have implications for phylogenetic hypotheses of hominoid evolution.

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Introduction

As the closest extant relatives of humans, great apes are often viewed as the most appropriate models for the extent and pattern of morphological variation to be expected in early fossil hominin species (LeGros Clark, 1964; Wolpoff, 1977; Kimbel and White, 1988; Wood et al., 1991; Daegling, 1993; Shea et al., 1993; Richmond and Jungers, 1995; Lockwood et al., 1996; Uchida, 1996; Lockwood, 1999; Silverman et al., 2001; Guy et al., 2003, 2008; Harvati, 2003a; Robinson, 2003; Harvati et al., 2004; Skinner et al., 2006; Lague et al., 2008; but see Jolly, 2001, 2009; Taylor, 2006 and references therein). Although some recent, and many earlier, studies suggested that all great ape species other than Pan paniscus could be split into two or more species (Groves, 1986, 2000, 2001, 2003; Morin et al., 1994; Ruvolo et al., 1994; Grine et al., 1996; Muir et al., 1998, 2000; Albrecht et al., 2003; Brandon-Jones et al., 2004; Thalmann et al., 2007; Bradley, 2008), Pan is currently the only extant great ape genus that researchers agree has multiple species (Badrian and Badrian, 1984; Thomson-Handler et al., 1984; Kano, 1992; Morin et al., 1994; Horai et al., 1995; Takahata et al., 1996; Burrows and Ryder, 1997; Gagneux et al., 1999; Kaessmann et al., 1999; de Waal, 2001; Stone et al., 2002; Yu et al., 2003). Thus, this taxon is valuable as a comparative model for assessing the taxonomic homogeneity of putative species in the hominin fossil record.

There have been many studies documenting craniodental and postcranial differences between the two Pan species (Johanson, 1974; Cramer and Zihlman, 1976; Cramer, 1977; Zihlman and Cramer, 1978; Corruccini and McHenry, 1979; McHenry and Corruccini, 1981; Shea, 1983a,b,c, 1984, 1985; Kinzey, 1984; Laitman and Heimbuch, 1984; Shea and Coolidge, 1988; Groves et al., 1992; Uchida, 1992, 1996; Shea et al., 1993; Braga, 1995; Lockwood et al., 2002, 2004; Guy et al., 2003; Pilbrow, 2006; Skinner et al., 2008, 2009; Singleton et al., 2011). Fewer studies have published data on differences between P. paniscus and Pan troglodytes in their mandibular morphology (Andrews, 1978;
Two of the three studies including all three chimpanzee subspecies described the differences between the two Pan species in their mandibular morphology as less extensive than the differences in their cranial shapes. These analyses presented data on 13 (Taylor, 2002) and 17 (Taylor and Groves, 2003) exclusively mandibular linear dimensions scaled to size, with over half of the measurements having at least one of their end points on the ramus. In the third study, Schmittbuhl et al. (2007) explored differences among extant hominoid taxa, including between P. paniscus and P. troglodytes, in the mean outline shapes of their entire mandibles using elliptical Fourier techniques. However, since complete mandibles are rarely found in the hominoid fossil record and the vast majority of specimens lack rami, it is useful to explore whether the morphology of the mandibular corpus on its own results in a similar or reduced ability to discriminate among hominoid species (Robinson, 2003; Lague et al., 2008). Moreover, the results of Taylor and Groves (2003) suggest that this region of the mandible may be especially important in differentiating bonobo and chimpanzee mandibles given that most of the significant differences they found between these two taxa were measurements taken on the mandibular corpus. Lague et al.’s (2008) analysis included eight linear measurements scaled to the geometric mean that are found on the more commonly preserved mandibular corpus to explore how effective these data were at grouping extant hominoid specimens in the correct genus, species, and subspecies. In the other recent study of Pan mandibular morphology using multivariate methods, Boughner and Dean (2008) focused on documenting ontogenetic changes in the three-dimensional (3D) shape of the mandible in Pan using geometric morphometric (GM) techniques and, consequently, they included only a small sample of adults for the two species.

This investigation builds on these studies by exploring differences between the two Pan species in the three-dimensional shape of the mandibular corpus using geometric morphometric techniques. Three-dimensional geometric morphometric methods have been used to quantify variation in modern human mandibular morphology, to explore differences among fossil hominid mandibles, and to investigate the ontogenetic development of the mandible in Pan (Rosas and Bastir, 2004; Oeltlé et al., 2005; Nicholson and Harvati, 2006; Boughner and Dean, 2008), but have not been employed, as of yet, to examine in depth differences between adults of the two Pan species in their mandibular shapes. One of the advantages of using 3D GM techniques is that it enables researchers to document shape differences in morphological features that have previously only been qualitatively described, often because they have been difficult to accurately quantify using traditional instruments (Dean, 1993; Harvati, 2001, 2003b; Robinson, 2003; Rosas and Bastir, 2004; Nicholson and Harvati, 2006). For example, the sizes of the symphyseal transverse tori have been assessed qualitatively in most studies of extant hominoids by noting how far they project posteriorly relative to the tooth row (Aitchison, 1965; Brown, 1989, 1997; Singleton, 2000). However, the positions of the tori relative to the dentition are strongly influenced by a number of factors, including the inclination of the symphysis. Accounting for symphyseal inclination when quantifying the size of the tori is difficult using standard techniques (Daegling, 1995; Daegling and Jungers, 2000; Robinson, 2003). GM methods provide one possible means of documenting variation in these kinds of morphological features.

The primary questions to be addressed using these data were: (1) How effectively can the mandibular corpora of Pan paniscus and P. troglodytes and those of the three P. troglodytes subspecies be differentiated from one another using the 3D shape data derived from GM analyses and how does this compare to previous multivariate studies of these taxa? (2) What features on the mandibular corpus are most useful for distinguishing Pan species from one another? (3) Are shape differences between the two Pan species and three P. troglodytes subspecies related to differences in the sizes of their mandibular corpora?

Materials and methods

Sample

The sample for this study was comprised of 126 mandibular specimens of P. paniscus and all three commonly recognized chimpanzee subspecies, Pan troglodytes schweinfurthii, Pan troglodytes troglodytes and Pan troglodytes verus (Table 1). Males and females were not sampled equally because at most of the museums visited all available specimens were digitized. Data were collected only on adult and wild-shot specimens, as determined by fully erupted permanent dentition, museum tags, and catalog information. Specimens showing obvious abnormalities or substantial resorption due to antemortem tooth loss were excluded since those factors would alter the shape of the mandibular corpus. These restrictions meant that, despite visiting the collections at nine museums, only six male bonobos could be included in the sample. In addition, four Australopithecus afarensis and three

![Table 1](image-url)
Australopithecus africanus specimens were included in a separate analysis using a subset of 12 of the 18 landmarks. The selection of these specimens was based on an attempt to minimize the number of landmarks that had to be excluded to avoid missing data and still have a small sample of each species.

