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Variation and diversity in *Homo erectus*: a 3D geometric morphometric analysis of the temporal bone

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Abstract

Although the level of taxonomic diversity within the fossil hominin species *Homo erectus* (*sensu lato*) is continually debated, there have been relatively few studies aiming to quantify the morphology of this species. Instead, most researchers have relied on qualitative descriptions or the evaluation of nonmetric characters, which in many cases display continuous variation. Also, only a few studies have used quantitative data to formally test hypotheses regarding the taxonomic composition of the "*erectus*" hypodigm. Despite these previous analyses, however, and perhaps in part due to these varied approaches for assessing variation within specimens typically referred to *H. erectus* (*sensu lato*) and the general lack of rigorous statistical testing of how variation within this taxon is partitioned, there is currently little consensus regarding whether this group is a single species, or whether it should instead be split into separate temporal or geographically delimited taxa.

In order to evaluate possible explanations for variation within *H. erectus*, we tested the general hypothesis that variation within the temporal bone morphology of *H. erectus* is consistent with that of a single species, using great apes and humans as comparative taxa. Eighteen three-dimensional (3D) landmarks of the temporal bone were digitized on a total of 520 extant and fossil hominid crania. Landmarks were registered by Generalized Procrustes Analysis, and Procrustes distances were calculated for comparisons of individuals within and between the extant taxa. Distances between fossil specimens and between *a priori* groupings of fossils were then compared to the distances calculated within the extant taxa to assess the variation within the *H. erectus* sample relative to that of known species, subspecies, and populations.

Results of these analyses indicate that shape variation within the entire *H. erectus* sample is generally higher than extant hominid intraspecific variation, and putative *H. ergaster* specimens are significantly different from other specimens in *H. erectus* (*sensu lato*). However, shape distances within geographical groups of *H. erectus* are also high, and OH 9 and Dmanisi 2280 are morphologically distinct from the Koobi Fora specimens that are sometimes classified as *H. ergaster*. These findings suggest that, although *H. erectus* may be composed of multiple species, the differentiation is complex, and specimens cannot easily be grouped geographically or chronologically. Consequently, more complicated scenarios seeking to explain the observed variation within *H. erectus* must be considered.

Keywords: Homo ergaster; Hominids; Hominins

Introduction

In the 1950s, researchers began to recognize that taxa such as *Pithecanthropus*, *Sinanthropus*, *Telanthropus*, and *Atlanthropus* could be subsumed under one species: *Homo erectus*. These researchers (Weidenreich, 1940, 1943; Mayr, 1950; Clark, 1955, 1964) stressed the importance of normal within-species variation in the analysis of fossil hominin taxa, and argued that the taxon *H. erectus* could accommodate all of the Asian and African specimens. Since that time, numerous additional fossils have been attributed to this taxon, and the geochronological framework for both previously and newly recovered specimens has been refined, greatly expanding the geographic and temporal ranges for this species. As

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currently delimited (e.g., Antón, 2003), *H. erectus* (*sensu lato*) ranges from southern and eastern Africa to China and Indonesia; chronologically, it existed as early as ca. 1.8 million years ago (Ma) and perhaps as late as 50 ka (Feibel et al., 1989; Swisher et al., 1994, 1996; Antón, 1999; Antón and Swisher, 2004). This range, which encompasses at least two continents and potentially ∼1.75 myr, is unparalleled by any other known hominin species, and the morphological variation within this fossil sample has engendered considerable debate regarding its taxonomic composition. The present study is designed to evaluate this variation in the context of extant hominid variation via temporal bone morphology.

There are currently two dominant positions regarding the status of *H. erectus* (*sensu lato*): 1) a single species, *H. erectus*; and 2) two distinct species, *H. ergaster* and *H. erectus*. The single species view considers *H. erectus* as a widespread, polytypic species that is diagnosed by a shared cranial configuration (e.g., Rightmire, 1990; Antón, 2003). Proponents of this view recognize regional and temporal morphs within this taxon, but argue that the degree of variation among these morphs is not significant enough to warrant identification of more than one species (Turner and Chamberlain, 1989; Rightmire, 1990, 1998; Kennedy, 1991; Kramer, 1993; Braüer, 1994; Asfaw et al., 2002; Kidder and Durband, 2004), although some researchers do divide the taxon into subspecies (i.e., *H. erectus soloensis*, *H. erectus pekinensis*, etc.; Antón, 2002a, 2003; Asfaw et al., 2002; Gilbert et al., 2003). Other researchers do not recognize *H. erectus* as a distinct biological species, but rather see these same fossil specimens as evidence of a widespread grade or stage in human evolution that is part of a single species, *H. sapiens*, that originated by ca. 1.8 Ma (Wolpoff et al., 1994; Wolpoff, 1999).

