Taxonomic Variation in the Supraorbital Region of Catarrhine Primates

Running title: Taxonomic variation in the primate supraorbital torus

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Abstract

Objectives

This study aimed to test the taxonomic utility of the catarrhine supraorbital region using 3D geometric morphometrics, with the aim of establishing its potential use in elucidating the position of more debated hominin groups.

Materials and Methods

230 3D coordinates were used to record the supraorbital morphology of two datasets: one containing 460 non-hominin catarrhine primates from species and subspecies of Gorilla, Pan, Papio, and Macaca; and the other containing 55 Pleistocene hominins from Homo, Australopithecus, and Paranthropus. Principal Component Analyses in tangent, form, and allometry-free shape space were used to assess differentiation of taxa, with biological distinctiveness of taxa being established using step-wise discriminant analysis with subsampling.

Results

Results indicated that the recorded supraorbital morphology could be used to separate non-hominin catarrhine primate genera, species, and subspecies, although accuracy was found to decrease with decreasing Linnaean rank. In addition, analyses in tangent space were found to produce the highest accuracy when classifying primates of known taxonomy. Biological distinctiveness of the middle and later Homo species was comparable to or higher than that of the non-hominin primates, and relatively lower for the earlier groups of Homo.
Discussion

This study indicates that the supraorbital region preserves taxonomic information that can be used to delineate between closely-related groups, both within hominins and wider catarrhine primates. Therefore, this region may be used to provide insight when assessing the taxonomic affiliation of disputed hominin specimens.

Key terms

Supraorbital morphology
Biological distinctiveness
Taxonomy
Primates
Hominins

Introduction

Assessment of craniofacial morphology is a primary method in establishing the taxonomy of hominin fossils (Athreya, 2006, 2009; Cramon-Taubadel, 2013; Lieberman, 2000; Lieberman, 1995, 2011). Fossil species play a dual role in palaeontology: they are a basis for the study of evolutionary processes giving rise to current groups (along with extant species); and they allow us to record past levels of biodiversity, and link this to changing factors such as geographic expansion and climate change (Tattersall, 1986). As such, the ability to identify and delineate different taxonomic groups is an important aspect of palaeontology (Tattersall, 1986). Classification of fossil specimens is intrinsically linked to the available evidence (Stringer, Howell, & Melentis, 1979), however the fossil record only preserves small, incomplete samples of hominins from which to build our understanding (Simpson, 1961). In addition, the fossil record typically only preserves hard-tissue evidence, yet many taxonomic differences in extant animals are only apparent in behavioural or soft-tissue evidence (Simpson, 1961; Smith, 1994; Tattersall, 1986, 1992), making application of popular taxonomic criteria to the fossil record extremely difficult.

Palaeoanthropologists use morphology to differentiate between hominin groups (Kimbel, 1991; Smith, 1994; Tattersall, 2005; Wood, 2010), for instance through the application of a morphological species concept. Such a concept can be applied by comparing levels of within- and between-group variation in skeletal morphology of fossil specimens to that of individuals of known taxonomic classification. In palaeoanthropology, non-hominin primates, and especially the Catarrhini, are generally used as reference taxa. Researchers have proposed the use of multiple model taxa when attempting to address taxonomic questions (Harvati, Frost, & McNulty, 2004), partly due to the great ecological and biological diversity found in animals, and primates in particular (Ackermann, 2002; Baab, 2008; Jiménez-Arenas, Palmqvist, & Pérez-Claros, 2011; O'Higgins & Dryden, 1993; Schaefer, Mitteroecker, Gunz, Bernhard, & Bookstein, 2004; Wood, Li, & Willoughby, 1991).

The inclusion of non-human apes provides an opportunity to model taxonomic variation in groups with different levels of sexual dimorphism, which is relevant to palaeoanthropology as studies have indicated that some extinct hominins may have been more sexually dimorphic than recent *Homo sapiens* (Garvin et al., 2017; Lockwood, 1996, 1999; Plavcan, 2012; Richmond & Jungers, 1995; Royer, Lockwood, Scott, & Grine, 2009). Non-human apes share a close relationship to *Homo*, with the *Pan* and *Homo* clades diverging approximately 6-9 Mya (Dos Reis et al., 2018; Langergraber et al., 2012; Perelman et al., 2011; Schrago & Voloch, 2013; Wilkinson et al., 2011), and the divergence between *Gorilla* and the *Pan/Homo* clade being dated to between 6-19 Mya (Glazko & Nei, 2003; Langergraber et al., 2012).
Papionins, as members of Cercopithecoidea, are more distantly related to hominins. Nevertheless, numerous researchers have suggested that they are appropriate models for the study of our evolutionary past (Baab, 2008; Delson, 1978; DeVore, 1963; Frost, Marcus, Bookstein, Reddy, & Delson, 2003; Harvati et al., 2004; Jolly, 1970; Jolly, 2001; Zinner, Groeneveld, Keller, & Roos, 2009). Their suitability arises from many characteristics, including: the numerous homologous traits they share with hominins; their phylogenetic distance to our own group, which may highlight possible parallelisms in primate evolution; their increased range in comparison to non-human apes, both geographically and ecologically; the existence of multiple species which diverged at similar time-depths and in broadly analogous habitats to hominins; the occurrence of hybridisation across different taxonomic boundaries; and the occurrence of relatively great biodiversity and craniofacial variation in some groups (Ackermann & Bishop, 2010; Alberts & Altmann, 2001; Baab, 2008; Frost et al., 2003; Harvati et al., 2004; Jolly, 2001; Pan, Oxnard, & Milne, 2002; Pan & Oxnard, 2002, 2004; Zinner et al., 2009; Zinner, Wertheimer, Liedigk, Groeneveld, & Roos, 2013).

This paper aimed to test whether the morphology of the supraorbital region can be used to detect taxonomic boundaries in primates, particularly at the species and subspecies level. The supraorbital region is one of the best-preserved in key periods of the hominin fossil record, potentially due to the robusticity of this area. It has also been suggested to document a moderate phylogenetic signal (McNulty, 2005; Smith, 2009; Weidenreich, 1947), and displays established phenetic differences between primate taxa (Aiello & Dean, 1990; Hublin et al., 2017; Lahr & Wright, 1996; Lieberman, 2000; Lieberman, 2011; Russell, 1985; Schwartz & Tattersall, 2010; Smith & Ranyard, 1980), indicating its potential usefulness for assessing the taxonomy of extinct hominins. Reference non-hominin primates included members of *Gorilla, Pan, Papio*, and *Macaca*. Following a test of the taxonomic information content of the supraorbital region in extant non-hominin primates, the same methods were applied to a dataset of Pleistocene hominin fossils, to test whether supraorbital morphology could provide valid insights into the hominin fossil record and, ultimately, the taxonomy of more debated hominin groups.

**Materials and Methods**

**Sample**

Only adult specimens were included in this study. Adult status was assessed dentally, by the full eruption of the third molars (both maxillary and mandibular, if present), and cranially, by full fusion of the basioccipital-basisphenoidal synchondrosis (Wood et al., 1991). When assessment of the fusion of the basioccipital-basisphenoidal synchondrosis could not be conducted, dental maturity was used as
the sole criterion. Specimens showing evidence of pathology or trauma in the cranium were excluded. Specimens with detailed geographical locations were favoured, although some with unknown origin were included when available specimen numbers were low.

**Non-Hominin Primate Dataset**

This study used a dataset of non-hominin primates consisting of 460 adult specimens from 10 species within *Gorilla*, *Pan*, *Papio*, and *Macaca* (see table 1 and SI-1). Previous researchers and collectors did not always recognise current subspecific distinctions within the non-hominin apes, therefore geographical information was used to establish subspecies categories of *Pan* and *Gorilla* specimens, using data on current taxonomic distribution from the IUCN (2017). Due to the relatively recent taxonomic separation of *Papio cynocephalus* and *Papio kindae*, geographic data from the IUCN was used to inform classification, although this was not possible for all specimens. Sex information was taken from collection material, and the ratio of males to females across the sample was approximately equal (225 females, 226 males, 9 unknown). Sample sizes varied between groups due to unequal representation of the included taxa in the various collections used. A maximum of 50 individuals were selected from each taxon. All non-hominin primate data was taken from original specimens, either in the form of 3D laser scans collected with a NextEngine Desktop Laser Scanner, or surface models generated from available CT data using 3D Slicer (Fedorov et al., 2012; see SI-1 and SI-2 in Supplementary Information).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Abbr.</th>
<th>Count</th>
<th>%</th>
<th>Total</th>
</tr>
</thead>
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<td></td>
<td>Female</td>
<td>Male</td>
<td>Unknown</td>
</tr>
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<td>25</td>
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<td>9</td>
<td>9</td>
<td>50.0%</td>
</tr>
<tr>
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<td>18</td>
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<tr>
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<td>25</td>
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<td>11</td>
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<td>2</td>
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<td>13</td>
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<tr>
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<td>1</td>
<td>2</td>
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</table>

Table 1 - Summary of non-hominin primate dataset (n=460) by taxon and sex. Abbr. indicates group abbreviations. Data for sex was taken from museum records. *Some Macaca fuscata and Papio cynocephalus sensu lato specimens could not be assigned a subspecies classification.
A Pleistocene hominin dataset was also used in this study, and consisted of 55 specimens from *Paranthropus, Australopithecus*, and *Homo* (see table 2 and SI-1). Earlier *Homo* and Late *Australopithecus* specimens, from purported species such as *Homo rudolfensis* and *Homo habilis*, were included, along with a reconstruction of Dinaledi Hominin 1 (DH1; *Homo naledi*). This specimen has been dated to the Middle Pleistocene (Dirks et al., 2017; Hawks & Berger, 2016), although its morphology indicates a closer relationship to Early Pleistocene hominins (Berger et al., 2015; Laird et al., 2017; Schroeder et al., 2017). *Homo erectus (sensu lato)* specimens from three subgroups (*Homo georgicus, Homo ergaster*, and *Homo erectus sensu stricto*) were also included, allowing modeling of craniofacial variation in a widespread and generally well-accepted hominin species with a considerable life span (over 1.5 million years (Antón, 2003)). Middle Pleistocene hominins (MPH) were included, although, while these hominins have previously been classified as *Homo heidelbergensis sensu lato*, they have an unresolved taxonomy, possibly constituting multiple species (Buck & Stringer, 2014; Harvati, 2007; Hublin, 2013; Stringer, 2012). As such, they were included to avoid inflating the morphological distance between earlier and later *Homo* species, but were not considered as a taxon for the purposes of this study. Late Pleistocene fossils included both *Homo neanderthalensis* and *Homo sapiens*, providing a model of variation between two sister-species. Hominin data were taken from research-quality casts of specimens, although original data were available in a number of cases (see table 2), either from 3D laser scans of the original fossil, or from surface models generated from available CT data (see SI-1 and SI-2).