**Methods**

Three-dimensional coordinates of 18 midline and left side mandibular landmarks were collected using a Microscribe 3DX portable digitizer (Table 2, Fig. 1). In geometric morphometrics, landmarks can be defined as ‘biologically meaningful’ points that can be consistently identified in all specimens (Richtsmeier et al., 1995; Valeri et al., 1998). Most of the landmarks digitized in this study were of either Type I or II (Bookstein, 1990; Valeri et al., 1998). Type I landmarks are contact points between structures, such as the intersection of two sutures, or the midpoints of foramina, while Type II landmarks are points at the maxima of curvature, such as points on the maxima of tori and the minima of sulci (Bookstein, 1990; MacLeod, 2001). Points that were digitized along the basal margin of the mandible directly inferior to the alveolar margin interdental septa are Type III landmarks (i.e., those at the ends of diameters). These coordinate points can be included as landmarks in some analyses using geometric morphometric techniques (Slice et al., 1996).

To assess whether the coordinate points along the base of the mandible could be reliably identified and, thus, treated as landmarks in this study, data were collected on the same male chimpanzee mandible (L18) from the Mammalogy Department at the American Museum of Natural History ten times following the protocols described above. The Euclidean distance from each landmark to the specimen’s centroid was determined for all replicates and the mean-square errors (MSEs) for each landmark were calculated in Microsoft Office Excel 2007 to determine the intra-observer error (Singleton et al., 2011). MSEs ranged from 0.05 mm to 1.64 mm, with an average for the 18 landmarks of 0.45 mm. The average MSE for the four Type III landmarks on the basal margin of the mandible was 0.50 mm, not appreciably larger than the overall mean, suggesting that these landmarks are no more difficult to reliably identify than the Type I and Type II landmarks that were included in this project.

A Generalized Procrustes analysis was run so that the relative positions of the landmarks could be compared among the specimens. In this method, superimposition of the specimens’ landmark configurations is accomplished by translating and rotating each specimen to a common coordinate system and orientation and scaling it to unit centroid size so that the differences they exhibit are due to shape (Rohlf, 1990; Rohlf and Marcus, 1993; Slice, 1996). Centroid size is defined as the square root of the sum of the squared Euclidean distances of all landmarks to a specimen’s centroid (Slice et al., 1996). Superimposition of the specimen configurations was performed using Morpheus (Slice, 1998).

The Procrustes aligned coordinates were analyzed using principal components analysis (PCA), which transforms the data to a new coordinate system, reducing the dimensionality of the dataset to focus on combinations of variables that are most informative for explaining the variation present within the sample. PCA was also used to graphically demonstrate how effective these data were at separating the various groups from one another. Changes in the relative positions of the landmarks along each PC axis were exhibited by linking the landmarks together using a wireframe in Morphologika (O’Higgins and Jones, 2004) (Fig. 2). A multivariate analysis of variance (MANOVA) was run on the PC scores to determine whether sex, subspecies, and species membership, and the interaction between these variables contributed significantly to variation on each PC axis.

To determine whether overall shape differences between the subspecies and species, and between males and females of each

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**Table 2**

List of mandibular landmarks digitized on each specimen. Landmarks 5, 6, 9, 10, 14, and 17 were removed in the fossil hominin analyses.

<table>
<thead>
<tr>
<th>Mandibular landmarks</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-4</td>
<td>Medial alveolus interdental points</td>
</tr>
<tr>
<td>7-10</td>
<td>Basal margin points directly inferior to alveolar interdental landmarks 3–6</td>
</tr>
<tr>
<td>11</td>
<td>Most projecting point of lateral prominence</td>
</tr>
<tr>
<td>12</td>
<td>Deepest point in lateral intertoral sulcus</td>
</tr>
<tr>
<td>13</td>
<td>Foramen mentale</td>
</tr>
<tr>
<td>14</td>
<td>Infrafrenalale</td>
</tr>
<tr>
<td>15</td>
<td>Gnathion</td>
</tr>
<tr>
<td>16</td>
<td>Mandibular orale</td>
</tr>
<tr>
<td>17</td>
<td>Most projecting point of superior transverse torus</td>
</tr>
<tr>
<td>18</td>
<td>Most projecting point of inferior transverse torus</td>
</tr>
</tbody>
</table>
species, were significant, two group random permutation tests were run on the Procrustes distances between the group mean configurations of the taxa and sexes using adaptations of SAS codes written by Kieran McNulty (2005). In each permutation, specimens were randomly placed into one of the two groups and the Procrustes distances between the resulting groups were then calculated. This process was repeated 1000 times and the frequency ($\alpha$) at which the permuted distances were less than the actual Procrustes distances ($\rho$) between the taxa or sexes was determined (Singleton et al., 2011).

A discriminant function (DF) analysis using cross-validation was performed on a subset of the principal components to explore how accurately mandibular specimens could be classified to the correct sex, subspecies, and species using these data. All groups were assigned equal prior probabilities and only the results for cross-validation classification were reported below. To determine the number of principal components to include within the DF analysis, a scree plot of the eigenvalues was created. This plot graphically exhibits the proportion that each principal component contributes to the overall variance. As is typical, the scree plot showed a steep drop over the first few PCs, with the percentage variance leveling off after PC 9. Thus, only the first nine PCs, which accounted for approximately 78% of the variance, were employed in the DF analyses.

Although geometric size is removed during Procrustes superimposition, size-related shape differences remain and can be important in differentiating taxa from one another. Since *P. paniscus* had a significantly smaller centroid size than *P. troglodytes* in this study (86.8 and 104.2, respectively, $p < 0.0001$), it was important to assess whether the differences identified below between the groups were size-related. To accomplish this, a multivariate linear regression of the data from all PC scores together on centroid size was performed. All statistical analyses were then re-run on the residual data for each specimen.