The second view, that *H. erectus* should be divided into two species, stems primarily from the early 1980s, when a number of researchers (e.g., Andrews, 1984; Stringer, 1984; Wood, 1984) began to question the lumping of variation within a broadly conceived *H. erectus*. These researchers proposed that the fossil materials subsumed under *H. erectus* should instead be separated into Asian (*H. erectus*) and African (*H. ergaster*) species based on a suite of autapomorphic features considered to be unique to the Asian fossils (Andrews, 1984; Stringer, 1984; Wood, 1984, 1994; Martinez and Arsuaga, 1997). These researchers argued that the presence of these autapomorphic features (which include sagittal keeling, angular torus on the parietal bone, reduced or absent postglenoid process, secondary loss of the styloid process, presence of a tympanomastoid fissure, and overall thickening of the cranial vault) preclude Asian *H. erectus* from a role in the ancestry of later human populations (Andrews, 1984; Rightmire, 1984, 1998; Stringer, 1984; Martinez and Arsuaga, 1997). In this view, the degree of expression of these traits is accorded higher significance in distinguishing between taxa than in the single-species model (Antón, 2003). However, proponents of the single-species model identify these traits in the African materials as well (Rightmire, 1990, 1998; Braüer, 1994) and therefore do not consider them to be a valid basis for dividing the sample at the species level.

Within this two-species view, some researchers argue for a purely Asian *H. erectus*, which would include all of the Chinese and Indonesian material (Andrews, 1984). However, the morphological similarity—primarily the overall greater cranial robusticity—between OH 9 and the Asian specimens complicates this scenario. Some researchers align OH 9 with the Asian *H. erectus* specimens, citing its incipient angular torus and overall increased cranial robusticity. The recently discovered, geologically younger (0.8–1 Ma) Daka calvaria clouds the issue even further, as this specimen has been aligned with both OH 9 and *H. ergaster* (i.e., KNM-ER 3733 and KNM-ER 3883; Asfaw et al., 2002; Gilbert et al., 2003; Manzi et al., 2003).

Interestingly, the Zhoukoudian material is characterized by a unique metric pattern that is not found in Africa or Indonesia (Antón, 2002a; Kidder and Durband, 2004), leading some to suggest that more than one taxon is present in Asia during the middle Pleistocene. However, most suggest that this "morph" is merely a geographic variant and not a separate species (Antón, 2002a, 2003; Kidder and Durband, 2004). This suggestion of morphological disjunction between the Asian samples, however, complicates interpretations of variation in *H. erectus* even further, and, coupled with the high levels of variation throughout the *H. erectus* (*sensu lato*) sample, has lead some researchers to suggest an even higher level of species diversity within *H. erectus* (*sensu lato*) (Schwartz, 2000; Schwartz and Tattersall, 2000, 2003).

Despite extensive analysis and discussion, little consensus has been reached regarding how many species are present within both Asian and African *H. erectus*. Numerous studies have examined variation in this group, using both metric and nonmetric characters (Andrews, 1984; Rightmire, 1984, 1998; Stringer, 1984; Wood, 1984, 1994; Kennedy, 1991; Kennedy et al., 1991; Braüer and Mbua, 1992; Kramer, 1993; Braüer, 1994; Delson et al., 2001; Antón, 2002a; Asfaw et al., 2002; Gilbert et al., 2003; Manzi et al., 2003; Kidder and Durband, 2004; Villmoare, 2005), but only a few have sought formally to test the statistical validity of hypotheses regarding the taxonomic composition of *H. erectus* (Kramer, 1993; Antón, 2002a; Villmoare, 2005).