### Table 2 - Summary of Pleistocene hominin dataset (n=55), showing species classifications and subgroup where applicable. Abbr. indicates group abbreviations. *indicates specimens where surface models were collected from the original fossil. # indicates specimens where surface models were generated from available CT data. *Homo sapiens* were separated into two subgroups based on their morphology. Older specimens not showing the full suite of *Homo sapiens* craniofacial traits were classified within Early Modern Humans (EMH), while later specimens showing modern craniofacial traits were classified as Anatomically Modern Humans (AMH).

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Species</th>
<th>Abbr.</th>
<th>Subgroup</th>
<th>Abbr.</th>
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<td>Cro-Magnon II</td>
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Reconstruction

Given the nature of the fossil record, it is unsurprising that most fossil hominin specimens included in this study were not intact across the region of interest, and some specimens had suffered post-depositional distortion. While efforts were made to select only the most well-preserved extant non-hominin primate specimens, this was not possible for members of the less numerous taxa, and a number of extant non-hominin primates in the final sample had missing data. While the simplest way to deal with missing data is to remove the affected landmarks from the dataset, this is unrealistic in larger samples. The alternative is to reconstruct the missing data so that the incomplete specimens may still be included in the analysis (Gunz, 2005). Each specimen was assessed individually in order to apply the most appropriate method given the above considerations. Details of the reconstruction methods and reference specimens can be found in SI-3. Effects of reconstruction methods and reference specimens were assessed (SI-4). These were found to have a non-significant impact on intragroup variation.

Landmarking

Landmarking was conducted in Stratovan Checkpoint. 230 3D landmarks and surface semilandmarks were used in this study. These included nine landmarks placed around the orbital area, and a mesh of 221 points across the supraorbital region, consisting of 11 control landmarks and 210 automatically generated semilandmarks. Two additional landmark points (Auriculare) were used to guide placement of the mesh but were not included in the final configuration (see figure 1 and table 3).

![Figure 1 - Diagrams showing location of landmarks used in this study, from frontal and left lateral view. Landmarks are numbered as in table 3. Points shown in blue were control landmarks for the mesh of surface semilandmarks. Points shown in red were independent landmarks used to record the orbital morphology. Points shown in grey were not included in the final configuration](image-url)
The final configurations of 230 3D points were registered using Generalised Procrustes Analysis (GPA) with a partial Procrustes fit (Rohlf, 1999; Rohlf & Slice, 1990) using the gpagen function in Geomorph (Adams, Otárola-Castillo, & Paradis, 2013). Surface semilandmarks were slid to minimise bending energy during this process. This method is favourable over the minimisation of Procrustes distances when samples include multiple taxa with significantly different morphology, as in the present study, as it maintains geometric homology (Gunz & Mitteroecker, 2013). This process was repeated for both the non-hominin primate and hominin datasets, and was conducted in tangent space (a Euclidean approximation of Kendall’s shape space), form space (where the effect of scaling was not removed, by scaling the Procrustes shape coordinates by Centroid size (Dryden & Mardia, 1998)), and allometry-free shape space (where the residuals from a regression of size (lnCS) on the Procrustes coordinates were used, using the procD.lm and shape.resid functions in Geomorph). Results from the three shape spaces can be usefully compared to bring to light dissociation between form and shape variation within a sample, and to assess the effect of both isometry and allometry (Mitteroecker & Gunz, 2009; Mitteroecker, Gunz, Windhager, & Schaefer, 2013).

Procrustes shape coordinates resulting from the above GPA were put through Principal Component Analysis (PCA), to reduce the datasets into a few dimensions which summarised the key aspects of variation (Mitteroecker & Gunz, 2009; O’Higgins, 2000). This study used the first two principal
components for preliminary assessment and visualisation, while including the loadings along the principal components accounting for over 95% of total sample variance combined in subsequent analyses, to avoid misinterpretation of morphological variation. Mean shapes were produced for each taxon, using the Procrustes coordinates and the mshape function in Geomorph, and were visualised as 3D scatterplots in SPSS 25. Mean pair-wise Procrustes distances were calculated within and between taxa.

Step-wise, cross-validated discriminant analyses with subsampling were performed for both datasets, using the principal components that accounted for over 95% of total variance, to assess biological distinctiveness following the methods of Cardini et al. (2009). Specimens which were the only representative of their species were excluded (i.e. Homo naledi, Homo rudolfensis, Australopithecus africanus, and Paranthropus aethiopicus), along with Paranthropus boisei due to the lack of closely-related specimens, resulting in a hominin dataset of 48 specimens. Discriminant analyses were repeated using three classification systems: the first and second classified specimens into genus and species, respectively, and were applied to both the non-hominin primate and hominin datasets; the third classified the non-hominin primate dataset into subspecies where applicable. 1000 random subsamples were taken from each taxonomic group. For the non-hominin primate dataset, subsample size was set to n=16 for genus-, n=8 for species-, and n=4 for subspecies-level analyses. These values were chosen due to low sample sizes for some of the subspecific groups, and to reflect the hierarchical composition of each increasing taxonomic rank. For the hominin dataset, sample size was set to n=7 due to the number of Homo erectus sensu lato included, except for the MPH where n=4, and Homo habilis where n=2 due to lower sample sizes, resulting in a total subsample of 27 individuals for each repeat. Classification accuracy was taken to reflect biological distinctiveness for each taxonomic rank (Cardini & Elton, 2011; Cardini et al., 2009). MPH and Homo habilis were excluded from the final calculation of cross-group hominin species-level classification accuracy, due to the uncertainties around the former group's taxonomic status, and the small sample size of the latter.

Intraobserver Error

All landmarking was conducted by SW. 26 specimens (18 non-hominin primates and eight Pleistocene hominins) were used in the assessment of intraobserver error (see table S13). Landmarks defined above in table 3 were placed on these 26 specimens on four occasions. As this study focused on morphological differences between genera, species, and subspecies, this study followed the method of Lockwood, Lynch, and Kimbel (2002). The repeats for the intraobserver specimens were added to the non-hominin primate and hominin datasets, after which both datasets were put through a GPA. Procrustes distances (which should approximate Euclidean distances from principal components) for
intraobserver repeats were then compared to intra- and inter-genus, species, and subspecies Procrustes
distances using a one-way ANOVA with post-hoc Tukey HSD (Honestly Significant Difference) tests
in SPSS 25. Results showed that intraobserver error was significantly lower than intra- and
intertaxonomic distances for both datasets (see tables S14 and S15). It was therefore concluded that
any intraobserver error should not significantly affect the outcome of later taxonomic analyses.

Results

Non-Hominin Primates

Group Morphology

Differences between the non-hominin primate genera are shown in figure 2 (figures are scaled to unit
centroid size, and therefore show differences in shape, not overall form). In comparison to Pan,
Gorilla were found to have more laterally flaring supraorbital tori that were more anteriorly
projecting, and wider nasal columns, narrower frontal bones, and deeper supraorbital sulci relative to
overall size. The differences between Papio and Macaca appear to be less marked, reflected in the
lower pairwise Procrustes distances (0.117 compared to 0.155 for Gorilla-Pan comparisons; see table
S16). Members of Papio were found to have shorter orbits, thicker supraorbital trigones, and less
vertical frontal squamae in comparison to Macaca.

There were slight differences apparent between the Gorilla gorilla subspecies (mean pairwise PrD:
0.112), which were largely focused in the lateral and inferior aspects of the supraorbital tori (figure 3).
Slightly larger differences (mean pairwise PrD: 0.119) were apparent between the Gorilla beringei
subspecies, with Gorilla beringei beringei having more superiorly placed dacryon points, more
anteriorly projecting frontal squamae and supraorbital tori, and slightly narrower frontal squamae than
Gorilla beringei graueri. The differences between the Gorilla species were more marked (mean
pairwise PrD: 0.123), with Gorilla gorilla having anteroposteriorly thicker lateral aspects of their

Figure 2 - Mean shapes of specimens of non-hominin primate genera. a - Gorilla (black) superimposed with Pan (red and white); b - Papio
(black) superimposed with Macaca (red and white)
supraorbital tori, more anteriorly projecting supraorbital tori in the midsagittal region, and more superiorly placed orbital points than *Gorilla beringei*.

Figure 4 shows minimal differences (mean pairwise PrD: 0.090) between the subspecies of *Pan troglodytes*. *Pan troglodytes troglodytes* was found to have more anteroinferiorly placed inferior aspects of the supraorbital tori, deeper post-toral sulci, and more vertical frontal squamae than the average *Pan troglodytes schweinfurthii* configuration. *Pan troglodytes elliotti* had slightly more laterally expanded supraorbital trigones, less anteriorly placed supraorbital tori and frontal squamae, and more posteriorly placed orbits than *Pan troglodytes troglodytes*. *Pan troglodytes verus* had slightly more anteriorly projecting supraorbital tori, which were taller in the midsagittal region, and less vertical frontal squamae than *Pan troglodytes elliotti*. In terms of species-level differences within *Pan* (mean pairwise PrD: 0.096), *Pan troglodytes* had more projecting supraorbital tori on average, with laterally expanded supraorbital trigones, and more posteriorly placed lower orbital margins, while the uppermost part of the frontal squama of the average *Pan paniscus* configuration was more anteroinferiorly placed.
Comparisons between the average shapes of the Papio groups are shown in figure 5. The differences between *Papio anubis* and *Papio cynocephalus* were relatively small (mean pairwise PrD: 0.098), with the latter having slightly narrower supraorbital tori and more anteriorly placed frontal squamae in the medial region, while the lateral aspects were relatively more inferiorly placed. *Papio anubis* had more anteriorly protruding supraorbital tori in the glabella region in comparison to *Papio cynocephalus*. Differences between *Papio anubis* and *Papio kindae* were more apparent (mean pairwise PrD: 0.106), with the latter having taller, more anteriorly and laterally projecting frontal squamae, and the former having more inferiorly placed supraorbital margins and orbits. The differences between *Papio cynocephalus* and *Papio kindae* were less apparent (mean pairwise PrD: 0.094), although the latter again was found to have a more superiorly and laterally projecting frontal squamae on average.