Finally, a preliminary analysis using the methods described above on the *Pan* specimens and a small sample of seven *Australopithecus* specimens (see Table 1) was run to assess whether these data could be used to accurately identify mandibles of *A. afarensis* and *A. africanaus* to species. So as to have a representative sample of landmarks but still include a small sample of each species, six landmarks were removed from the dataset to avoid missing data (see Table 2). The DF analyses and permutation tests were run using the remaining 12 landmarks and including the seven hominins in the dataset.

All statistical analyses were run using SAS 9.2 (SAS Institute Inc.).

Results

Principal components analysis

PC 1 accounted for 24.3% of the total variance and was significant for species ($p < 0.0001$) and sex ($p < 0.01$) effects, but not subspecies or interaction effects ($p > 0.05$). Bonobos tended to have more positive scores on PC 1, although their range overlapped that of chimpanzees (Fig. 3). Female *P. troglodytes* specimens tended to be located closer to the positive end of this axis and, thus, closer to *P. paniscus*, than male *P. troglodytes* specimens. No differences were readily apparent between male and female bonobo specimens on PC 1.

The shape differences between the wireframes at the extreme ends of PC 1 included a deeper mandibular corpus and symphysis, a less projecting superior transverse torus, a more anteriorly positioned lateral intertoral sulcus, and a more elongated postincisive planum for specimens closer to the negative end of this axis (i.e., *P. troglodytes*) than for those closer to the positive end of this axis (i.e., *P. paniscus*).

PC 4 was significant for species ($p < 0.001$), but not subspecies, sex, or interaction effects ($p > 0.05$) and accounted for 6.5% of the total variance. *P. paniscus* specimens tended to be located nearer to the negative end of this axis compared with those of *P. troglodytes*, although there was substantially more overlap in their ranges on this axis than on PC 1 (Fig. 3). The shape differences between specimens on the positive end of PC 4 (*P. troglodytes*) and those on the negative end (*P. paniscus*) included a more posteriorly oriented symphyseal axis, a more elongated postincisive planum, and a more posteriorly positioned mental foramen for those on the positive end of this axis.

PC 2, accounting for 17.2% of the total variance, did not exhibit significant taxonomic, sex or interaction effects ($p > 0.05$) and the two *Pan* species and three *P. troglodytes* subspecies overlapped extensively on this axis.

PC 3, which accounted for 8.7% of the total variance, only exhibited significant subspecies effects ($p < 0.0001$) with all other categories non-significant ($p > 0.05$). PC 5 was also significant for subspecies effects and also sex effects ($p < 0.0001$), but not for any other categories ($p > 0.05$). This axis accounted for 5.8% of the total variance. *P. t. schweinfurthii* specimens tended to be located closer to the positive end of PC 3, while *P. t. verus* specimens were primarily located on the opposite end of this axis. On PC 5, *P. t. verus* specimens were mostly placed on the positive end while specimens of the other two subspecies, particularly males, were typically located on the negative end (Fig. 4).

Figure 2. Lateral view of a *Pan troglodytes* mandible exhibiting all landmarks that were digitized and a wireframe connecting the landmarks. The wireframe is used to help visualize shape differences along each principal components axis in Morphologika (e.g., Fig. 3).
Permutation tests

The Procrustes distances between the mean mandibular shapes of all species and subspecies were significant. As expected, the shape differences were greatest between *P. paniscus* and *P. troglodytes* ($r = 0.0952$). The Procrustes distance between the mean shapes of *P. t. schweinfurthii* and *P. t. troglodytes* ($r = 0.0339$) was just barely significant ($r = 0.035$) and their mean shapes were much more similar to one another than either was to *P. t. verus* (Table 3). The mandibular shape of *P. t. verus* could be easily differentiated from those of the other subspecies ($r < 0.05$) (Table 3).

The Procrustes distances between males and females were similar for the two *Pan* species, although it is interesting to note that the Procrustes distance was greater between males and females of *P. paniscus* than between the *P. troglodytes* sexes (Table 3). However, males and females of *P. paniscus* could not be significantly differentiated from one another ($r = 0.075$) while *P. troglodytes* sexes could be ($r = 0.023$). These results were likely influenced by the small sample of male bonobos included in this study.

The Procrustes distance between bonobos and chimpanzees using the residual data was substantially reduced compared to the distance between them using the original size-adjusted dataset (Table 3). The two taxa could no longer be significantly differentiated and, in fact, their distance was less than all pairwise distances between the *P. troglodytes* subspecies. It seemed possible that the reason for this result was that the dispersion of individuals of the chimpanzee subspecies was such that they generated a mean value for the species as a whole that was similar to that of bonobos, even though the means of the individual subspecies were not particularly close to that of *P. paniscus*. This hypothesis was assessed by re-running the permutation tests on the residual data and determining the Procrustes distances between *P. paniscus* and each of the *P. troglodytes* subspecies individually. In these tests, the pairwise distances between bonobos and each of the chimpanzee subspecies were significantly different ($r < 0.05$) and the distances were similar to or greater than the pairwise distances between the *P. troglodytes* subspecies. However, the distances between *P. paniscus* and the three subspecies were still quite reduced compared with the Procrustes distance between the species that was found using the original dataset. This suggests that size-related shape differences are important in differentiating *P. paniscus* and *P. troglodytes*. The multivariate regression of all PC scores together on centroid size found that size was significantly associated with the data ($r < 0.001$). The correlation coefficient ($r^2$) was 0.7338, showing that size accounts for a substantial amount of the variance in the dataset.

The Procrustes distances between the *P. troglodytes* subspecies using the residual dataset were also less than those using the original data, although the most substantial reductions were in the pairwise distances between *P. t. verus* and the other two subspecies. The reduction in Procrustes distance was such that *P. t. verus* and *P. t. schweinfurthii* were no longer significantly different. These results suggest that shape differences between *P. t. verus* and the other two subspecies are, to some extent, size-related.

Procrustes distances between males and females, particularly between male and female chimpanzees, were also reduced using the residual dataset. The sexes could not be significantly

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Figure 3. Scatterplot of the principal components scores for each specimen on PC 1 and PC 4. Lateral views of the wireframe shape configurations representing the extreme shapes along each axis are provided. Black squares — *Pan paniscus* females; black triangles — *Pan paniscus* males; white diamonds — *Pan troglodytes schweinfurthii* females; grey diamonds — *Pan troglodytes schweinfurthii* males; white circles — *Pan troglodytes troglodytes* females; black triangles — *Pan troglodytes troglodytes* males; black Xs — *Pan troglodytes verus* males; grey circles — *Pan troglodytes troglodytes* females; grey circles — *Pan troglodytes troglodytes* males; black Xs — *Pan troglodytes verus* males; shaded grey Xs — *Pan troglodytes verus* males.
differentiated in either species using these data. These results also imply that size is an important factor in shape differences between males and females, especially for *P. troglodytes*.