The purpose of this study, therefore, is to test different hypotheses for how variation within *H. erectus* (*sensu lato*) can be partitioned quantitatively through the use of three-dimensional (3D) landmark data of the temporal bone. The temporal bone is used here in part because this bone has a high recovery rate in the fossil record, and a good sample is available for *H. erectus*. Also, numerous authors have previously used features of the temporal bone to diagnose *H. erectus* or to divide the species into multiple taxa (Weidenreich, 1943; Andrews, 1984; Rightmire, 1984, 1990; Stringer, 1984; Wood, 1984; Kennedy, 1991; Braüer and Mbua, 1992; Braüer, 1994; Martinez and Arsuaga, 1997; Antón, 2002a, 2003). Because temporal bone morphology has proven difficult to quantify, these features have for the most part been qualitatively assessed, which has led to varying descriptions and interpretations. These qualitative results may create the *a priori* expectation of high temporal bone variation within *H. erectus* (*sensu lato*) relative to extant hominoids, but the research presented here aims to assess the statistical strength of these results using geometric morphometric methods by drawing on evidence of taxonomically structured temporal bone variation within the great ape-human clade (Lockwood et al., 2002, 2004).

Although 3D geometric morphometric representations of temporal bone morphology are not all-inclusive, landmark methods are particularly well-suited to temporal bone anatomy and have recently been very successful in capturing the morphology of this portion of the cranium. Lockwood et al. (2002, 2004) and Harvati (2001, 2003a,b) have previously shown the effectiveness of these methods in distinguishing human and great ape populations based on temporal bone morphology, and Lockwood et al. (2004) found that the hominid[1] temporal bone manifests a phylogenetic signal that reflects the current consensus of molecular data regarding the evolutionary relationships among extant hominids.

In this context, the primary objectives of the present study are threefold: to 1) quantify shape variation in *H. erectus* (*sensu lato*) and evaluate whether shape variation is comparable to that seen in extant hominid species, 2) determine whether geographic and/or temporal subsets of the *H. erectus* sample are more consistent with the variation expected for a single species, and 3) determine whether subsets of *H. erectus* are significantly different from one another. Three-dimensional landmark data allow the quantification of features expressed on the ectocranial surface of the temporal bone that have previously been difficult to assess objectively. Additionally, this method of analysis allows for the identification of unique aspects of temporal bone shape that distinguish the fossil hominin samples in question.

Materials

Landmarks were digitized on specimens from 15 different groups of extant hominids from 5 species (Table 1), 3 original fossil specimens, and 12 fossil casts (Table 2). Taxa within *Gorilla* and *Pongo*, although elevated to species status by some researchers (Janczewski et al., 1990; Garner and Ryder, 1996; Rowe, 1996; Xu and Arnason, 1996; Saltonstall et al., 1998; Zhang et al., 2001), were treated here as subspecies, in part to take a conservative approach to intraspecific variation and to use these subspecific differences as an analogy for geographic and chronological variation in the fossil record. Data for the extant nonhuman samples and the original fossil specimens were collected by C.A.L. and W.H.K. All other specimens (the modern human and cast fossil specimens) were digitized by C.E.T.

The use of casts in this analysis, although not ideal, is justified here for several reasons. First, several of the specimens included in this analysis (i.e., the Zhoukoudian crania) are only available as casts due to loss of the original fossils. Second, for those specimens where the original was able to be digitized, comparison of these trials to digitized casts of the same specimen revealed no systematic error in landmark orientations or configurations. Error between these trials was noted, however, and was approximately at the level of interobserver error as documented and discussed below. Finally, the authors are aware of the difficulty of including reconstruction cast specimens such as Sangiran 4 in this analysis. Like many of the earliest Indonesian specimens from the Pucangan formation, this specimen was badly fragmented and telescoped (Weidenreich, 1945; Antón, 2003), and was subsequently reconstructed by Weidenreich (1945). However, careful examination of this specimen and comparison of the reconstruction to photographs of the original indicate that, while there is slight distortion to portions of the cranial base, the temporal bones are largely undistorted. Therefore, we believe that the use of this specimen has not introduced any undue error into this analysis. Nevertheless, results pertaining to this specimen should be viewed in light of its reconstruction.