Figure 5 - Mean shapes of specimens of *Papio* taxa: a - *Papio anubis* (black) superimposed with *Papio cynocephalus* (sensu stricto) (red and white); b - *Papio cynocephalus* (sensu stricto) (black) superimposed with *Papio kindae* (red and white)

Figure 6 shows the differences between the *Macaca* taxa. There were slight differences between the *Macaca* species (mean pairwise PrD: 0.099), which were largely found in the supraorbital trigones and superior frontal squama region. *Macaca fascicularis* was found to have the most anteriorly projecting supraorbital tori in the medial region, while the lateral aspects of the supraorbital tori in *Macaca fuscata* were more projecting. The orbits of *Macaca mulatta* showed a higher degree of orbital frontation than in the other two species, and the frontal squamae in this group were more vertically aligned. Differences between the *Macaca fuscata* subspecies were relatively low (mean pairwise PrD: 0.087). *Macaca fuscata yakui* specimens had slightly more laterally thickened supraorbital trigones and mediolaterally narrower frontal squamae, which were more vertically aligned than seen in *Macaca fuscata fuscata*.
Principal Component Analysis

Only the results of the tangent space analyses are presented here as they provide the most reliable levels of taxonomic differentiation (see Discriminant Analysis). The results of the form and allometry-free shape space analyses are available in Supplementary Information (SI-6).

Principal Component Analysis on the non-hominin primate dataset resulted in 46 principal components (PCs), with the first 32 accounting for >95% of the total sample variation combined, and the first 13 accounting for >1% of variation individually. The first PC accounted for 40.4% of sample variation. More negative values on PC1 were associated with less laterally flaring and anteriorly projecting supraorbital tori, a minimal postorbital sulcus, a higher degree of orbital frontation, a narrower nasal column, and a smaller degree of postorbital constriction (figure 7). The second PC accounted for 14.9% of sample variation. Negative values on this component were associated with superoinferiorly thicker supraorbital tori, a lack of a post-toral sulcus, and a particularly narrow nasal column.

The non-hominin primates were spread along two parallel trajectories in this plot, with one comprising the non-human apes, which had lower values on PC2, and the other the papionins. At genus level, Gorilla and Pan were separated along both PC1 and PC2, although with some overlap, with Gorilla having lower-values for PC1 and higher values for PC2 (figure S3). Papio and Macaca overlapped to a larger extent, with Papio having slightly lower values along PC1 and higher values on PC2.

Figure 6 - Mean shapes of specimens of Macaca taxa: a - Macaca fascicularis (black) superimposed with Macaca fuscata (red and white); b - Macaca fascicularis (black) superimposed with Macaca mulatta (red and white); c - Macaca fuscata fuscata (black) superimposed with Macaca fuscata yakui (red and white)
Figure 7 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 55.4% of variation, for PCA in tangent space using dataset of 460 non-hominin primates. Specimens are identified by symbols shown in legend. See table 1 for list of abbreviations. Convex hulls are shown and correspond to species groups. Shape changes are shown for minimum, median, and maximum sample values for both axes, in frontal and left lateral view.
At species level, *Gorilla beringei* specimens were found to have lower values along PC2 combined with slightly higher values on PC1 in comparison to *Gorilla gorilla* (figure S4). *Pan paniscus* was differentiated from *Pan troglodytes* by slightly higher values along PC1 and lower values on PC2. *Papio cynocephalus* was mostly encompassed by *Papio anubis*, while *Papio kindae* was somewhat differentiated by higher values for PC1. The three *Macaca* species showed considerable overlap for values on both PC1 and PC2.

In terms of subspecific differences, *Gorilla beringei beringei* had higher values along PC2, while *Gorilla beringei graueri* had lower values along this component, and a wider range of values along PC1 (figure S5). *Gorilla gorilla diehli* was almost fully encompassed by *Gorilla gorilla gorilla*, although they sat towards the lower end of this taxon’s range for PC2. *Pan troglodytes verus* and *Pan troglodytes ellioti* were almost fully encompassed by the *Pan troglodytes schweinfurthii* specimens, while *Pan troglodytes troglodytes* was somewhat differentiated by lower values along PC1 and higher values along PC2. *Macaca fuscata yakui* was found to have slightly lower values along PC1 than *Macaca fuscata fuscata*.

**Discriminant Analysis**

Results of the discriminant analyses in the three shape spaces are shown in table 4. Primate taxa were found to have the highest biological distinctiveness using principal components from analyses in tangent space at the subspecies and species levels, and form space at the genus level (although biological distinctiveness was similar when using PCs from tangent space analysis at the genus level). Results of the discriminant analyses using principal components from PCA in form and allometry-free shape space can be found in SI-6. Using results from the PCA in tangent space, classification accuracy was highest for the genus-level analysis (97.5%), followed by the species-level analysis (75.4%), and the subspecies-level analysis (45.2%). Genus classification accuracy, taken to reflect biological distinctiveness, ranged from 96.6% in *Papio* to 98.9% in *Pan* (table 5). The range of biological distinctiveness for the species groups was broader; from 56.4% in *Papio cynocephalus* to 83.9% in *Gorilla gorilla* (table 6). Biological distinctiveness for the included subspecies showed a similarly broad range, with *Pan troglodytes ellioti* having the lowest classification accuracy at 30.7%, and *Gorilla beringei graueri* the highest at 63.3% (table 7).
Table 4 - Comparison of results of step-wise cross-validated discriminant analysis with subsampling using principal components that accounted for over 95% of total sample variance from PCA in tangent space, form space, and allometry-free shape space with dataset of 460 non-hominin primates. Percentage classification accuracy across the 1000 subsamples (n=16, for Genus; n=8 for Species; n=4 for Subspecies) is shown by taxon. See table 1 for list of abbreviations. See tables in SI-6 for detailed results for form and allometry-free shape space analysis.

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Table 5 - Results of step-wise cross-validated discriminant analysis with subsampling using first 32 principal components that accounted for over 95% of total sample variance from PCA in tangent space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples (n=16) is shown by taxon. Specimens were classified by genus, and overall genus classification accuracy was 97.5%.

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Table 6 - Results of step-wise cross-validated discriminant analysis with subsampling using first 32 principal components that accounted for over 95% of total sample variance from PCA in tangent space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples (n=16) is shown by taxon. Specimens were classified into species groups, and overall species classification accuracy was 75.4%. See table 1 for list of abbreviations. See tables in SI-6 for detailed results for form and allometry-free shape space analysis.

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Table 7 - Results of step-wise cross-validated discriminant analysis with subsampling using first 32 principal components that accounted for over 95% of total sample variance from PCA in tangent space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples (n=4) is shown by taxon. Specimens were classified into subspecies groups where possible, and overall subspecies accuracy was 45.2%. See table 1 for list of abbreviations.

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Hominins

Group Morphology

Large differences, reflected by a mean pairwise PrD of 0.127 (see table S23), were found between the average Homo sapiens and Homo neanderthalensis shapes (figure 8). Homo sapiens had taller frontal squamae, which were more vertically aligned, their orbits were more anteriorly placed, and their supraorbital tori were narrower mediolaterally. In addition, Homo sapiens had more superiorly placed nasion landmarks and thinner supraorbital trigones in comparison to Homo neanderthalensis. The shape differences were even larger between Homo erectus sensu lato and Homo sapiens (mean pairwise PrD: 0.172), with the latter having parallel frontal squamae and lateral aspects of the supraorbital tori, thin supraorbital trigones, high, vertical frontal squamae, more superiorly located nasion points, and less protruding supraorbital tori. The differences between the mean Homo neanderthalensis and Homo erectus sensu lato configurations were less visible (mean pairwise PrD: 0.117), with Homo neanderthalensis having slightly taller and more vertical frontal squamae, less anteriorly projecting supraorbital tori, and slightly thinner, less laterally flaring supraorbital trigones.

Comparisons between early Homo and related hominins are shown in figure 9. The Homo rudolfensis specimen (KNM-ER 1470) showed a more superoinferiorly bulging frontal squama in comparison to the Homo habilis specimens (mean pairwise PrD of 0.100), with more inferiorly placed orbits, and a more superiorly located nasion. Homo naledi showed closer affinities to early Homo in the PCA plots (and especially to KNM-ER 3733 and OH 24), and lower mean pairwise PrD to Homo erectus sensu lato and Homo rudolfensis (0.118 and 0.119, respectively) in particular despite its Middle Pleistocene age, so it is also considered here. DH1 had a slightly taller supraorbital torus than the mean Homo
Homo habilis shape, with much more angled orbits which were also wider, and a shorter frontal squama. Homo habilis had a more angled frontal squama in this orientation (i.e. a narrower angle between mid-frontotemporale-nasion-orbitale) than that found in the Australopithecus africanus specimen (Sts 5; mean pairwise PrD of 0.114), as well as more superiorly placed orbits and inferior supraorbital torus, and a mediolaterally wider frontal squama.

There are fairly large visible shape differences between Sts 5 and the Paranthropus aethiopicus specimen (KNM-WT 17000; figure 10), reflected in the mean pairwise PrD of 0.133. For instance, KNM-WT 17000 had thick, laterally flaring, and posteriorly rotated supraorbital trigones, and a lower frontal squama than Sts 5. Differences between the Paranthropus species were less pronounced (mean pairwise PrD: 0.116): Paranthropus boisei was found to have less posteriorly rotated supraorbital trigones, slightly more vertical frontal squamae, slightly wider orbits and nasal columns, and slightly more anteriorly projecting supraorbital tori than seen in Paranthropus aethiopicus. Caution must be taken when interpreting these results, due to the low sample sizes available for the earlier hominins.
Principal Component Analysis

PCA in tangent space resulted in 54 principal components, with the first 17 accounting for over 95% of the total sample variance combined, and the first 10 accounting for >1% of variance individually. Figure 1 shows a plot of specimens by PC1 and PC2, accounting for 55.5% and 11.1% of variance, respectively. PC1 broadly corresponded with robusticity of the supraorbital region, with the more robust specimens (e.g. *Paranthropus*) having more negative values along this axis, and the more gracile *Homo sapiens* having the most positive values. Positive values corresponded to taller and more curved frontal squamae which occupied a larger area of the recorded morphology, minimal expression of the supraorbital tori in all dimensions, an absence of a supraorbital sulcus, a relatively superiorly positioned nasion, and a higher degree of orbital frontation. PC2 separated the early *Homo sapiens*, *Homo neanderthalensis*, MPH, and *Homo erectus sensu lato*, which had lower values along this axis, from the later *Homo sapiens* and earlier hominins. Specimens with higher values were associated with more laterally flaring supraorbital trigones, less projecting supraorbital tori with minimal post-toral sulci, more vertical frontal squamae, lower positions of dacyron points, and more vertically oriented orbits. *Homo sapiens* had the highest values along PC1 and PC2, with some earlier members (Omo 1, Jebel Irhoud 1, and Skhūl V) falling within the *Homo neanderthalensis* convex hull due to their lower values on PC1. The *Homo erectus sensu lato* specimens were separated from *Homo neanderthalensis* due to their relatively lower values along PC1. The MPH largely overlapped with the *Homo erectus sensu lato*, although they fell more towards the *Homo erectus sensu stricto* end of the convex hull, due to their higher values along PC1.
Figure 11 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 66.3% of variation, for PCA in tangent space using sample of 55 Pleistocene hominin specimens. Specimens are identified by symbols shown in legend. See table 2 for list of abbreviations. Convex hulls are shown and correspond to species groups: black - Homo sapiens; green - Homo neanderthalensis; blue - Homo erectus sensu lato; purple - Paranthropus boisei. Shape changes are shown for minimum, median, and maximum sample values for both axes, in frontal and left lateral view.
**Discriminant Analysis**