**Discriminant function analysis**

In the discriminant function analysis, all of the *P. paniscus* and 91.3% of the *P. troglodytes* specimens were correctly identified to species. Nine chimpanzee specimens were misclassified as bonobos: one *P. t. schweinfurthii* female, four females and one male *P. t. troglodytes*, and two females and one male *P. t. verus*. When the linear discriminant scores are plotted, there is only a slight overlap between *P. paniscus* and *P. troglodytes* on Canonical 1 (Fig. 5), while the species extensively overlap and cannot be differentiated from one another on Canonical 2 or 3 (Fig. 6).

Only 52.9% of female and 33.3% of male bonobos were identified to the correct sex, while 65.9% of chimpanzee females and 67.8% of males were correctly identified to sex.

For the chimpanzee subspecies, 44.8% of the *P. t. schweinfurthii*, 59.6% of the *P. t. troglodytes*, and 74.1% of the *P. t. verus* specimens could be accurately identified. Only 10.3% and 17.0% of the misidentified *P. t. schweinfurthii* and *P. t. troglodytes* specimens were classified as *P. t. verus* specimens, respectively. Thus, just as in the permutation tests, the most substantial differences among the *P. troglodytes* subspecies were between *P. t. verus* and the other two taxa.

**Table 3**

Results from two group random permutation tests.

<table>
<thead>
<tr>
<th>Pairwise comparison</th>
<th>Original data</th>
<th>Residuals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Procrustes distance (p)</td>
<td>Frequency (α)</td>
</tr>
<tr>
<td><em>P. paniscus</em> — <em>P. troglodytes</em></td>
<td>0.0952</td>
<td>0.000</td>
</tr>
<tr>
<td><em>P. t. schweinfurthii</em> — <em>P. t. troglodytes</em></td>
<td>0.0339</td>
<td>0.000</td>
</tr>
<tr>
<td><em>P. t. schweinfurthii</em> — <em>P. t. verus</em></td>
<td>0.0541</td>
<td>0.000</td>
</tr>
<tr>
<td><em>P. t. troglodytes</em> — <em>P. t. verus</em></td>
<td>0.0472</td>
<td>0.000</td>
</tr>
<tr>
<td><em>P. paniscus</em> males — females</td>
<td>0.0373</td>
<td>0.673</td>
</tr>
<tr>
<td><em>P. troglodytes</em> males — females</td>
<td>0.0306</td>
<td>0.023</td>
</tr>
</tbody>
</table>

The Procrustes distances (p) between the taxa using both the original size-adjusted data and the residual data derived from the linear regression of the data from all PC scores combined on centroid size are provided, along with the frequency (α) at which the Procrustes distances between 1000 randomly selected groups are less than that between the taxa.

<sup>a</sup> The Procrustes distances between *Pan paniscus* and *Pan troglodytes schweinfurthii*, *P. t. troglodytes*, and *P. t. verus* using the residual dataset are 0.0364, 0.0323, and 0.0468, respectively (α < 0.05).
When the DF analyses were run on the residuals, only 60.9% of the bonobo specimens and 59.2% of the chimpanzee specimens could be correctly identified to taxon. The discriminatory power also decreased in the P. troglodytes subspecies analysis with only 24.1%, 51.1%, and 44.4% of the P. t. schweinfurthii, P. t. troglodytes, and P. t. verus specimens, respectively, correctly allocated to subspecies. These results suggest that, similar to the permutation test results, shape differences among these taxa, are, to some degree, size-related.

In the DF analyses of males and females of the two Pan species using the residual data, 61.4% of P. troglodytes females and 72.9% of males could be correctly identified to sex. For bonobos the percentages correctly allocated were 64.7% for females and 33.3% of males. These figures are similar to those reported above using the non-residual data.

Fossil hominin results

In the permutation test using the subsample of 12 landmarks, the Procrustes distance between the P. paniscus and P. troglodytes mean mandibular shapes was still significant and was, in fact, slightly greater than when all 18 landmarks were included in the analysis (ρ = 0.103; α = 0).

The Procrustes distance between the A. afarensis and A. africanus mean shapes was similar to, but greater than, that between the two Pan species and the two fossil hominin species could be significantly differentiated from one another even with the small sample size (ρ = 0.136; α = 0.023).

Even after removing six of the landmarks, chimpanzees and bonobos were identified with nearly the same accuracy as with the full complement of landmarks in the discriminant function analysis, with the only difference being one bonobo that was misclassified as a chimpanzee instead of none of them being misidentified. All of the hominin fossils were classified as hominins. However, only 75% of the A. afarensis and 33% of the A. africanus specimens were accurately allocated to their putative species. Further tests were run that included additional A. afarensis specimens by reducing the number of landmarks further, but this did not substantially improve the classification accuracy for the hominin specimens.

Discussion

Interspecific differences

In the PCA, the mandibular corpus specimens of P. paniscus and P. troglodytes were significantly separated from one another on PCs 1 and 4, although there was some overlap of the species’ ranges on both axes. Previous multivariate analyses of Pan mandibular morphology also were able to clearly discriminate between P. paniscus and P. troglodytes (Taylor, 2002; Taylor and Groves, 2003; Schmittbuhl et al., 2007; Boughner and Dean, 2008; Lague et al., 2008).

Using 11 of their 17 linear mandibular measurements scaled to size, Taylor and Groves (2003) were able to accurately identify 76% of their P. paniscus and 96% of their P. troglodytes specimens. They were able to achieve 100% discrimination for both taxa by including the additional six variables in the analysis, but argued that doing so led to problems with multicollinearity. Schmittbuhl et al. (2007) did an elliptical Fourier analysis of the entire mandibular outline scaled to size. They were able to correctly allocate approximately 97% of their P. paniscus and 91–98% of their P. troglodytes specimens to the correct species in their discriminant function analysis using

![Figure 5. Scatterplot of Can 1 and Can 2 for the linear discriminant scores. Symbols as in Fig. 3.](image-url)
cross-validation. In their discriminant analysis, Lague et al. (2008), using data from eight linear measurements only on the mandibular corpus scaled to the geometric mean, were able to allocate approximately 91% of their specimens to the correct Pan species. It should be noted that unlike the current study and that of Taylor and Groves (2003), Lague et al. did not include P. t. verus in their sample, which, according to genetic analyses of chimpanzees (Morin et al., 1994; Horai et al., 1995; Gonder et al., 1997, 2006; Gagneux et al., 1999; Guy et al., 2003; Taylor and Groves, 2003; Caswell et al., 2008; Fischer et al., 2011), is more distantly related to the other two subspecies than they are to one another. Given that this study and others (Taylor and Groves, 2003; Schmittbuhl et al., 2007) found P. t. verus to have the most distinct mandibular morphology of the three chimpanzee subspecies, including western chimpanzees in a dataset is likely to increase the extent of intraspecific variation in the chimpanzee sample and could make it more difficult to differentiate chimpanzees from bonobos.

