

Variation in early hominin temporal bone morphology and its implications for species diversity

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Temporal bone morphology features prominently in discussions of fossil hominin taxonomy and phylogeny. However, the complex morphology has led to different ways of interpreting features and, as a result, different conclusions regarding systematics. Here we use temporal bone anatomy and geometric morphometric techniques to ask how much disparity exists among early hominin temporal bones and whether levels of intra- and interspecific variation among fossil hominins are consistent with those among modern apes and humans. Using 3D ectocranial landmarks, Euclidean distances based on Procrustes coordinates were determined for all pairwise comparisons among 15 fossil specimens representing *Australopithecus* species and early *Homo*. These were then compared to distributions of intraspecific pairwise comparisons for five great ape and human samples, and interspecific comparisons for ten species pairs. Overlap between intra- and interspecific differences is pronounced in the extant as well as the fossil sample. On the whole, differences between fossil specimens matched the central tendency of differences between extant ape species or genera. In some cases the differences among fossils can also be found within highly variable extant species, even when the fossils are commonly recognised as different species. We conclude that the overall level of disparity among hominin specimens supports arguments that the clade is relatively speciose, but the pronounced overlap between intra- and interspecific variation suggests that classifications based largely on morphometrics would be unreliable.

INTRODUCTION

One of the enduring debates regarding human evolution concerns how variation is patterned within and between species in the fossil record. Decisions about diversity have implications for central questions, for example, the origin of the genus *Homo* (Wood, 1991, 1992) and the nature of the earliest hominin radiation (Haile-Selassie *et al.*, 2004). Ultimately the number of species conveys the level of morphological disparity among hominins and – by virtue of the link between morphology and behaviour – speaks to the ecological breadth of the group.

Generally speaking, qualitative skeletal features are used to diagnose fossil hominin species, whereas quantitative features are used to test established hypotheses that a given sample represents a single species. Over the last fifteen years or so, many studies have analysed cranial variation in fossil samples using a variety of quantitative techniques (e.g. Aiello *et al.*, 2000; Grine *et al.*, 1993, 1996; Kramer *et al.*, 1995; Lockwood, 1999; Miller, 2000). These studies have examined the more well-known samples, such as *Australopithecus afarensis*, *A. africanus*, *A. boisei*, and the early *Homo* species. At the same time, an array of new species has been announced, which raises the issue of how accurately hominin classifications reflect species diversity.

In this paper we ask the following questions:

- What is the general level of disparity among early hominin temporal bones?
- Are conspecific hominin fossils substantially more similar to each other than are those thought to belong to different species?

- How do levels of variation among fossil taxa compare to differences observed among extant apes and humans?

The target of our study is the temporal bone. A benefit of choosing a narrowly defined region is that we are not restricted to relatively complete skulls, and therefore the sample size is larger than it would be in a study of the cranium as a whole. In addition, the temporal bone is an element whose features have been used extensively in systematic studies without comprehensive quantitative methods. It is therefore an interesting test case of whether morphometric methods, when applied at a high level of landmark resolution, confirm or reject conclusions about variation that have been based on qualitative features. Moreover, the temporal bone features prominently in some taxonomic debates, particularly those concerning the earliest members of the genus *Homo* (e.g. Hill *et al.*, 1992; Tobias, 1993; Kimbel & Rak, 1993; Ahern, 1998; Sherwood *et al.*, 2002).

MATERIALS AND METHODS

For this study, our extant hominoid sample consisted of one subspecies from each of the five great ape species (wild-shot individuals) and a human sample of African-Americans from the Hamann-Todd Osteological Collection (Cleveland Museum of Natural History) (Table 1). Females and males were pooled in all analyses, so that the analyses of intraspecific variation included the effects of sexual dimorphism.

The fossil sample comprised fifteen early hominin specimens representing several *Australopithecus* species and early *Homo* (Table 2). These provided a total of 105 comparisons between individuals. Sample size for each species was small, and for that

Table 1. Extant hominoid comparative samples.

Species	Males	Females	Abbreviation	Source*
<i>Pongo pygmaeus pygmaeus</i>	17	20	Popyg	NMNH
<i>Gorilla gorilla gorilla</i>	36	35	Ggor	CMNH, PCM
<i>Pan troglodytes troglodytes</i>	39	39	Ptrog	CMNH, PCM
<i>Pan paniscus</i>	19	23	Ppan	RMCA
<i>Homo sapiens</i>	32	29	Hs	CMNH

*CMNH, Cleveland Museum of Natural History; RMCA, Royal Museum for Central Africa, Tervuren, Belgium; NMNH, National Museum of Natural History, Washington, DC, USA; PCM, Powell-Cotton Museum, Birchington, England

reason only 12 of the comparisons were intraspecific (based on our classification).