The results of the hominin tangent space discriminant analysis are shown in table 8. Species classification accuracy was 87.3% across the 1000 subsamples. Classification accuracy was highest for *Homo neanderthalensis* (92.2%) and *Homo sapiens* (87.6%), followed by *Homo erectus sensu lato* (82.3%). 20 of the 22 *Homo sapiens* were classified correctly in the majority of repeats (table S24), although Skhūl V was only correctly classified in 47.2% of subsamples in which it was randomly selected (and was classified as *Homo neanderthalensis* in 39.3% of cases). Jebel Irhoud 1 and Omo 1 were most frequently classified as *Homo neanderthalensis* (in 73.6% and 48.7% of cases, respectively). All of the *Homo neanderthalensis* and *Homo erectus sensu lato* were most frequently correctly classified when included in subsample repeats. OH 24 was classified as *Homo habilis* in 49.0% of subsamples, while KNM-ER 1813 was classified as *Homo erectus sensu lato* in 64.1% of cases, reflecting its placement in the PC plot.

![Table 8](image)

**Discussion**

A proper understanding of biological variation is fundamental to the study of evolutionary processes, however the accurate documentation of phenotypic variation in the fossil record is particularly challenging due to its fragmentary nature. Studies have found that different elements of the primate craniofacial complex have varying levels of effectiveness in differentiating groups at different taxonomic levels (Bjarnason, Chamberlain, & Lockwood, 2011; Bjarnason, Soligo, & Elton, 2015, 2017; Cardini & Elton, 2008a; Lockwood, Kimbel, & Lynch, 2004; von Cramon-Taubadel & Smith, 2012). As such, it is important to establish the extent to which aspects of the craniofacial morphology that are relatively well documented in the fossil record reflect taxonomic differentiation in extant primates. The supraorbital torus is one such region, being particularly well-preserved in the hominin fossil record, potentially due to the robusticity of this cranial superstructure.
This study identified notable differences between accepted non-hominin primate taxa in the recorded morphology, indicating that the primate supraorbital region can be used in taxonomic differentiation. Larger differences were noted at the genus level, although this varied between families and analyses; *Pan* and *Gorilla* were more separated in the principal component plots than *Papio* and *Macaca*, although all genera showed relatively high biological distinctiveness (97.5% in tangent space). Differences between species were less substantial (75.4% in tangent space), especially in the case of *Papio cynocephalus*, *Papio anubis*, and *Macaca fascicularis*. Differences between non-hominin primate subspecies were even more subtle, with several subspecies groups being fully encompassed within other closely-related subspecies in terms of key principal components, and with subspecies groups having lower biological distinctiveness (45.2% in tangent space).

This pattern of increasing biological distinctiveness with increasing taxonomic rank is not unexpected. Subspecies are considered by some to be incipient species, populations which have begun to diverge from their conspecifics but which have not achieved full speciation and are genetically reticulate (Boggs, 2001; Groves, 2004; Mayr, 1982; Simpson, 1961). As such, the morphological divergence between subspecies groups is predicted to be lower than that between fully diverged species. Species, in contrast, are considered by many researchers to reflect biological entities (Balakrishnan, 2005; Cracraft, 1983; Eldredge & Cracraft, 1980; Ghiselin, 1974; Tattersall, 1992), and should therefore be expected to have more distinct boundaries than those between subspecies (Simpson, 1961). Genera are classified among the higher taxa, and in turn are expected to show a greater degree of biological divergence (Tattersall, 2017).

It is important to put the biological distinctiveness of the catarrhine supraorbital region into its wider context. Genus-level results were very similar to those found for hairy armadillos (weighted average of 98.5% classification accuracy; Abba et al., 2015), although no comparable studies could be found within the primates. The values for species-level analyses were comparable to those found for marmots (87.4%; Cardini et al., 2009) and *Cercopithecus* (88.3%; Cardini & Elton, 2008b), at least for the non-hominin apes, but lower than those for red colobus monkeys (97.0%; Cardini & Elton, 2011) and hairy armadillos (94.1%; Abba et al., 2015). For subspecies-level analyses, the values of the present study lay between those for marmots (36.6%; Cardini et al., 2009) and red colobus monkeys (80.1%; Cardini & Elton, 2011). Nevertheless, comparisons to other studies are imperfect as some used anatomical landmarks across the cranium and mandible (Cardini & Elton, 2008b, 2011), rather than focusing on specific areas of the craniofacial complex. As studies indicate that different craniofacial regions may differentially preserve phylogenetic histories (Bjarnason et al., 2011; Bjarnason et al., 2015; von Cramon-Taubadel, 2009), it could be predicted that they may also preserve different taxonomic signals. Future research could investigate the taxonomic utility of other well-
represented regions, such as the temporal bone and basicranium, to further contextualise the results of the current study.

As shown by the group morphologies, differences between non-hominin primate and hominin taxa in supraorbital morphology are frequently subtle, especially in the case of the lower taxa (i.e. species and subspecies). Despite this, the above discriminant analyses resulted in relatively high classification accuracy in some groups. This contrasting result highlights the efficacy of geometric methods which allow quantitative analysis of morphology, especially when differences between taxa may be difficult to detect through qualitative assessment of craniofacial morphology. Regardless of whether primate subspecies are sufficiently biological distinct, at least in the supraorbital region, and the ability of geometric morphometric methods to distinguish between these groups, researchers have suggested that the likelihood of having sufficient samples of primate fossil specimens to identify subspecific distinctions is low (Kimbel, 1991; Simpson, 1943, 1961; Tattersall, 1986, 1992).

Analyses were performed in tangent, form (with size added as a variable), and allometry-free (with the effect of allometric scaling removed) shape space. Taxonomic differentiation was found to be highest in tangent space, as shown by the higher rates of biological distinctiveness of known taxa, indicating that tangent space may be more useful for primate taxonomic differentiation when considering the supraorbital region. This was somewhat unexpected, as form space has been hypothesised to be preferable when size is integral to the morphology under assessment, including classification studies such as this one which include organisms that vary in both size and shape (Mitteroecker and Gunz, 2009; Mitteroecker et al., 2013). The results of the present study did note comparable levels of taxonomic differentiation between form and tangent space analysis at the genus level, which could support this argument as size differences are less pronounced within the genera studied. However, several of the taxa analysed here are characterised by pronounced levels of sexual dimorphism and, hence, intraspecific size variation, which is likely to blur taxonomic distinctiveness based on size. As such, future work should explore the possibility that form space might more accurately distinguish between taxa that lack pronounced levels of sexual dimorphism.

The *Papio kindae* specimens were found to be more clearly separated from *Papio anubis* than *Papio cynocephalus* in principal component plots, and had higher biological distinctiveness. This may be partially affected by the relatively small size of the *Papio cynocephalus* sample, as research indicates that *Papio kindae* and *Papio cynocephalus* are more closely related to each other than they are to *Papio anubis* (Jolly, Burrell, Phillips-Conroy, Bergey, & Rogers, 2011; Zinner et al., 2009; Zinner et al., 2013), although this does not adequately explain the difference in biological distinctiveness as subsampling would have mitigated against differences in sample size. An alternative hypothesis is that this distinction is affected by the smaller physical size of *Papio kindae*, which are suggested to be
paedomorphic in comparison to *Papio cynocephalus* (Dunn, Cardini, & Elton, 2013; Frost et al., 2003; Singleton, Seitelman, Krescoh, & Frost, 2017). Tangent space, while unaffected by isometric scaling, can be influenced by allometry. *Papio kindae* specimens were distinguished in terms of the key components of morphology in both form and allometry-free shape space (see Supplementary Information), indicating that their biological distinctiveness in the supraorbital region may be unrelated to any allometric scaling.

*Macaca fuscata yakui* was found to have higher biological distinctiveness than *Macaca fuscata fuscata* overall (although not in form space), which is contrary to the fact that genetic data indicate low differentiation of this group relative to other populations of *Macaca fuscata* not currently given subspecific status (Marmi, Bertranpetit, Terradas, Takenaka, & Domingo-Roura, 2004). Biological distinctiveness was higher for the *Macaca fuscata* subspecies in form space, unlike all other non-hominin primate subspecies studied here. Research has shown that *Macaca fuscata yakui* is the smaller of the two subspecies (Napier, 1981; Yano, Egi, Takano, & Ogihara, 2018), indicating that further research into allometric differences between these taxa is required.

Of the *Pan troglodytes* subspecies, *Pan troglodytes troglodytes* was found to have the highest biological distinctiveness in supraorbital morphology, while *Pan troglodytes ellioti* had the lowest. Genetic analysis has indicated that the first phylogenetic split within *Pan troglodytes* was between *Pan troglodytes schweinfurthii* and *Pan troglodytes troglodytes* on the one hand, and *Pan troglodytes ellioti* and *Pan troglodytes verus* on the other (Prado-Martinez et al., 2013). This phylogenetic pattern was not reflected in the supraorbital morphology, with the largest distinction being found between *Pan troglodytes schweinfurthii* and *Pan troglodytes troglodytes*. These subspecies appear to have diverged later on than *Pan troglodytes ellioti* and *Pan troglodytes verus*, although there is more substantial genetic evidence to support their subspecific status, while the separation of *Pan troglodytes ellioti* is more debated (de Manuel et al., 2016; Lobon et al., 2016; Stone et al., 2010).

The largest differences between closely related species and subspecies, as measured by pairwise-Procrustes distances, were found within *Gorilla*. While genetic evidence indicates considerable differentiation between the two *Gorilla* species, it also shows that hybridisation between *Gorilla* taxa occurred until fairly recently (Ackermann & Bishop, 2010; Thalmann, Fischer, Lankester, Pääbo, & Vigilant, 2007; Thalmann et al., 2011). Lower levels of biological distinctiveness were found for *Gorilla beringei beringei* in comparison to *Gorilla beringei graueri* in all shape space analyses. While both subspecies are known to have complicated phylogenetic histories, including periods of hybridisation, previous analysis indicates that only the latter group show evidence of this in their craniodental morphology (Ackermann & Bishop, 2010). In addition, *Gorilla beringei beringei* have relatively small habitats with few remaining individuals, and show strong evidence of inbreeding
(Fossey, 1983; Xue et al., 2015), which would be expected to lead to higher homogeneity in craniofacial morphology. Further analysis is required to confirm whether this pattern of inter-specific biological distinctiveness is consistent across the craniofacial complex.