In the above DF analyses, using data from only the mandibular corpus, like Lague et al. (2008), bonobo and chimpanzee specimens were identified to species with approximately 93% accuracy after the data were scaled to unit centroid size. Thus, the discriminatory power of these data was similar to those of previous multivariate studies that included data from the ramus (Taylor and Groves, 2003; Schmittbuhl et al., 2007). These results and those from most of the other research cited above would appear to suggest that the shape of the mandibular corpus may be more effective for discriminating between these taxa than the ramus. Unlike the current study and that of Lague et al. (2008), approximately half of Taylor and Groves’ (2003) linear measurements included at least one endpoint on the ramus and their dataset provided the lowest discriminatory power for differentiating the Pan species from one another. Moreover, Taylor and Groves (2003) found that most of the significant differences between P. paniscus and P. troglodytes subspecies for size-adjusted linear measurements were on the mandibular corpus, with few significant differences between those taxa for measurements that included a point on the ramus. The results of Schmittbuhl et al. (2007) could be viewed as evidence against this hypothesis since they were able to achieve the most accurate classification of bonobo and chimpanzee mandibles although they included data from the ramus in their analyses. However, their classification accuracy was only slightly better than that of this study and that of Lague et al. (2008) suggesting that most of the important differences between these species are on the mandibular corpus.

It may be that the ability to significantly differentiate bonobos and chimpanzees in this study was influenced by the substantially larger number of female, compared with male, bonobo specimens. In the MANOVA, the overall female mean PC score was found to be significantly different from that of males on PC 1 and it could be that if more male bonobos were included in the analysis, the interspecific differences would have been less evident. However, when the MANOVA was run on the species separately, no significant differences were found between the mean PC scores of males and females of either species on this axis. While female chimpanzees tended to be located closer to the bonobos on PC 1, the six male bonobos were not positioned any closer to the chimpanzee specimens on this axis than female bonobos were (see Fig. 3). Moreover, the Procrustes distance between male and female bonobos was not significant and in the DF analysis male and female bonobos could be differentiated at only slightly better than chance. This result is not surprising given the recent studies showing a lack of significant sexual dimorphism in P. paniscus for any measurements taken on
the mandibular corpus or for any shape ratios derived from those measurements (Taylor, 2006) and no significant differences between the outline shapes of the mandibles of male and female bonobos (Schmittbuhl et al., 2007). This suggests that it is unlikely that the skewed sex ratio of bonobos is the factor that led to the finding of significant interspecific diversity in mandibular morphology documented above. If bonobos are ‘essentially monomorphic’ in mandibular size and shape (Taylor, 2006), then including more males should not alter the results significantly.

It should be noted that Taylor and Groves (2003) and Schmittbuhl et al. (2007) in their discriminant function (DF) analyses separated the *P. troglodytes* specimens into subspecies for comparison with *P. paniscus*, while in this study and that of Lague et al. (2008) all *P. troglodytes* subspecies were grouped together. To test whether this difference could influence the results of the current analysis, a DF analysis was run with four groups (i.e., specimens of the three *P. troglodytes* subspecies separated from one another). In this re-analysis, the data were slightly better at allocating specimens to the correct species with 93.2% of the *P. troglodytes* and 95.7% of the *P. paniscus* specimens correctly identified. Thus, this methodological difference would not seem to be an influence on the ability of this study to allocate a specimen to the correct species.

Researchers have found in some studies that 3D landmark-based methods were more effective than using size-adjusted linear data for identifying and quantifying morphological differences among species (Hartman, 1989; Adams et al., 2004; Singleton et al., 2011). This study does not refute that hypothesis and, if anything, provides tentative support for it. More importantly, it demonstrates that 3D GM studies are important for providing complementary data to results derived from 2D linear measurements to help better understand morphological differences among taxa.

**Subspecific differences**

In the above analysis, *P. t. verus* specimens could be accurately identified to taxon almost 75% of the time, while fewer than 60% of the other two subspecies could be correctly allocated, with most of them incorrectly identified as *P. t. schweinfurthii* or *P. t. troglodytes* specimens. Moreover, the Procrustes distances between *P. t. verus* and the other two subspecies were considerably greater than the distance between *P. t. schweinfurthii* and *P. t. troglodytes*. This is consistent with genetic evidence suggesting that *P. t. schweinfurthii* and *P. t. troglodytes* are more closely related to one another than either is to *P. t. verus* (Morin et al., 1994; Horai et al., 1995; Gonder et al., 1997, 2006; Gagneux et al., 1999; Caswell et al., 2008; Fischer et al., 2011).

The percentage of *P. t. verus* specimens that were correctly identified in this study is nearly identical to that of Taylor and Groves (2003) and greater than that of Schmittbuhl et al. (2007). However, Taylor and Groves’ (2003) data were somewhat more accurate at allocating *P. t. troglodytes* and *P. t. schweinfurthii* to their correct groups than either this study or that of Schmittbuhl et al. (2007), with *P. t. schweinfurthii* being the most difficult subspecies to place in the correct taxon in all three studies. It is worth noting that Lague et al. (2008) had much greater success differentiating *P. t. schweinfurthii* and *P. t. troglodytes* from one another (80% accuracy) than any of the other three studies. This could potentially be because they did not include *P. t. verus* in their analysis given that over 10% of *P. t. schweinfurthii* and *P. t. troglodytes* specimens in the other three studies were misidentified as *P. t. verus* specimens. Overall, multivariate analyses using linear measurements were somewhat more effective at correctly identifying mandibular specimens of the two closely related subspecies, *P. t. schweinfurthii* and *P. t. troglodytes*. However, the current study was undertaken to explore whether shape differences in the mandibular corpus could be used to differentiate fossil species, not subspecies. Consequently, the rest of the discussion will be focused on species-level differences.