Geometric morphometric methods were used to study 3D ectocranial landmarks. Twenty-one ectocranial landmarks were included in the analysis, representing the glenoid, petrous, tympanic, and mastoid parts of the temporal bone. These are defined in Lockwood *et al.* (2002a), where an error analysis is also presented. A difference from our previous work (Lockwood *et al.*, 2002a, 2004) is that the tip of the mastoid was not used here, in order to maximise fossil sample size. Landmarks were collected using Microscribe 3D and 3DX digitizers, and all data were collected by the first author.

All individuals were subjected to generalized Procrustes analysis (GPA) in *Morphologika* (O'Higgins & Jones, 1998). The GPA is a least squares superimposition method that translates, rotates, and scales the landmarks for each individual (Rohlf & Slice, 1990; Goodall, 1991). The new coordinate data are informally referred to as Procrustes coordinates. While Procrustes coordinates represent shape data, they are still subject to potential allometric effects.

We calculated Euclidean distances between individuals using the Procrustes coordinates, thereby obtaining a summation of all shape differences between two individuals. Strictly speaking, these are not the same as Procrustes distances, but use of the programme tpsSmall (Rohlf, 1998) showed that for our data they are correlated at levels greater than $r = 0.99$. All possible inter-individual intraspecific comparisons were determined for each extant species sample. Furthermore, we determined all between-species distances for individuals of the following taxa: *Homo sapiens*, *Gorilla gorilla gorilla*, *Pan troglodytes troglodytes*, *P. paniscus* and *Pongo pygmaeus pygmaeus*. Thus, the interspecific comparisons represent 10 species pairs.

Euclidean distances were also calculated between all fossil specimens, and these results were compared to the distributions for the modern taxa. We report these comparisons in a descriptive way and did not apply statistical tests to establish

Table 2. Fossil specimens and classification used here.

<i>A. afarensis</i>	AL 444-2*
<i>A. africanus</i>	Sts 5*, Sts 19*, MLD 37/38*
<i>A. aethiopicus</i>	KNM-WT 17000*
<i>A. robustus</i>	TM 1517
<i>A. boisei</i>	KNM-WT 23000*, KNM-ER 406, KNM-ER 407, KNM-ER 732
<i>H. habilis</i>	Stw 53
<i>H. erectus</i>	KNM-ER 3733*, KNM-ER 3883*, KNM-WT 15000
Unknown	KNM-BC 1 (<i>Homo?</i>)

*Indicates that the specimen is relatively complete and was used in both sets of analyses. All specimens were used in the analysis of ten landmarks.

whether the differences in distributions are significant. This informal approach was adopted because the study is partly exploratory; we are not testing specific hypotheses and did not construct the comparisons to do so.

Two sets of landmarks were used for each analysis: 1) a complete list of 21 landmarks and a fossil sample size of eight, and 2) 10 landmarks and the whole fossil sample of 15 (Table 2). The ten landmarks represent primarily the glenoid and tympanic regions [landmarks 5–9, 15, 19, 21, 22 in Lockwood *et al.* (2002a)]. All extant species were included in each set of analyses.

RESULTS

Extant species

In the analysis of complete specimens, chimpanzees, bonobos, and lowland gorillas show comparable levels of intraspecific variation (Figure 1), while the human and orangutan samples are somewhat more variable. In the case of orangutans, this variation is due to pronounced sexual dimorphism in shape. In the human sample, the variation is largely intra-sexual, individual variation.

Intraspecific differences overlap substantially with interspecific differences among apes. For example, individual bonobos and chimpanzees are often morphometrically more similar to each other than are many individuals within the same species. The median distance between individual chimpanzees and bonobos is actually less than the median distance among humans or among orangutans. Differences among ape genera – *Pan*, *Gorilla*, and *Pongo* – tend to be somewhat greater, and the highest degrees of shape distance occur between the human sample and each of the ape species. Only the human-ape comparisons are clearly greater than the levels of within-species variation.

The analysis of 10 landmarks provides largely similar results (Figure 2). Humans and orangutans show greater intraspecific variation than do the other species, and again there is substantial overlap between intra- and interspecific variation.