The biological distinctiveness of the supraorbital morphology of *Homo sapiens* and *Homo neanderthalensis* was higher than that of all of the non-hominin primate species, and the value for *Homo erectus sensu lato* was comparable to the highest of those for the non-hominin primate species. This is somewhat unexpected, as the inclusion of individuals from across the lifespan and geographical range of a species may blur the boundaries between species, although not in all cases (Baab, 2016). In addition, the inclusion of the Middle Pleistocene hominins, which may include transitional and early members of these middle and later *Homo* species, could have been predicted to reduce the biological distinctiveness of these taxa. The relatively high biological distinctiveness for *Homo erectus sensu lato* is also surprising due to the considerably wider time range from which these specimens were sampled, and the ongoing taxonomic debate around this group (Antón, 2003; Baab, 2008; Baab, 2016; Bilsborough, 2005; Etler, 2004; Lordkipanidze et al., 2013; Rightmire, Lordkipanidze, & Vekua, 2006). The effect of low sample sizes for early *Homo* limits interpretation of the frequent misclassification of the KNM-ER 1813 specimen.

The results of the present study would indicate that the hominin supraorbital region is particularly taxonomically informative relative to the wider catarrhine primates. This could be in part due to the higher variability, particularly in the supraorbital torus, in hominins, as well as the later changes in the frontal squama seen in modern *Homo sapiens*. The supraorbital torus has been acquired, lost, and modified in various populations of hominins (Lahr & Wright, 1996), and has been shown to document distinctive morphologies between species (Athreya, 2006, 2012; Fiscella & Smith, 2006; Gonzalez, Perez, & Bernal, 2010; Lahr & Wright, 1996; Lieberman, 2000; Moss & Young, 1960; Russell, 1985; Schwartz & Tattersall, 2010; Smith & Ranyard, 1980; Weidenreich, 1947). At present, few studies have assessed the evolutionary significance of the hominin brow ridge. The fossils included in the present study indicate that there may have been a transition from a more general hominid form (protruding, bar-like supraorbital tori that are short superoinferiorly) in earlier hominins such as *Australopithecus*, to a more variable form in *Homo* (e.g. the swollen, rounded tori in *Homo neanderthalensis* and MPH), potentially linked to the latter groups increased orthognathy, relatively high levels of craniofacial robusticity, and associated large cranial superstructures (Gonzalez et al., 2010; Lieberman, 2011; Weidenreich, 1941).

This study supported the suggestion of previous studies that *Homo sapiens* are particularly distinct in their frontal bone morphology (Athreya, 2009; Bruner, Athreya, de la Cuétara, & Marks, 2013; Godinho, Spikins, & O’Higgins, 2018; Kurten, 1979; Lieberman, 2000; Russell, 1985; Schwartz &
Tattersall, 2010; Smith & Ranyard, 1980). This distinction appears to be due to the minimally expressed supraorbital torus in our species, along with our tall, bulging frontal squamae. Nevertheless, earlier members of *Homo sapiens* were found to overlap with *Homo neanderthalensis*, and Jebel Irhoud 1 and Omo 1 were more frequently misclassified as *Homo neanderthalensis* in the discriminant analysis. This is likely due to the presence of more plesiomorphic browridges in earlier *Homo sapiens* (Hublin et al., 2017; Lahr & Wright, 1996; Lieberman, 2000; Russell, 1985; Tattersall & Schwartz, 2008), although the possibility of interbreeding has also been raised in the case of the Jebel Irhoud assemblage (Mounier & Mirazón Lahr, 2019).

*Homo neanderthalensis* has been described as one of the most clearly defined and delineated extinct hominin species (Tattersall, 1992; Tattersall & Schwartz, 2006; White, Gowlett, & Grove, 2014), and the results of this study would seem to support this conclusion. While DNA analyses have shown that *Homo neanderthalensis* and *Homo sapiens* interbred on a number of occasions (Green et al., 2010; Prüfer et al., 2014; Racimo, Sankararaman, Nielsen, & Huerta-Sanchez, 2015; Sankararaman et al., 2014; Sankararaman, Patterson, Li, Pääbo, & Reich, 2012), this interbreeding does not seem to have led to increased similarity in the supraorbital morphology of these taxa, at least in the specimens studied here. Indeed, the results of the current study would support the specific status of *Homo neanderthalensis* (White et al., 2014). This group had a biological distinctiveness comparable to, and even somewhat higher than, that of *Homo sapiens*, along with a higher proportion of the sample being most frequently correctly classified across the subsamples. These groups were also clearly separated in terms of key morphology.

**Conclusion**

This study found that supraorbital morphology can be used to differentiate between closely-related, extant non-hominin primate genera, species, and subspecies, although with a reduced accuracy in the latter taxon. Hypothesised late Middle-to-Late Pleistocene hominin species were found to have relatively higher biological distinctiveness in this region than the extant catarrhine non-hominin primate species, while the *Homo erectus sensu lato* specimens had biological distinctiveness which was comparable to the higher range of the non-hominin catarrhine species. Overall, the results support the use of supraorbital morphology to assess the taxonomic affiliation of fossil hominins and catarrhines of unknown or debated taxonomy, and suggest that hominin taxa may be more readily distinguished by their morphology in this region. Future studies should explore the different aspects of the supraorbital morphology recorded here to determine which are the most useful for taxonomic differentiation, and compare the efficacy of supraorbital morphology to that of other regions suggested to reflect phylogeny, such as the temporal bone and basicranium.
Acknowledgements

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.
References


Sankararaman, S., Patterson, N., Li, H., Pääbo, S., & Reich, D. (2012). The date of interbreeding between Neandertals and Modern humans. *PLOS Genetics, 8*(10), e1002947. doi:10.1371/journal.pgen.1002947


# Supplementary Information

## SI-1: Details of Specimens

### Non-Hominin Primate Specimens

Table S1 - Details of non-hominin primate specimens, showing taxonomic classification, institution, sex, type of data used, and whether the specimen required reconstruction for the purposes of this study.

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| Merfield 372 | Gorilla gorilla gorilla | Powell Cotton Museum | M | Cranium | N |
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| USNM 176209 | Gorilla gorilla gorilla | Smithsonian | M | Cranium | Y |
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## Hominin Specimens

Table S2 - Details of hominin specimens, showing taxonomic classification, subgroup, institution, type of data used, and whether the specimen required reconstruction for the purposes of this study

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<td>MPH NHM (Pal) Cast Y</td>
<td>MPH BioAnth (UCL) Cast Y</td>
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<td>Sangiran 17</td>
<td>Homo erectus (sensu stricto) HEss</td>
<td>Homo erectus (sensu stricto) NHM (Pal) Cast Y</td>
<td>Homo erectus (sensu stricto) NHM (Pal) Cast Y</td>
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<td>Homo ergaster HEss</td>
<td>Homo ergaster HEss</td>
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<td>KNM-ER 3773</td>
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<td>Homo ergaster HEr</td>
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<td>Homo georgicus HG</td>
<td>Homo georgicus HG</td>
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<td></td>
<td>Dmanisi D4500</td>
<td>Homo naledi</td>
<td>Homo naledi</td>
<td>Homo naledi</td>
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<td></td>
<td>Dmanisi D2282</td>
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<td>Homo rudolfensis</td>
<td>Homo rudolfensis</td>
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<td></td>
<td>Sts 5</td>
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<td>Paranthropus boisei</td>
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</table>
SI-2: Laser and CT Scan Parameters

Details of the scanning parameters for the hominin specimens for which CT data were acquired are shown in table S3. Unfortunately, this information was not available for the non-hominin primate specimens.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>CT Scanner</th>
<th>Slice thickness (mm)</th>
<th>Voxel size (mm)</th>
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<td>Phillips Mx8000IDT</td>
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<td>Skhul V</td>
<td>Siemens multidetector scanner</td>
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<td>Spy 1</td>
<td>Siemens Somatom 64</td>
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<td>0.465 x 0.465</td>
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<td>Sts 5</td>
<td>Siemens Somatom Plus 4</td>
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<td>0.390625 x 0.390625</td>
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A set protocol was used to collect non-CT data (from both casts and crania) using the NextEngine 3D laser scanner. Crania were placed on the NextEngine rotating platform which was positioned at a distance of 17 inches from the scanner itself, to maximise performance (see NextEngine user manual). The software was set to collect surface scans at 10,000 points/inch² to achieve sufficiently detailed meshes at a reasonable speed, given the size of the required sample. Different combinations of scans were collected based on the type of specimen being examined. These were then aligned using the Align function in ScanStudio.
SI-3: Details of Reconstruction Methods

This study used a combination of reconstruction methods, with each specimen being assessed individually in order to apply the most appropriate method.

Geometric Reconstruction

When only a few points required reconstruction, geometric reconstruction methods were applied using the estimate.missing function in the Geomorph package in R, using reference samples that were matched by sex and species for non-hominin primates, and for time period and taxon for the hominins (Adams, Otárola-Castillo, & Paradis, 2013; see table S4). 49 of the specimens (45 of the non-hominin primates and four of the hominins) required this type of reconstruction (table S5).

<table>
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<th>Taxon</th>
<th>Sex</th>
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<td>Gorilla gorilla gorilla</td>
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<td>15</td>
<td>Pan troglodytes schweinfurthii</td>
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<td>Pan troglodytes troglodytes</td>
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Table S5 - Details of 49 specimens for which points were reconstructed using geometric method. 
# indicates the number of points that needed to be reconstructed for each specimen

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Manual Virtual Reconstruction

A peculiarity of the process of generating 3D models from CT data meant that some automatic semilandmarks were placed on endocranial surfaces in the Checkpoint Stratovan software. 3D models generated from CT data, including all of the specimens from the Smithsonian collection, were therefore put through the Mesh Doctor function in Geomagic (uk.3dsystems.com). This automatically detects any errors in the polygon mesh and was used to fill holes, remove non-manifold edges, and smooth the mesh, which reduced the number of semilandmarks that fell through the ectocranial surface of the frontal bone during the landmarking process. The remaining misplaced semilandmarks were reconstructed manually in the Checkpoint software by using the surrounding points and the grid template to place single landmarks in the appropriate location. The exported landmark file was then amended, with the affected semilandmarks being replaced with the reconstructed coordinates. The process of sliding removed any effects this reconstruction method may have had on the homology of the semilandmarks (Gunz & Mitteroecker, 2013; Mitteroecker & Gunz, 2009). A total of 59 specimens (52 non-hominin primates and seven hominins) required this type of reconstruction (Table S6).