**Mandibular shape differences between Pan species**

In the principal components analysis, shape differences between the two *Pan* species remained after specimens were scaled to unit centroid size. In particular, variation on PCs 1 and 4 was related to mandibular shape differences that included *P. troglodytes* having a deeper, more posteriorly inclined mandibular symphysis with a longer postincisive planum, a less projecting superior transverse torus, a mandibular corpus that deepens more substantially anteriorly, a more posteriorly positioned mental foramen, and a more anteriorly positioned lateral intertoral sulcus. These differences are demonstrated graphically in Fig. 7, which superimposes the mean shapes generated in Morpheus (Slice, 1998) for the bonobo and chimpanzee specimens in this study.

Most of these differences are due to characters that are present on the mandibular symphysis. Guy et al. (2008) contended, as a number of other researchers have suggested (Biegert, 1963; Schultz, 1963, 1969; Simons and Pilbeam, 1965; Simons, 1972; Andrews, 1978; Logan et al., 1983; White et al., 2000), that variation in the symphysis is such that using symphyseal morphology alone to allocate specimens to taxon is unsatisfactory and that misclassification should be expected. This was based on their only being able to allocate approximately 87% of their gorilla and orangutan specimens to the correct genus using data from an elliptical Fourier analysis of the outline of the mandibular symphysis. It may be that it is necessary to include data from the rest of the mandibular corpus to more accurately identify hominoid mandibular species to taxon or that, as suggested previously (Daegling and Jungers, 2000; Sherwood et al., 2005), particular morphological characters, or combinations of characters, on the symphysis are useful for allocating fossil specimens to the correct species. Further exploration of this issue is currently being undertaken in a separate project using a larger and more taxonomically diverse sample (Robinson et al., 2012).

Some of the morphological traits found to distinguish chimpanzees from bonobos in the above analyses have not previously been studied in both of these species (e.g., symphyseal axis orientation and postincisive planum length). For other mandibular features it is possible to compare these results with those from the mandibular corpus...
other studies. For example, other researchers have also found that bonobos and chimpanzees are significantly different from one another for relative symphysal depth, with chimpanzees having a deeper symphysis (Taylor and Groves, 2003; Bougner and Dean, 2008; Lague et al., 2008). Taylor and Groves (2003) also found that P. paniscus could be differentiated from males and females of some, but not all, P. troglodytes subspecies for relative corpus height at M3, while for relative corpus height at M9 of the six pairwise comparisons only P. t. schweinfurthii males were significantly different from P. paniscus males. This is consistent with the above results that found differences between the two Pan species for relative corpus depth to be more pronounced anteriorly.

In the above analyses, P. paniscus was also found to have a relatively shorter postincisive planum and a relatively more projecting superior transverse torus than P. troglodytes. Singleton (2000) coded the position of the superior transverse torus as the same relative to the dental arcade in P. paniscus and P. troglodytes. However, if the symphyseal axis is inclined postero-inferiorly, a more posteriorly positioned torus can result from a number of different factors including a longer postincisive planum, a more posteriorly inclined symphysis, a deeper symphysis, and an increase in the size of the torus relative to the midline of the symphysis (i.e., a more projecting torus). The results of the current study confirm Singleton’s (2000) characterization of the position of the torus relative to the dentition as the same in P. paniscus and P. troglodytes. However, the way in which the torus comes to be positioned in the same place is different in P. paniscus and P. troglodytes. In chimpanzees, the postincisive planum is more elongated and the symphysis more posteriorly inclined than in bonobos, while in bonobos the projection of the torus relative to the midline symphysal axis is greater than in chimpanzees. These results support the suggestions by Daegling (1993) and Daegling and Jungers (2000) that differentiation of hominoid taxa using symphysal tural morphology may be possible (contra Simons, 1972) using a quantitative approach.

A lateral hollow (or intertoral sulcus) lies between the lateral superior torus and the marginal torus on the lateral corpus of most hominoids. It is bounded posteriorly by the lateral prominence. Anteriorly, it is frequently delimited by the canine or P3 jugum. Studies of this structure in hominoids have qualitatively described the depth and extent of this hollow on the lateral corpus without mention of any differences between the two Pan species (White, 1977; Brown, 1989; Kramer, 1988; Strait et al., 1997; Singleton, 2000). The finding above that the deepest point of the lateral intertoral sulcus tends to be more posteriorly positioned in P. paniscus may suggest that its sulcus extends further posteriorly than that of P. troglodytes. However, this merits a more detailed quantitative analysis.

Variation on PC 4 was in part related to the mental foramen being relatively more posteriorly positioned in P. troglodytes. Qualitative studies have typically described the modal position of the mental foramen along the dental arcade as the same (inferior to P4) in all great ape species and modern human populations (Simonton, 1923; Schulz, 1933; Tebo and Telford, 1950; Wood and Chamberlain, 1986; Brown, 1989; Trinkaus, 1993). However, a quantitative analysis of mental foramen position relative to dental arcade length found significant differences among great apes, with P. troglodytes exhibiting a relatively posteriorly positioned mental foramen compared with other hominoids (Robinson and Williams, 2010).

Size and scaling in Pan mandibular morphology

It has been argued that much of the diversity in skeletal shape among great apes is due to allometric scaling of morphological features in taxa of varying sizes (Shea, 1983a,b,c) and morphological differences between the two Pan species have often been attributed to allometric effects (Corruccini and McHenry, 1979; McHenry and Corruccini, 1981; Shea, 1983a,b,c; Shea et al., 1993; Uchida, 1996; Taylor and Groves, 2003; Singleton et al., 2011). Since, as expected, the centroid size of P. paniscus in this study was significantly smaller than that of P. troglodytes, it was important to explore whether the differences described above between P. paniscus and P. troglodytes in the three-dimensional shape of the mandibular corpus might be size-related.