Specimens of extant taxa that lacked fully erupted third molars were excluded from this study, although adults with an unfused spheno-occipital synchondrosis were included in the analysis, since differences between them and adults are minimal compared to taxonomic differences. However, it should be noted that two subadult fossil specimens were included (KNM-ER 15000 [Walker and Leakey, 1993], and

Table 1
Comparative taxa used in this study

Species	Population/subspecies	Source*	Number		
			Female	Male	Total
H. sapiens	Nubian (Egypt)	ASU	21	22	43
	Native American (Utah)	AMNH	10	10	20
	East African (Tanzania)	AMNH	11	8	19
	Southeast Asian (Singapore)	AMNH	11	10	21
	Medieval European (Hungary)	AMNH	10	11	21
	Australian Aborigine	AMNH	11	10	21
	Native Alaskan	AMNH	10	10	20
Pan troglodytes	*P. t. troglodytes*	CMNH, PCM	39	38	77
	P. t. schweinfurthii	RMCA	20	20	40
	P. t. verus	PM	24	24	48
P. paniscus	Zaire	RMCA	21	19	40
Gorilla gorilla	*G. g. beringei*	NMNH, RMCA	6	11	17
	G. g. gorilla	CMNH, PCM	36	36	72
Pongo pygmaeus	*P. p. pygmaeus*	NMNH	21	15	36
	P. p. abelli	NMNH	5	5	10
Total			256	249	505

* AMNH—American Museum of Natural History, New York, NY; ASU—Arizona State University, Tempe, AZ; CMNH—Cleveland Museum of Natural History, Cleveland, OH; PCM—Powell-Cotton Museum, Birchington, UK; RMCA—Royal Museum for Central Africa, Tervuren, Belgium; PM—Peabody Museum, Harvard University; NMNH—National Museum of Natural History, Washington, DC.

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[1] As used here, hominid refers of the genera *Homo*, *Pan*, *Gorilla*, and *Pongo*, and all descendants of their last common ancestor, whereas the term hominin includes modern humans and fossil taxa more closely related to humans than to any other extant taxon.

Table 2
Fossil specimens used in this study

Specimen No./name	Abbreviation	Locality	Age (Ma)+	Source*	Original or cast
Africa					
KNM-ER 3733	3733	Koobi Fora, Kenya	1.78	NMK	Original
KNM-ER 3883	3883	Koobi Fora, Kenya	1.5–1.65	NMK	Original
KNM-WT 15000	15000	West Turkana, Kenya	1.51–1.56	NMK	Original
OH 9	OH9	Olduvai Gorge, Tanzania	1.47	IHO	Cast
Eurasia					
Dmanisi 2280	D2280	Dmanisi, Georgia	1.7	AMNH	Cast
Indonesia					
Sangiran 4	San4	Sangiran, Java	>1.6	AMNH	Cast
Sangiran 17	San17	Sangiran, Java	1.3	AMNH	Cast
Sambungmacan 1	SM1	Sambungmacan, Java	0.1–0.05	AMNH	Cast
Sambungmacan 3	SM3	Sambungmacan, Java	0.1–0.05	AMNH	Cast
Ngandong 6**	Ng6	Ngandong, Java	0.1–0.05	IHO	Cast
Ngandong 7**	Ng7	Ngandong, Java	0.1–0.05	AMNH	Cast
Ngandong 12**	Ng12	Ngandong, Java	0.1–0.05	AMNH	Cast
Continental Asia					
Zhoukoudian III	SinIII	Zhoukoudian, China	0.58	AMNH	Cast
Zhoukoudian XI	SinXI	Zhoukoudian, China	0.42	AMNH	Cast
Zhoukoudian XII	SinXII	Zhoukoudian, China	0.42	AMNH	Cast

+ Dates are from Wood, 1991; Walker and Leakey, 1993; Swisher et al., 1994; Swisher et al., 1996; Grun et al., 1997; Gabunia et al., 2000; Larick et al., 2001; Shen et al., 2001; Antón, 2003.

* IHO- Institute of Human Origins, Tempe, AZ; NMK- National Museum of Kenya, Nairobi, Kenya; AMNH- American Museum of Natural History, New York, NY; National Natural History Museum, Arusha, Tanzania.