Fossil hominins

The early hominin species represented here show levels of differentiation generally comparable to differences among great ape genera. This is true whether the complete or partial list of landmarks is used. That said, the pronounced overlap between intra- and interspecific variation means that many of the fossil pairs fall in the range of both sets of distributions.

In the analysis of all 21 landmarks, the two smallest shape distances are intraspecific, based on current classifications. These are between Sts 5 and Sts 19, and Sts 5 and MLD 37/38. Sts 19 and MLD 37/38 are more distinct, with a shape distance of 0.229. The similarity between Sts 5 and the other two *A. africanus* specimens is only marginally greater than the similarity between KNM-WT 17000 and either Sts 5 or Sts 19 (the two leftmost comparisons in Figure 1). On the other hand, the difference between two African *H. erectus* specimens – KNM-ER 3733 and KNM-ER 3883 – is relatively high compared to differences within modern species.

The analysis of a smaller set of landmarks permits eleven intraspecific comparisons and in particular the comparison of individuals within *A. boisei*, a species whose hypodigm is rarely questioned (but see Groves, 1989). Again, the general level of disparity among early hominins is similar to that among great ape genera (Figure 2). The *A. africanus* specimens give similar results to the previous analysis, with the exception that Sts 5 and Sts 19 have virtually identical proportions for the smaller set of landmarks and a low shape distance.

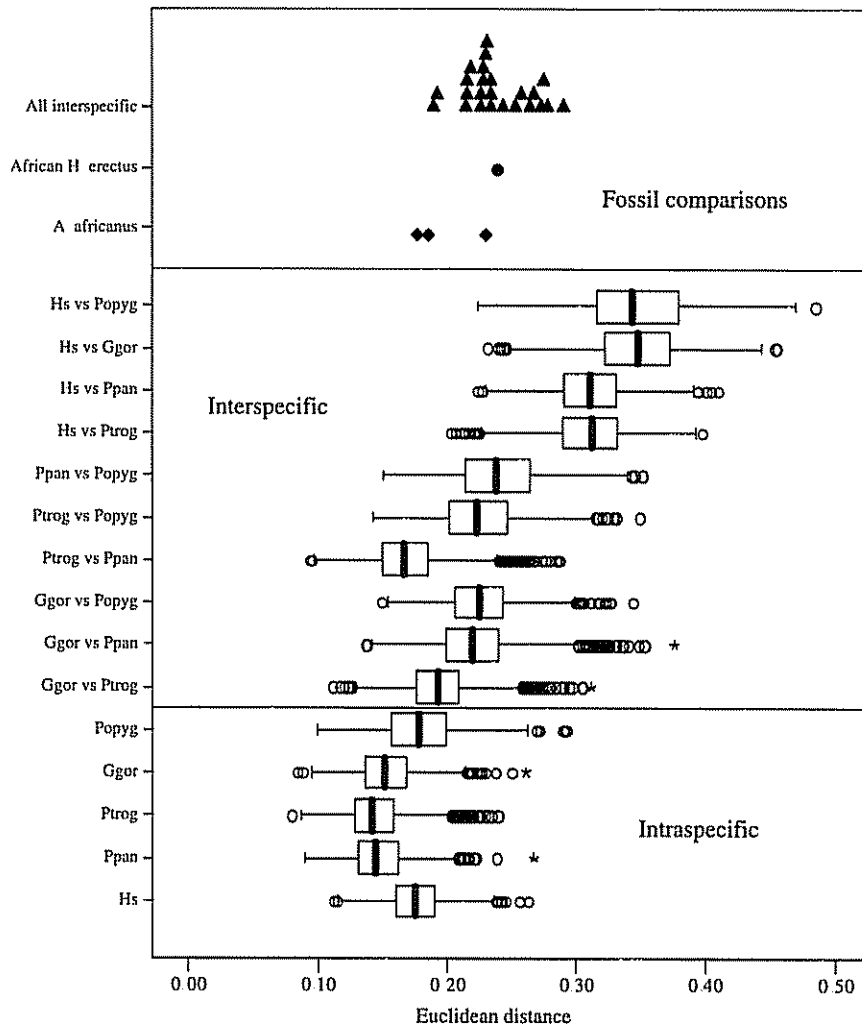


Figure 1 Results from the analysis of 21 landmarks. Each point represents a comparison between two individuals. Intraspecific distributions are at the bottom of the chart, with the interspecific comparisons in the middle, and the distribution of fossil comparisons shown at the top. Abbreviations for extant taxa are given in Table 1. Each box indicates the median and the lower and upper quartiles. The endpoints are maxima and minima, with circles being outlier comparisons.