Using the residual data approximately 60% of the Pan specimens could be correctly identified to species, a substantial loss of discriminatory power compared with the results from the original dataset. Moreover, the Procrustes distances between P. paniscus and the P. troglodytes subspecies were reduced, with differences in their mean shapes being significant for only two of the three pairwise comparisons. Finally, the linear regression of the combined PC scores on centroid size found a significant correlation between the data and size, with a high correlation coefficient ($r^2 = 0.7338$). These results would seem to indicate that the mandibular corpus shape differences captured by these landmarks between the Pan species are, to some extent, size-related shape differences. Size is clearly an important factor in differentiating the mandibles of these two species, although there are some shape differences between them that are not related to size. This is consistent with the results of Bougner and Dean (2008) who argued that chimpanzee mandibles are not just scaled up versions of bonobo mandibles and also with those of other studies that found similar scaling patterns for many, but not all, bonobo and chimpanzee mandibular measurements (Taylor, 2002; Taylor and Groves, 2003). As noted by Shea et al. (1993), the finding that some of the shape differences between the two Pan species are due to ontogenetic scaling does not in any way change the validity of the taxonomic assignment of P. paniscus. By contrast, it underscores the importance of size and allometry in differentiating closely related species.

Australopithcine results

A number of studies have described differences between the mandibular morphologies of A. afarensis and A. africanaus (Johanson et al., 1978, 1982; Johanson and White, 1979; White et al., 1981; White and Johanson, 1982; Kimbel et al., 1984, 1994; Chamberlain and Wood, 1985, 1987; Kramer, 1986; Kimbel and White, 1988; Daegling and Grine, 1991; Wood, 1991; Wood and Richmond, 2000; Ward et al., 2001). In this study, nearly 60% (four out of seven) of the fossil hominin species were allocated to the correct putative species in the DF analysis, with all specimens correctly identified as hominins, even with a reduced set of 12 landmarks. It is possible with a larger sample size, particularly including additional specimens from both species that these methods could be used to accurately place specimens into the correct taxon. This hypothesis is supported by the two groups’ random permutation test, which shows their Procrustes distance to be greater than that between the two Pan species and finds them to be significantly different from one another. Further study of differences in the 3D shape of fossil hominin mandibles using larger extant and fossil hominoid datasets is currently being undertaken (Robinson et al., 2012).

Implications for fossil hominin studies

Other than teeth, mandibles are the most common skeletal elements recovered at most hominin-bearing localities, and most of these specimens lack rami (White, 1977; White and Johanson, 1982; Tobias, 1991; Wood, 1991; Ward et al., 2001; Robinson, 2003). Because of this, characters on the mandibular corpus have been
important in both taxonomic and phylogenetic analyses of fossil hominins (Johanson et al., 1978, 1982; Johanson and White, 1979; Tobias, 1980; White et al., 1981; Skelton et al., 1986; Wood and Chamberlain, 1986; Chamberlain and Wood, 1987; Wood, 1991, 1992; Skelton and McHenry, 1992, 1998; Leakey et al., 1995; Brunet et al., 1996; Strait et al., 1997; Straig and Grine, 1998, 2001, 2004; Senut et al., 2001; Ward et al., 2001; Robinson, 2003; Schmittbuhl et al., 2007; Guy et al., 2008; Lague et al., 2008). Improving our understanding of mandibular corpus variation in the only two extant hominoid species that researchers agree are congeneric has the potential to improve our models of the extent and pattern of variation to be expected in the mandibular corpora of fossil hominins. One cannot necessarily make the assumption that the features of the mandibular corpus that are found to differentiate extant hominoid species will be the same as those that are effective for attributing fossil hominid mandibular specimens to species. However, this study, and that of Lague et al. (2008), provide evidence that the extent of intraspecific variation in the mandibular corpus of *Pan* is not so great that it is difficult to differentiate these species from one another. This suggests that the mandibular corpus is potentially informative for studies of fossil hominin taxonomy. This also supports the research of Collard and Lyckett (2009), and contrasts with that of Wood and Lieberman (2001), who argued that removing characters, such as most of those on the mandible, based on their likelihood of being phenotypically plastic does not necessarily lead to more reliable taxonomic hypotheses.

Taylor (2006) has argued that using great apes as models for the extent of variation to be expected in the mandibles of fossil hominins seems ill-advised, given her study of great apes showing that the dimorphism patterns of mandibular dimensions and ratios based on those dimensions exhibit great variability even among subspecies of the same species. Using extant hominoids as exemplars for resolving whether fossil hominid samples are taxonomically heterogeneous has been questioned for a number of reasons, including the relative paucity of comparative extant ape species, by other researchers (Martin, 1991; Grine et al., 1996; Kelley and Plavcan, 1998; Jolly, 2001, 2009). However, most studies continue to use extant hominoids as the most appropriate model taxa for fossil hominins, principally because their phylogenetic proximity makes it more likely that they share similar patterns of variation (Wood et al., 1991; Daegling, 1993; Shea et al., 1993; Richmond and Jungers, 1995; Lockwood et al., 1996; Uchida, 1996; Silverman et al., 2001; Guy et al., 2003; Robinson, 2003; Harvey, 2007a; Harvati et al., 2004; Skinner et al., 2006; Lague et al., 2008). Exploring this topic in any depth is beyond the scope of this paper as the potential to improve our models of the extent and pattern of variation to be expected in the mandibular corpora of fossil hominins seems ill-advised, given her study of great apes showing that the dimorphism patterns of mandibular dimensions and ratios based on those dimensions exhibit great variability even among subspecies of the same species. Using extant hominoids as exemplars for resolving whether fossil hominid samples are taxonomically heterogeneous has been questioned for a number of reasons, including the relative paucity of comparative extant ape species, by other researchers (Martin, 1991; Grine et al., 1996; Kelley and Plavcan, 1998; Jolly, 2001, 2009). However, most studies continue to use extant hominoids as the most appropriate model taxa for fossil hominins, principally because their phylogenetic proximity makes it more likely that they share similar patterns of variation (Wood et al., 1991; Daegling, 1993; Shea et al., 1993; Richmond and Jungers, 1995; Lockwood et al., 1996; Uchida, 1996; Silverman et al., 2001; Guy et al., 2003; Robinson, 2003; Harvey, 2007a; Harvati et al., 2004; Skinner et al., 2006; Lague et al., 2008). Exploring this topic in any depth is beyond the scope of this paper as the theory behind allocating fossils to particular species is a complex and contentious subject. However, to address specifically using our understanding of great ape mandibular variation to allocate fossil hominin mandibular specimens to species, Taylor (2006: 94) quite appropriately suggests that particular “combinations of mandibular variables may fare better” in taxonomic analyses. This is one of the potential advantages of 3D multivariate analyses: to identify such combinations of variables, including ones that are difficult to quantify using traditional morphometrics, that may be useful for differentiating taxa. The above results using 3D geometric morphometrics suggest regions of the mandibular corpus that may be especially informative for taxonomic analyses (e.g., the shape of the mandibular symphysis) and should be studied in more detail in extant and fossil hominoids.