Table S6 - Details of 59 specimens for which points were reconstructed using manual virtual reconstruction. # indicates the number of points that were reconstructed for each specimen.

<table>
<thead>
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<th>Specimen</th>
<th>#</th>
<th>Group</th>
<th>Sex</th>
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</tr>
<tr>
<td>KNM-ER 1813</td>
<td>12</td>
<td>Homo habilis</td>
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<tr>
<td>Sts 5</td>
<td>8</td>
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</table>

**Reconstruction by Mirroring Across an Empirical Midplane**

The method of mirroring landmarks across an empirical midplane, estimated with orthogonal regression, was applied to specimens which were missing one of a pair of bilateral single landmarks. This method was used on six specimens (five non-hominin primates and one hominin; Table S7). The midplane was estimated by placing a curve of semilandmarks using three control landmarks: nasion, glabella, and post-toral sulcus. These points were used to generate a plane in Checkpoint software, and were manipulated until this plane estimated the midsagittal plane. The process of orthogonal regression was performed in R and Microsoft Excel.
Specimens with larger areas of damage or distortion were reconstructed by digital reconstruction methods. 27 of the hominin specimens (Table S8) required digital reconstruction, either due to their fragmentary nature or because of taphonomic distortion. Fossil reference specimens were chosen based on species, geographic region, time period, and overall similarity of morphology, which was visually assessed. In cases where areas were missing on only one side of the cranium, a reflection of the specimen was also used as a reference for digital reconstruction. Homologous, standard craniofacial landmarks were placed on the target and reference specimen crania, after which one of two methods were used. In the first, the reference and target surface models were aligned using a Generalised Procrustes Analysis in Evan Toolbox (Phillips, O'Higgins, & Bookstein, 2010). In the second, the reference surface model was warped onto the target specimen in Evan Toolbox using the homologous landmarks and a mesh of semilandmarks covering the frontal bone. In both cases, the resulting reference and target surfaces were then exported and loaded into CloudCompare (version 2; www.cloudcompare.org). Distorted and damaged areas were removed on the target specimen, and superfluous areas were removed on the reference specimen. The alignment of the two surface models was refined using manual manipulation. The surface models were then exported and merged in Geomagic, and the Mesh Doctor function was used to correct for any defects in the merged surface model. Finally, the reconstructed model was scaled back to its original size in Meshlab in an iterative process where distances between two homologous points were measured on the original and reconstruction, and the reconstruction was scaled until the distances were approximately equal (to 0.01mm). Details of reconstruction methods and points affected can be found below.
Table S8 - Details of 27 fossil specimens which were digitally reconstructed, including reference specimen(s) used to guide reconstruction. Number and percentage (%) of landmarks and semilandmarks affected by digital reconstruction are shown. *See SI-4 for tests of effect of reference specimen on Brno II

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Group</th>
<th>Reference Specimen(s)</th>
<th>Landmarks affected</th>
<th>Semilandmarks affected</th>
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<tr>
<td>Liujiang</td>
<td>Homo sapiens</td>
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<td>0.0%</td>
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<tr>
<td>Qafzeh 9</td>
<td>Homo sapiens</td>
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<td>40.0%</td>
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<tr>
<td>Jebel Irhoud 1</td>
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<tr>
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**Brno II**

Brno II was missing regions of the left and right frontal squama interior to the temporal lines, as well as the nasal region of the frontal bone inferior to glabella, both maxillae, and the left zygomatic. There was also a depression to the right lateral side of the frontal squama. First, Brno II was reflected missing regions of the original were taken and merged with the original model in Geomagic. Brunn III was then warped on to the Brno II reconstruction, and parts of the warped Brunn III surface model were used to reconstruct the missing regions in the lateral frontal bone. The reconstructed areas affected seven landmarks and 27 semilandmarks. The effect of the reference specimen was tested for Brno II, and results are shown in SI-4.
**Předmostí IV**

Předmostí IV was missing a section of bone in the right lateral trigone region. This was reconstructed by merging the original model with the corresponding region of the reflected model, with eight semilandmarks affected by digital reconstruction.

**Cro-Magnon II**

Cro Magnon II had a mediolateral depression to the superior right frontal squama. It was also missing the inferior orbital margin on the left zygomatic, the frontal process of the left maxilla, and the left lacrymal. The affected regions of the original model were reconstructed using the corresponding areas of the reflected model. This affected two landmarks and seven semilandmarks.

**Mladeč 2**

The original fossil of Mladeč 2 was missing both zygoma, maxillae and lacrymals, as well as the inferior border of the lateral frontal squama on both sides. The lower face of Mladeč 1 was transformed, aligned and merged with Mladeč 2, affecting four of the landmarks.

**Liujiang**

Liujiang had a defect in the left frontal squama, superior to the midorbit, extending medially to be parallel with the left medial orbital rim. This was reconstructed by using corresponding regions of the reflected aligned surface model and affected 11 of the semilandmarks.

**Qafzeh 9**

Qafzeh 9 was missing areas of the left frontal squamous surface superior to the lateral aspects of the orbit, as well as some of the midsagittal region on the superior part of the squama extending to laterally to the left. There were also small missing regions in the left superior orbital margin (towards the trigone) and the right superior orbital margin (above midorbit). The depressed regions of the frontal squamous were raised to the level of the surrounding bone and merged in Geomagic. The reconstruction was then aligned with its reflection to reconstruct missing regions of the left and right supraorbital margin. Nasion was estimated using the reconstructed region on the cast. Finally, the reflected model was warped onto the reconstruction to patch the missing area of bone superior to the left trigone. This affected one of the landmarks and 24 of the semilandmarks.
**Jebel Irhoud 1**

Jebel Irhoud 1 had a depressed region in the left lateral frontal squama superior to midorbit extending laterally, which also affected the supraorbital trigone. This was reconstructed by using the relevant region from the right side of the specimen. This affected two landmarks and 54 semilandmarks.

**Gibraltar 1**

Gibraltar 1 was missing lateral portions of the left frontal squama, along with the left trigone region. This was reconstructed by using the appropriate areas of the reflected model. Two landmarks and 35 semilandmarks were affected by the reconstruction.

**Guattari**

The original Guattari model was missing the right anterolateral aspect of the frontal including all of right trigone. It was also missing the right zygomatic and the lateral aspect of the right inferior orbital rim. Missing areas were reconstructed by aligning the original model with its reflection and merging the two. In total, seven landmarks and 35 semilandmarks were affected by reconstruction.

**Krapina C**

Krapina C was missing most of the left half of the frontal squama, superior to the supraorbital torus. This extended into the midsagittal region on the superior aspect of the squama. It was also missing part of the left maxilla, affecting the inferior orbital rim, and the right zygomatic was displaced anterolaterally. The original model and its reflection were aligned with Shanidar I to aid realignment of the zygoma. The reflected model was then used to reconstruct the missing regions of the left frontal squama and maxilla. Shanidar I was then warped on to the reconstruction to reconstruct the missing superior midsagittal region of the frontal squama. Four landmarks and 25 semilandmarks were affected.

**Krapina E**
Krapina E was missing a large region of the left frontal squama, superior to the supraorbital torus, and some of the right supraorbital torus in the trigone area. It was also missing the right zygomatic, the right nasal bone and both maxillae, and the left zygomatic was misaligned. The alignment of the left zygomatic was corrected by aligning the original model with Shanidar I. The frontal bone and the right zygomatic were then reconstructed by aligning the original model, with the corrected zygomatic, with its reflection. The lower face was reconstructed by using the aligned Shanidar I model. This reconstruction affected five of the landmarks and 17 of the semilandmarks.

**Le Moustier 1**

Le Moustier 1 had a defect on the left supraciliary region, lateral to glabella and extending medially to affect the superomedial orbital rim. There was also a depression in the right trigone. These areas were reconstructed by using the corresponding regions from the reflected model. 22 semilandmarks were affected by the reconstruction.

**Saint Césaire**

The Saint Césaire fossil was missing all of the left frontal squama up to midsagittal region, as well as the left lateral supraorbital torus. The left zygomatic, and all of the left orbital margin. There was also a defect in the right frontal squama. This specimen was reconstructed firstly by using the relevant sections of its aligned reflection, followed by merging the resulting model with the lower face of the Shanidar 1 fossil, and finally by warping the frontal squama of Shanidar I on to the reconstructed model’s surface to reconstruct the remaining defects. This affected nine landmarks and 85 semilandmarks.

**Shanidar V**

There was some erosion of the nasal region on Shanidar V, extending to the frontal processes of the maxillae. This specimen also had a defect on the left frontal squama, on the superior aspect above midorbit. It was reconstructed by using the corresponding regions from the reflected model. Three landmarks and five semilandmarks were affected by the reconstruction.

**Spy 1**
Spy 1 was missing both maxillae and nasal bones as well as the left zygomatic. The right zygomatic, while present, was displaced. First, the right zygomatic was aligned using La Chapelle as a reference. Then, the model was reflected to reconstruct the left zygomatic. Finally, the model was aligned with La Chapelle again to reconstruct the lower face. Six landmarks were affected.

**Bodo**

Bodo was missing the right zygomatic, the right lateral maxilla, affecting the inferior orbital margin, and sections of the frontal squama in the right and posterosuperior midsagittal region. It was also missing a section of bone around the left temporal line, and there was a crack of missing bone in the right temporal line region. These areas were reconstructed by using the corresponding regions of the reflected model to create a composite surface, then by warping the frontal squama of Kabwe 1 on to this model to reconstruct the missing areas. One landmark and 35 semilandmarks were affected.

**Sima de los Huesos**

There was damage to the right lateral supraorbital torus and trigone region of Sima de los Huesos 5, which also affected the frontal squama posterior to this area. This specimen was reconstructed by using the corresponding morphology of the reflected model. Three landmarks and 45 semilandmarks were affected.

**Solo VI**

The Solo VI fossil was missing the left lateral supraorbital torus region, extending onto the frontal squama in the lateral aspect. There was also damage to the lateral part of the right trigone, and it was missing both zygomatics and maxillae. The trigone and frontal squama were reconstructed by using a reflected surface model, while the face and the anterior aspects of the zygomatic processes of the frontal were reconstructed by using Sangiran. Seven landmarks and 15 semilandmarks were affected by the reconstruction.

**Zhoukoudian XII**
Zhoukoudian XII was missing both maxillae, the right zygomatic, and the inferomedial portion of the left zygomatic. These areas were reconstructed by using the reflected right zygomatic, and raising the preserved inferomedial portion to the level of the inferior orbital rim. Six landmarks were affected.