Perhaps surprisingly, the *A. boisei* specimens include several comparisons that illustrate high levels of intraspecific variation in this taxon. KNM-ER 732 shows a high level of shape difference from other specimens, particularly KNM-ER 407 and KNM-ER 23000. KNM-ER 732 is nonetheless more similar to KNM-ER 406 (indicated by the lowest pairwise shape distance) than to any other hominin specimen included here. The African *H. erectus* specimens, which in this analysis include KNM-WT 15000, also show high levels of shape difference. These differences are still within the range of the most variable extant species, orangutans and humans.

The three lowest distances between individuals considered to be of different species occur between the following pairs: AL 444-2 vs KNM-WT 23000, KNM-BC 1 vs TM 1517, and KNM-BC 1 vs AL 444-2 (these are the leftmost interspecific comparisons in Figure 2). Each of these comparisons shows greater similarity than is seen in any of the intraspecific comparisons, save that of Sts 5 vs Sts 19.

DISCUSSION AND CONCLUSIONS

As shown elsewhere, great ape species form distinct clusters in the morphometric space represented by temporal bone

morphology (Lockwood *et al.*, 2002a). By contrast, the present study shows pronounced overlap between intra- and interspecific differences, when examined by pairwise differences among apes and humans. These two findings are more consistent than they appear to be. Individuals towards the periphery of morphospace represented by a species may be diagnosable to that species, but they will be more phenetically similar to some members of different species than they are to some members of their own species. For that reason, the intra- and interspecific distributions of pairwise comparisons will overlap. In this respect our results mirror those of Aiello *et al.* (2000), who conducted a similar study based on linear dimensions of the skull.

With regard to the fossil sample, several key points emerge from the results presented above: low levels of shape difference among *A. africanus* specimens, higher levels of variation among *A. boisei* and African *H. erectus* specimens, and similarity between some specimens routinely assigned to different species [the latter point again echoing Aiello *et al.* (2000)]. Taken together, these results lead to somewhat contradictory conclusions: on the one hand, the level of disparity among hominin species illustrates why palaeoanthropologists routinely assign