It is important to emphasize that fossil hominin specimens are frequently fragmentary and do not typically retain all of the landmarks used in this study. Like other multivariate methods, GM techniques cannot include specimens with missing data. However, sometimes similar discriminatory power can be achieved even when removing some of the landmarks because of missing data, as was shown above for the two *Pan* species in the analysis of the reduced landmark dataset that included fossil hominins. Also, it is possible to use subsets of landmarks to explore variation in specific morphological features on the mandibular corpus that have been identified as potentially useful for assessing fossil hominoid taxonomy (e.g., Robinson and Williams, 2010). Other options for dealing with missing data that have been suggested in the literature are to substitute species-specific mean values for the missing data (Slice, 1996; Singleton et al., 2011), to use various algorithms, information on structural constraints and morphological integration, and data from more complete specimens to reconstruct missing or deformed areas of a specimen (Gunz et al., 2004, 2009; Mitteroecker and Gunz, 2009), or to use regression equations to estimate landmark coordinates (Adams et al., 2004; Gunz et al., 2004; Bastir et al., 2008).

Analyses of great ape skeletal morphology have been important in helping researchers reconstruct the phylogenetic relationships of fossil hominin taxa by providing data to aid in the determination of character polarity and mandibular features have frequently been included in the lists of characters used by researchers to test phylogenetic hypotheses (Skelton et al., 1986; Chamberlain and Wood, 1987; Wood, 1991; Groves et al., 1992; Skelton and McHenry, 1992, 1998; Lieberman et al., 1996; Strait et al., 1997; Strait and Grine, 1998, 2001, 2004; Wood and Collard, 1999). Thus, studies like this one that document which features of the mandible differ significantly among extant hominoid species could also help in refining phylogenetic hypotheses of fossil hominins. For example, if the two *Pan* species are found to exhibit shape differences for a particular morphological feature on the mandibular corpus, it would be useful to re-examine how the genus *Pan*, one of the outgroups in almost any hominin phylogenetic analysis, should be coded for that character.

In the present study, one of the shape differences identified between *P. paniscus* and *P. troglodytes* was the more posteriorly inclined symphysial axis of chimpanzees. Phylogenetic analyses of fossil hominins have typically coded all great apes as having receding symphyses (Skelton and McHenry, 1992; Strait et al., 1997; Strait and Grine, 2001, 2004). While extant hominoids generally have more receding symphyses than most hominins, this study demonstrates that there is diversity among hominoid taxa that could prove informative if taken into account in phylogenetic analyses that include this character. As noted by White et al. (2000), there is substantial variation for this character in extant hominoid species that encompasses the range supposedly separating some putative fossil hominin species (e.g., *Australopithecus bahrelghazali* and *A. afarensis*). Some fossil hominins, particularly some of the early Pliocene specimens (e.g., the *Australopithecus anamensis* mandibular specimens, LH 4, and a number of the Hadar mandibles), have symphyseal axes that are similar to, or more receding than, those of extant hominoids (Robinson, 2003). Thus, it would seem that a re-examination of the coding scheme for this character is warranted. For most fossil specimens preserving the mandibular symphysis, the data for this character could be readily collected using 3D GM since only four landmarks would need to be preserved for a specimen to be included in the analysis.

Another example of a character whose coding in phylogenetic analyses of hominins might be affected by the results of this study is the depth of the mandibular corpus. Lucas et al. (2008) characterized the mandibular corpus height as ‘tall’ in both *P. troglodytes* and in the last common ancestor (LCA) of humans and *Pan*. However, given that *P. paniscus* was found to have a relatively shallower mandibular corpus than *P. troglodytes* in this study and that of Taylor and Groves (2003) and that stem hominins are coded as having a ‘moderately tall’ mandibular corpus by Lucas et al. (2008), it may be that it is more parsimonious to code the LCA as having a ‘moderately tall’ corpus.
By undertaking additional studies of hominoid skeletal variation and diversity, researchers can further refine the character states and polarities of morphological characters, likely leading to more accurate phylogenies. Criticisms of hominoid phylogenetic hypotheses that are based on skeletal data (e.g., Collard and Wood, 2000, 2001) have often made an implicit assumption that morphological diversity among extant hominoids was well documented. However, it would seem that more extensive research on intraspecific variation and interspecific diversity in extant hominoid skeletal morphology is likely to improve our understanding of hominin evolution.

Conclusions

Significant differences in the three-dimensional form of the mandibular corpus were documented in this study between *P. paniscus* and *P. troglodytes* after scaling the specimens for size. The following features were found to differentiate bonobos from *P. troglodytes*: a more vertical symphysis axis, a more projecting superior transverse torus, a reduced postincisive planum, a shallower mandibular symphysis and corpus, particularly anteriorly, a more anteriorly positioned mental foramen and a more posteriorly positioned lateral intertoral sulcus. *P. paniscus* was found to have a significantly smaller mandibular corpus than *P. troglodytes* and the differences between these taxa appear to be, at least to some extent, size-related. This underscores that size and allometry can be important in the morphological divergence of closely related taxa.

In the discriminant function analysis, specimens were identified to species with approximately 93% confidence after they were scaled for size using Procrustes superimposition and permutation tests found the Procrustes distance between the two Pan species to be significant. This supports the results of Lague et al. (2008), suggesting that the morphology of the mandibular corpus can be useful for differentiating between closely related hominoid taxa. The preliminary findings from the analysis of mandibles attributed to *A. afarensis* and *A. australopithecus* are promising in terms of the potential of these methods for allocating the relatively commonly preserved fossil hominin mandibular corpus specimens to the appropriate species.

The identification of significant differences between the mandibular morphologies of *P. paniscus* and *P. troglodytes* in this study and others (Taylor and Groves, 2003; Schmittbuhl et al., 2007; Boughner and Dean, 2008; Lague et al., 2008) also suggest that we should not use a single species (i.e., chimpanzees) to define the character states for a genus in phylogenetic analyses, as this may affect interpretations of the polarity of morphological characters and reconstructions of the ancestral morphotype of the *Homo–Pan* clade. By using data from this and similar studies of extant hominoid skeletal morphology, particularly from larger, more geographically diverse samples, it is hoped that researchers will be able to further refine phylogenetic hypotheses of fossil hominins.

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