** The numbering system of the Ngandong specimens used here follows that outlined by Oakley et al. (1975) where Ngandong 6 = Solo V, Ngandong 7 = Solo VI, and Ngandong 12 = Solo XI.

Zhoukoudian III [Black, 1931; Antón, 2002b]), in order to maximize the available sample. The use of these specimens is considered acceptable here for several reasons, most importantly because of the frequent comparison of these specimens to adult *H. erectus*. Consequently, the inclusion of KNM-WT 15000 and Zhoukoudian III is necessary in order to test previous statements about variation within this taxon and specifically the affinity of KNM-WT 15000 to other specimens in the sample. However, given the possibility that ontogenetic and taxonomic variation may consequently be conflated in the fossil sample, results for these specimens will also be discussed in light of ontogenetic variation in the temporal bone.

Methods

A total of 18 landmarks were analyzed (Table 3; Fig. 1). Landmarks were chosen to record as many clearly defined and repeatably identifiable ectocranial points as possible, as well as to allow the maximum number of fossil and extant specimens to be included in the study. These landmarks were originally patterned after the 23 landmarks described by Lockwood et al. (2002), but due to incomplete preservation of the fossil specimens a number of landmarks were excluded. In addition, the most lateral point on the supramastoid crest was analyzed here, as it is applicable to features described as unique to *H. erectus* (i.e., well-developed supramastoid crests, small biasterionic breadth).

Data were obtained using a MicroScribe (Immersion Corp., San Jose, CA) digitizer (model 3D or 3DX, depending on when data were collected). Landmarks were identified and marked using pencil or artist's putty prior to the collection of data and each specimen was mounted in a stable elevated ring so that all landmarks could be obtained in a single series.

Three-dimensional geometric morphometrics

Three-dimensional (3D) geometric morphometric methods have recently seen widespread use in physical anthropology (Lynch et al., 1996; Yaroch, 1996; O'Higgins and Jones, 1998; Delson et al., 2001; Harvati, 2001, 2003a,b; Hennessy and Stringer, 2002; Lockwood et al., 2002, 2004; Guy et al., 2003; etc.). Accordingly, these methods are discussed here only to briefly explain and justify their use in this study.

For this analysis, landmark configurations were standardized using Generalized Procrustes Analysis (GPA), a method of superimposition that minimizes differences between forms (Zelditch et al., 2004). This method works by centering, scaling, and rotating objects so that the sum of the squared distances between equivalent landmarks in a group of forms is minimized (Rohlf, 1990; Zelditch et al., 2004). Following GPA, landmark coordinates are represented as points in Kendall's shape space, where each point represents the shape of a configuration of points in space, irrespective of size, position, and orientation (Slice et al., 1998). Procrustes residuals—the set of vectors connecting the landmarks in the final Procrustes rotated consensus configuration (Slice et al., 1998)—then form the basis for all subsequent statistical analyses.

Because Kendall's shape space is curved (non-Euclidean), tangent projection of these coordinates into a linear (Euclidean)

Table 3
Landmark definitions

LMK No.	Definition
1	Intersection of the infratemporal crest and sphenosquamosal suture
2	Most anterior point on the articular surface of the articular eminence
3	Most inferior point on the medial margin of the articular surface of the articular eminence
4	Center of the articular eminence
5	Deepest point within the mandibular fossa
6	Most inferior point on the postglenoid process
7	Point on the anterior margin of the tympanic element that is closest to the carotid canal
8	Most lateral point on the vagina of the styloid process (whether process is present or absent)
9	Most lateral point on the margin of the stylomastoid foramen
10	Most lateral point on the jugular fossa
11	Most inferior point on the external acoustic porus
12	Most inferolateral point on the tympanic element of the temporal bone
13	Point of inflection where the braincase curves laterally into the supraglenoid gutter, in the coronal plane of the mandibular fossa
14	Point on the lateral margin of the zygomatic process of the temporal bone at the position of the postglenoid process
15	Auriculare
16	Porion
17	Most lateral point on the supramastoid crest
18	Asterion

space is necessary for analysis (Dryden and Mardia, 1993; O'Higgins and Jones, 1998). If variation within the sample is relatively small compared to the complete shape space for the number of landmarks (as is true for most biological data), then this projection is valid, and it is possible to apply traditional statistical analyses to the study of shape variation (Bookstein, 1996; Slice et al., 1998). For a temporal bone dataset similar to that used here, Lockwood et al. (2004) showed that Euclidean distances of Procrustes data were highly correlated ($r > 0.9999$) with true Procrustes distances.