*KNM-ER 3733*

KNM-ER 3733 had a defect in the region of the supraboral sulcus, superior to glabella and extending to the left midorbit. There was also a slight defect in the left superior orbital rim on the medial side. This was reconstructed by using the corresponding regions from the reflected model. 15 semilandmarks were affected.

*KNM-ER 3883*

There was a depression on the left frontal squama of KNM-ER 3883. This specimen was also missing the left frontal process of maxilla and most of the left zygomatic, with the preserved areas being somewhat misaligned. This specimen was reconstructed by using the aligned reflected model. Three landmarks and 22 semilandmarks were affected.

*D2282*

D2282 showed some post-depositional changes. The lower face was misaligned, being shifted to the left. This specimen was missing the anteroinferior aspect of the supraorbital torus in the glabella region, the medial aspects of the supraciliary region, the nasal region, and the frontal processes of both maxillae. The right lateral frontal squama appeared to be deformed in the area of the temporal line region. To reconstruct this specimen, first the left zygomatic process of the frontal was moved medially into its correct alignment. Then the model was reflected to reconstruct the right lateral squama in the area of the temporal line and the posterior region of the zygomatic process. Next, the lower face, including the zygomatics, was moved to the right to be aligned with the calvarium. Finally, D4500 was used to reconstruct the nasal column, anterior glabella region, and inferomedial orbital rim. In total, 13 landmarks and 29 semilandmarks were affected.

*KNM-ER 1813*
KNM-ER 1813 was missing the left zygomatic, left inferior orbital margin on the maxilla, and the left lateral trigone region. These areas were reconstructed by using an aligned reflected model of the specimen. Four landmarks and five semilandmarks were affected by the digital reconstruction.

**KNM-ER 1470**

KNM-ER 1470 was missing some of the frontal process of the right zygomatic, and a section of the right supraorbital torus area above midorbit, affecting the supraorbital rim. This specimen was reconstructed by using the corresponding morphology of its own reflection, affecting one landmark and nine semilandmarks.

**KNM-WT 17000**

There was a slight circular defect in the frontal squama of KNM-ER 17000, isolated on the right hand side, inferior to the temporal line. This defect was reconstructed by using an aligned reflection of the specimen, with two landmarks being affected in total.

**KNM-ER 406**

KNM-ER 406 had a circular defect along the left temporal line on the frontal squama. It was also missing the left inferior orbital rim on the left maxilla. Both areas were reconstructed by using the corresponding areas of a reflection of the specimen. One landmark and seven semilandmarks were affected.

**KNM-ER 732**

KNM-ER 732 had a defect in the left supraciliary region, as well as some on the right squama between the midsagittal region and the temporal line. In addition, it was missing the lateral portion of the left frontal squama, the left supraorbital trigone, and the left zygomatic and maxilla. This specimen was therefore reconstructed by using the reflected left frontal squama to reconstruct the defects in the right squama, then by reflecting the reconstructed right side to reconstruct the majority of the left side. All of the left bilateral landmarks (eight in total) were affected, along with all left semilandmarks and 24 of those on the right side of the specimen (123 in total).

**Reconstruction in ScanStudio**
One non-hominin primate specimen required reconstruction by manipulation of the original ScanStudio file. RMCA 9220, a male *Gorilla beringei graueri*, had a small defect which was removed using the Trim function, after which the Fill function was used to fill in the area. This method only works for suitably small areas and uses the surrounding morphology to generate gaps in the 3D surface model. Sliding of semilandmarks in later analysis removed any effect on the homology of the affected points.
SI-4: Testing the Effect of Digital Reconstruction

Effect of Reference Specimen: Brno II

To test the effect of choice of reference specimen on the reconstructed morphology, one specimen, Brno II (*Homo sapiens*), was reconstructed using five different reference specimens: Brno III (taken as the control reconstruction, as Brno III was not included in the entire *Homo sapiens* sample), Mladeč 1, Předmostí IV, Dolní Věstonice III, and Abri Pataud. These specimens are from a similar time period (Upper Palaeolithic) and region (Europe), and are therefore suitable reference specimens for Brno II. The configuration of landmarks and semilandmarks for all five reconstructions was included in a dataset containing the remaining 54 Pleistocene hominins. The dataset was aligned using GPA, and PCA was used on the resulting Procrustes coordinates (see Materials and Methods).

Figure S1 shows a plot of PC1 and PC2 (67.5% of total sample variance combined) for the Brno II reconstruction dataset, in which the Brno II reconstructions are tightly clustered. Examination of Procrustes distances showed that the Brno II reconstruction using Mladeč 1 as a reference was closer to the reference specimen than the control reconstruction (table S9). For the other reconstructions of Brno II (using Dolní Věstonice III, Předmostí III, and Abri Pataud as references), the distance to the reference specimen was larger in comparison to the distance between the control Brno II reconstruction and the respective reference specimens. A one-way ANOVA with post-hoc Tukey HSD tests in SPSS 25 (table S10) showed that the Procrustes distances between the Brno II reconstructions and their reference specimens were not significantly different than either the distance between the Brno II control reconstruction and the other reference specimens (*p*=0.991), or between the other *Homo sapiens* specimens and the four Brno II reference specimens (*p*=0.132). A second one-way ANOVA (table S11) showed that the Procrustes distances between the five Brno II reconstructions was significantly lower (*p*=0.031) than the intraobserver error distances (see SI-5), and the intra-specific distances for the other *Homo sapiens* specimens (*p*<0.001). It was therefore concluded that the choice of reference specimen for digital reconstructions did not have an effect on the results of this study. The Brno II reconstruction which used Brno III as a reference was used in all subsequent analyses.
Figure S1 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 67.5% of variation combined, for PCA in tangent space using dataset of 54 Pleistocene hominins combined with the five reconstructions of Brno II. See table 2 for list of abbreviations, and legend for identification of specimens. Convex hulls are shown and correspond to species; see figure 11 for identification.
Table S9 - Procrustes distances between control reconstruction (using Brno III as a reference) and other reference specimens, and between reconstructions and their references

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<thead>
<tr>
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<th>Control - Reference</th>
<th>Recon. - Reference</th>
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</tr>
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</tr>
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<td>Mladeč I</td>
<td>0.109</td>
<td>0.108</td>
<td>-0.001</td>
</tr>
<tr>
<td>Předmostí III</td>
<td>0.112</td>
<td>0.114</td>
<td>0.001</td>
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</table>

Table S10 - Results of Post-Hoc Tukey HSD comparisons of Procrustes distances between the Brno II reconstructions and their reference specimens compared to those between the control Brno II reconstruction and the reference specimens, and between the other Homo sapiens (HS) and the reference specimens

<table>
<thead>
<tr>
<th></th>
<th>Mean Difference</th>
<th>Std. Error</th>
<th>p</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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</tr>
<tr>
<td>Recon. vs. Reference</td>
<td>0.002</td>
<td>0.015</td>
<td>0.990</td>
<td>-0.034</td>
</tr>
<tr>
<td>Control vs. Reference</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>HS vs. Reference</td>
<td>0.021</td>
<td>0.011</td>
<td>0.135</td>
<td>-0.005</td>
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</tbody>
</table>

Table S11 - Results of Post-Hoc Tukey HSD comparisons of Procrustes distances within the five Brno II reconstructions, versus those within intraobserver error (IOE) repeats (see SI-5) and intra-Homo sapiens (HS) distances

<table>
<thead>
<tr>
<th></th>
<th>Mean Difference</th>
<th>Std. Error</th>
<th>p</th>
<th>95% Confidence Interval</th>
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</thead>
<tbody>
<tr>
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<td>Lower Bound</td>
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<tr>
<td>Intra-Recon.</td>
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</tr>
<tr>
<td>Intra-IOE</td>
<td>-0.021</td>
<td>0.008</td>
<td>0.031</td>
<td>-0.041</td>
</tr>
<tr>
<td>Intra-HS</td>
<td>-0.061</td>
<td>0.008</td>
<td>&lt;0.001</td>
<td>-0.079</td>
</tr>
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</table>
Exclusion of a Specimen: Saint Césaire I

Saint Césaire I required approximately half of the frontal bone to be reconstructed (see SI-3); as such, it was one of the specimens which required the most extensive digital reconstruction. To test that the reconstruction method did not impact the overall results, analyses were run with a dataset where Saint Césaire I was excluded, and results were compared to those for the full dataset. Figure S2 shows a plot of PC1 and PC2 (66.9% of total variation combined) for the dataset where Saint Césaire I was excluded. As can be seen, the exclusion of this specimen has a negligible effect on the plot when compared to figure 11. Saint Césaire I’s exclusion also had minimal effect on the results of the discriminant analysis (table S12), and the Procrustes distance between the Saint Césaire I reconstruction and the *Homo neanderthalensis* centroid (0.056) was very close to the mean distance to the centroid for the other *Homo neanderthalensis* specimens (0.055; st. dev. = 0.016).

| Table S12 - Results of step-wise cross-validated discriminant analysis with subsampling (n=7, except for MPH where n=4 and *Homo habilis* where n=2 due to sample size) using first 17 principal components that accounted for over 95% of total sample variance from PCA in tangent space with dataset of 54 hominins (with Saint Césaire I excluded). Percentage classification accuracy is shown across 1000 repeats. Specimens were classified into species groups, and overall weighted species classification accuracy (excluding MPH and *Homo habilis*) was 87.5%. See table 2 for list of abbreviations |
|---------------------------------|--------|---------|------|------|-------|--------|
|                  | HS     | HN      | MPH  | HE   | HHa   | Species |
| HS                | 87.4   | 8.5     | 2.5  | 0.8  | 0.8   | 87.4   |
| HN                | 4.8    | 89.8    | 0.8  | 4.6  |       | 89.8   |
| MPH               | 0.1    | 12.4    | 72.6 | 14.2 | 0.8   |        |
| HE                | 7.2    | 3.3     | 85.5 | 4.0  |       | 85.5   |
| HHa               | 0.4    | 8.2     | 47.8 | 43.8 |       |        |
Figure S2 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 66.9% of variation, for PCA in tangent space using dataset of 54 Pleistocene hominins (with Saint Césaire I excluded). See table 2 for list of abbreviations, and legend for identification of specimens. Convex hulls are shown and correspond to species; see figure S11 for identification.
### SI-5: Intra-observer Error