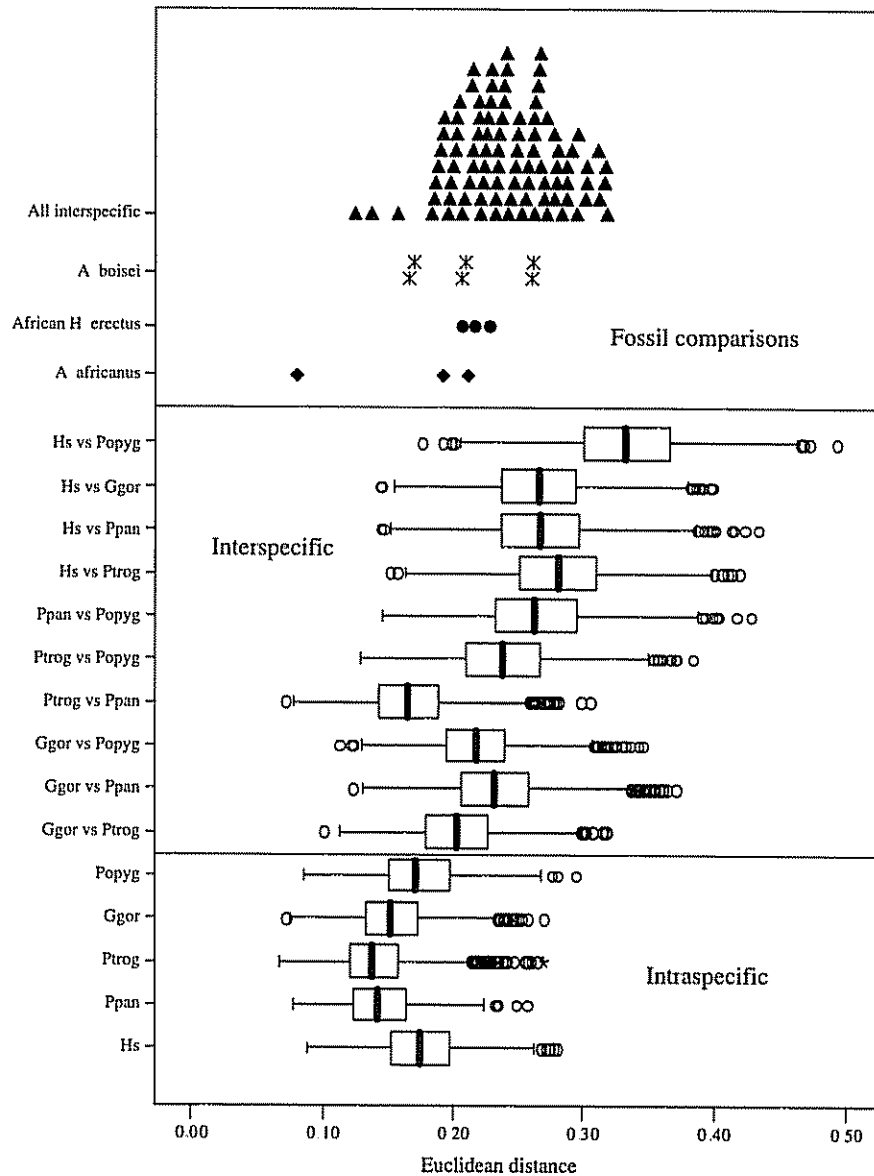


Figure 2. Results from the analysis of 10 landmarks. For other details, see legend for Fig. 1.

most of these specimens to different species but, on the other hand, the pronounced overlap between intra- and interspecific variation suggests that classifications may be unstable, particularly for small samples or isolated specimens.

Similarity among *A. africanus* specimens occurs despite arguments that Sts 19 may be a member of the genus *Homo* (Kimbel & Rak, 1993). In a separate study devoted to early *Homo* in particular, we show that the phenetic position of Sts 19 is equivocal, as similarities to both Sts 5 and *Homo* specimens such as KNM-ER 1813 can be discerned (Lockwood *et al.*, in prep.; see also Lockwood *et al.*, 2002b).

Shape variation in *A. boisei* could stem from the allometric effects of high levels of size dimorphism in the skull. In this case, sexual dimorphism in orangutans may provide a partial analogue. However, KNM-ER 732, usually considered a female specimen, is most similar to the large, presumably male KNM-ER 406. In any event, KNM-ER 732 is more similar to *A. boisei* specimens than it is to specimens in other hominin species. This finding provides an example where clustering of

individuals may occur despite the similarity of some individuals to members of other species. Nonmetric analyses of the anatomy of KNM-ER 732 also leave little doubt that it belongs to *A. boisei* (Wood, 1991; Kimbel *et al.*, 2004; *contra* Groves, 1989).

In the case of African *H. erectus*, it is visually apparent that KNM-ER 3733 has a shallower mandibular fossa than KNM-ER 3883, and the tympanic is less anteriorly projecting. Among other differences, these contribute to a high level of shape difference (see also Terhune, 2005), whereby KNM-ER 3733 comes to resemble *Homo* cranium Stw 53 and some *Australopithecus* specimens.

On the whole, differences among hominin specimens traditionally belonging to different species appear to match the central tendency of differences among great ape species. Strictly speaking, in many individual cases, pairwise comparisons do not fall outside the 95% confidence limits of intraspecific variation. However, it is equally true that virtually none of the fossil comparisons made here fall outside the lower 95% confidence limits of interspecific variation. As shown else-

where with respect to calliper measurements, intra- and inter-specific differences overlap enough so that it is often unclear using these methods whether two individuals can be considered different species (Aiello *et al.*, 2000).

Part of the explanation of why temporal bones of different hominin species are in some cases similar to each other may simply be that species-level differences are reflected in other parts of the skeleton. In addition, the morphometric analysis probably does not capture all of the features that palaeo-anthropologists use to distinguish species qualitatively. For example, in our analysis of ten landmarks, the finding of low levels of shape difference among AL 444-2, KNM-ER 23000, TM 1517, and KNM-BC 1 suggests a situation where the reduced landmark sampling may have missed key features, particularly those derived aspects of the glenoid region that set KNM-ER 23000 apart from the other specimens (Kimbel *et al.*, 2004).

In conclusion, the temporal bone provides an informative test case in which morphometrics can be used to gauge differentiation at the level of anatomical detail typically used by palaeo-anthropologists. Our results support views that early hominins were morphologically diverse, based on shape differences usually on a par with those among great ape species or genera. At the same time, the lack of a clear separation of intra- and interspecific variation, when based on pairwise comparisons, suggests that morphometrics alone is unlikely to yield reliable classifications.

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