Variation within a sample can be evaluated and summarized using principal components analysis (PCA), also referred to as relative warp analysis. Relative warps are the principal components of a distribution of shapes in tangent shape-space (Slice et al., 1998), where axes are interpreted as shape changes around the mean form (or consensus configuration; Slice et al., 1998; Zelditch et al., 2004). Principal components (PCs), or factors, summarize information concerning the distribution of specimens. PCA was used here to explore overall variation within both the extant and fossil samples, to provide an overview of morphological variation within and among all included specimens, and to assist in the visualization of fossil groupings, rather than as a statistical method of hypothesis testing. Shape changes along PC axes were visualized using both wireframe diagrams that represent the morphology being analyzed, as well as thin-plate spline analysis (TPSA) which uses a Cartesian transformation grid (Thompson, 1917; Bookstein, 1991) to visualize changes in relative landmark placement between landmark configurations.

Finally, Procrustes distances were calculated in order to statistically evaluate variation within the sample. These distances were measured by estimating the Euclidean distance between Procrustes coordinates for two specimens or groups (Slice et al., 1998; Zelditch et al., 2004). Procrustes distances were used in two ways in this study: 1) comparing distributions of distances among fossil specimens to distributions of intra- and interspecific distances among extant specimens, and 2) testing whether groups were significantly different from one another, based on permutation tests.

To compare distributions, frequencies of the distribution of Procrustes distances were calculated to illustrate the variation observed within and among living apes and humans. Once these distributions were calculated for the samples of extant taxa, the distributions of distances among individual specimens within groups of fossils were compared to the distributions observed for the extant taxa. This method quantified the "morphological distance" within and between two groups by providing a measure of intra- and inter-group variation. For instance, if a fossil group samples a single taxon, then one would expect the variation within that group to be consistent with the distributions of Procrustes distances observed within extant taxa. However, if a fossil group samples more than one species, then the Procrustes distance distribution for the fossil group will be greater than that observed for intraspecific variation in the samples of extant species. Correspondingly, the more divergent the specimens sampled and collapsed into a single group, the higher the mean value for the Procrustes distances.

To assess whether a given fossil distribution was statistically indistinguishable from any of the extant intra- or interspecific Procrustes distance distributions, a Kruskal-Wallis test was used with a two-tailed multiple (*post hoc*) comparisons test to determine the significance of the comparisons. To obtain distributions for statistical comparison, the mean Procrustes distances from each specimen to all others was calculated. This procedure was necessary to reflect the correct degrees of freedom, which would be artificially inflated if all pairwise distances were used. For example, to obtain a distribution of Procrustes distances for intraspecific variation in *Homo*, the distance from specimen 1 to all other specimens was averaged, as was the distance from specimen 2 to all other specimens, and for specimen 3, and so on. This resulted in the same number of mean values in the distribution as there were specimens included. If a fossil sample was statistically significantly different (at the $p < 0.05$ level) from all of the intraspecific distributions, but indistinguishable from one or more interspecific distributions, then it can be reasonably argued that the variation within the fossil sample is consistent with sampling multiple species.

In order to measure the morphological distance between groups, Procrustes distances were also used in this study through a comparison of the mean Procrustes distances among extant and fossil taxa. Permutation tests, where null distributions are generated by randomly allocating individuals to groups, were carried out in order to assess the significance of a Procrustes distance (Harcourt-Smith, 2002). For each comparison, the observed distance between two groups (i.e., the test statistic) was compared to the distribution of distances between randomly allocated groups. The observed distance was