#### Details of Specimens

Table S13 - Details of 26 specimens used for intra-observer error assessment

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Species</th>
<th>Sex</th>
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<tr>
<td>RMCA 2260</td>
<td><em>Gorilla beringei beringei</em></td>
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<tr>
<td>RMCA 27840</td>
<td><em>Gorilla beringei graueri</em></td>
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<td>USNM 590946</td>
<td><em>Gorilla gorilla diehli</em></td>
<td>Female</td>
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<tr>
<td>ZD.1878.12.14.1</td>
<td><em>Gorilla gorilla gorilla</em></td>
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<tr>
<td>RMCA 27012</td>
<td><em>Pan paniscus</em></td>
<td>Female</td>
</tr>
<tr>
<td>RMCA 29036</td>
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</tr>
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<td>RMCA 29074</td>
<td><em>Pan troglodytes schweinfurthii</em></td>
<td>Female</td>
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<tr>
<td>ZD.1939.3365</td>
<td><em>Pan troglodytes troglodytes</em></td>
<td>Male</td>
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<td>ZD.1908.8.9.42</td>
<td><em>Papio anubis</em></td>
<td>Female</td>
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<tr>
<td>ZD.1925.5.12.1</td>
<td><em>Papio anubis</em></td>
<td>Male</td>
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<tr>
<td>ZD.1961.772</td>
<td><em>Papio kindae</em></td>
<td>Female</td>
</tr>
<tr>
<td>ZD.1961.734</td>
<td><em>Papio kindae</em></td>
<td>Male</td>
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<td>M-30622</td>
<td><em>Macaca fascicularis</em></td>
<td>Female</td>
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<td>ZD.1919.11.12.8</td>
<td><em>Macaca fascicularis</em></td>
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<td>ZD.1905.11.3.2</td>
<td><em>Macaca fascata</em></td>
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<td><em>Macaca fascata yakui</em></td>
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<td>ZD.1914.7.10.3</td>
<td><em>Macaca mulatta</em></td>
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<tr>
<td>ZD.1931.1.11.8</td>
<td><em>Macaca mulatta</em></td>
<td>Male</td>
</tr>
<tr>
<td>Zhokoudian UC 102</td>
<td><em>Homo sapiens</em></td>
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<tr>
<td>Border Cave 1</td>
<td><em>Homo sapiens</em></td>
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<tr>
<td>Gibraltar 1</td>
<td><em>Homo neanderthalensis</em></td>
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<tr>
<td>Bodo</td>
<td>MPH</td>
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<td>KNM-ER 3733</td>
<td><em>Homo ergaster</em></td>
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<td>D4500</td>
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<td>OH 24</td>
<td><em>Homo habilis</em></td>
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<tr>
<td>KNM-ER 732</td>
<td><em>Paranthropus boisei</em></td>
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</table>
Results

Table S14 - Descriptive statistics for within-group Procrustes distances for analysis of intra-observer error (IOE) for non-hominin primate and hominin datasets. All values reported to 3 decimal places

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<th></th>
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<th>Median</th>
<th>Min.</th>
<th>Max.</th>
<th>St. Dev.</th>
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<tr>
<td>IOE</td>
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<td>0.043</td>
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<td>0.040</td>
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<td>0.095</td>
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<td>0.026</td>
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<td>0.034</td>
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<td>Hominins</td>
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<td>IOE</td>
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<td>0.093</td>
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<td>0.057</td>
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<td>Intra-genus</td>
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<td>0.017</td>
<td>0.305</td>
<td>0.045</td>
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<tr>
<td>Inter-genus</td>
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<td>0.148</td>
<td>0.097</td>
<td>0.240</td>
<td>0.033</td>
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Table S15 - Results of Post-Hoc Tukey HSD comparisons of intra-observer Procrustes distances to intra- and inter-taxonomic Procrustes distances for the non-hominin primate and hominin datasets

<table>
<thead>
<tr>
<th></th>
<th>Mean Difference</th>
<th>Std. Error</th>
<th>p</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>Lower Bound</td>
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<tr>
<td>Non-Hominin Primates</td>
<td>IOE</td>
<td>-0.055</td>
<td>0.003</td>
<td>&lt;0.001</td>
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<tr>
<td>Intra-subspecies</td>
<td>-0.052</td>
<td>0.003</td>
<td>&lt;0.001</td>
<td>-0.060</td>
</tr>
<tr>
<td>Inter-subspecies</td>
<td>-0.051</td>
<td>0.003</td>
<td>&lt;0.001</td>
<td>-0.059</td>
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<tr>
<td>Intra-species</td>
<td>-0.059</td>
<td>0.003</td>
<td>&lt;0.001</td>
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<tr>
<td>Inter-species</td>
<td>-0.055</td>
<td>0.003</td>
<td>&lt;0.001</td>
<td>-0.063</td>
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<tr>
<td>Intra-genus</td>
<td>-0.096</td>
<td>0.003</td>
<td>&lt;0.001</td>
<td>-0.104</td>
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<td>IOE</td>
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<td>0.006</td>
<td>&lt;0.001</td>
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<td>-0.099</td>
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<td>&lt;0.001</td>
<td>-0.122</td>
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### SI-6: Non-Hominin Primates - Additional Results

**Mean Pairwise Procrustes Distances**

Table S16 - Mean pairwise Procrustes distances (PrD) for inter-taxon comparisons for non-hominin primate dataset. See table 1 for list of abbreviations. PrD shown to 3 decimal places

<table>
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<th>subspecies</th>
<th></th>
<th>PrD</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Gorilla-Pan</td>
<td>GB-GG</td>
<td>PP-PT</td>
<td>PA-PC</td>
<td>PA-PK</td>
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<tr>
<td></td>
<td>Papio-Macaca</td>
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<tr>
<td>Pairwise PrD</td>
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<td>0.123</td>
<td>0.096</td>
<td>0.098</td>
<td>0.106</td>
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Figure S3 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 55.4% of variation, for PCA in tangent space using dataset of 460 non-hominin primates. See table 1 for list of abbreviations. Convex hulls are shown and correspond to genus; see legend for identification.
Figure S4 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 55.4% of variation, for PCA in tangent space using dataset of 460 non-hominin primates. See table 1 for list of abbreviations. Convex hulls are shown and correspond to species; see legend for identification.
Figure S5 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 55.4% of variation, for PCA in tangent space using dataset of 460 non-hominin primates. See table 1 for list of abbreviations. Convex hulls are shown and correspond to subspecies; see legend for identification.
Principal Component Analysis: Form Space

Figure S6 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 94.8% of variation, for PCA in form space using dataset of 460 non-hominin primates. Specimens are identified by symbols shown in legend. See table 1 for list of abbreviations. Convex hulls are shown and correspond to species groups. Shape changes are shown for minimum, median, and maximum sample values for both axes, in frontal and left lateral view.
Figure S7 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 94.8% of variation, for PCA in form space using dataset of 460 non-hominin primates. Convex hulls are shown and correspond to genera; see legend for identification.
Figure S8 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 94.8% of variation, for PCA in form space using dataset of 460 non-hominin primates. See table 1 for list of abbreviations. Convex hulls are shown and correspond to species; see legend for identification.
Figure S9 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 94.8% of variation, for PCA in form space using dataset of 460 non-hominin primates. Only subspecies are shown. See table 1 for list of abbreviations. Convex hulls are shown and correspond to subspecies; see legend for identification.
Discriminant Analysis: Form Space

Table S17 - Table showing results of step-wise cross-validated discriminant analysis with subsampling (n=16) using first three principal components that accounted for over 95% of total sample variance from PCA in form space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples is shown by taxon. Specimens were classified by genus, and overall genus classification accuracy was 99.2%

Table S18 - Table showing results of step-wise cross-validated discriminant analysis with subsampling (n=8) using first three principal components that accounted for over 95% of total sample variance from PCA in form space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples is shown by taxon. Specimens were classified by species, and overall species classification accuracy was 64.1%. See table 1 for list of abbreviations
S19 - Table showing results of step-wise cross-validated discriminant analysis with subsampling (n=4) using first three principal components that accounted for over 95% of total sample variance from PCA in form space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples is shown by taxon. Specimens were classified by subspecies, and overall subspecies classification accuracy was 33.2%. See table 1 for list of abbreviations.

<table>
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<th>GGD</th>
<th>GGG</th>
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<th>PTT</th>
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<th>PTV</th>
<th>PTE</th>
<th>PA</th>
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</thead>
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Principal Component Analysis: Allometry-free Shape Space

Figure S10 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 46.6% of variation, for PCA in allometry-free shape space using dataset of 460 non-hominin primates. Specimens are identified by symbols shown in legend. See table 1 for list of abbreviations. Convex hulls are shown and correspond to species groups. Shape changes are shown for minimum, median, and maximum sample values for both axes, in frontal and left lateral view.
Figure S11 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 46.6% of variation, for PCA in allometry-free shape space using dataset of 460 non-hominin primates. Convex hulls are shown and correspond to genera; see legend for identification.
Figure S12 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 46.4% of variation, for PCA in allometry-free shape space using dataset of 460 non-hominin primates. See table 1 for list of abbreviations. Convex hulls are shown and correspond to species; see legend for identification.
Figure S13 - Plot of PC1 (x-axis) and PC2 (y-axis), accounting for 46.4% of variation, for PCA in allometry-free shape space using dataset of 460 non-hominin primates. See table 1 for list of abbreviations. Convex hulls are shown and correspond to subspecies; see legend for identification.
**Discriminant Analysis: Allometry-free Shape Space**

S20 - Table showing results of step-wise cross-validated discriminant analysis with subsampling (n=16) using first 39 principal components that accounted for over 95% of total sample variance from PCA in allometry-free shape space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples is shown by taxon. Specimens were classified by genus, and overall genus classification accuracy was 83.2%.

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<th>Macaca</th>
<th>Genus</th>
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S21 - Table showing results of step-wise cross-validated discriminant analysis with subsampling (n=8) using first 39 principal components that accounted for over 95% of total sample variance from PCA in allometry-free shape space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples is shown by taxon. Specimens were classified by species, and overall species classification accuracy was 64.9%. See table 1 for list of abbreviations.

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See table 1 for list of abbreviations.
S22 - Table showing results of step-wise cross-validated discriminant analysis with subsampling (n=4) using first 39 principal components that accounted for over 95% of total sample variance from PCA in allometry-free shape space with dataset of 460 non-hominin primates. Mean percentage classification accuracy across the 1000 subsamples is shown by taxon. Specimens were classified by subspecies, and overall subspecies classification accuracy was 39.9%. See table 1 for list of abbreviations.

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<th>PTT</th>
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<th>PTV</th>
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SI-7: Hominins - Additional Results

Mean Pairwise Procrustes Distances

Table S23 - Mean pairwise Procrustes distances (PrD) for inter-taxon comparisons for Pleistocene hominin dataset. See table 2 for list of abbreviations. PrD shown to 3 decimal places

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Table S24 - Percentage classifications for hominin specimens from discriminant analysis shown in table 8. See table 2 for abbreviations. n shows number of subsamples in which specimen were randomly selected.

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