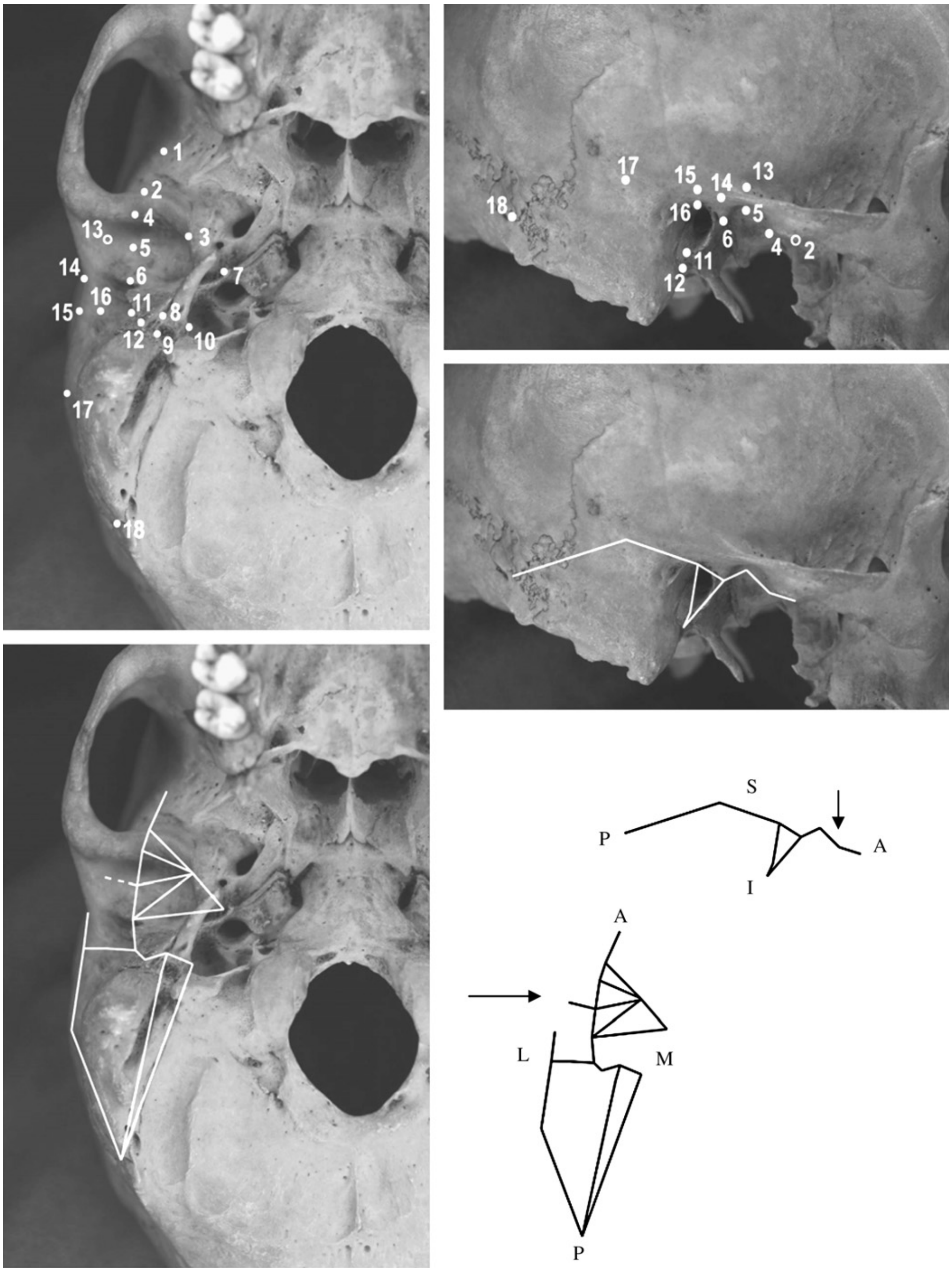

Fig. 1. Inferior (left) and lateral (above right) views of a human cranium showing landmarks and wireframe diagrams used in this study. Numbers correspond to those listed in Table 3. A: anterior; P: posterior; S: superior; I: inferior; L: lateral; M: medial.

considered statistically significant when it was greater than 95% of the permuted distances. In each analysis, 10,000 iterations were calculated for each pair of taxa, giving a minimum possible *p*-value of 0.0001.

For both of the Procrustes distance analyses discussed above, the extant taxa examined are defined in Table 1. For the fossils, *a priori* scenarios or groupings of fossils to be tested were taken from the literature (Table 4). These groups include a single species scenario, two species (with two different configurations of the species where the placement of OH 9 changes between configurations), and geographical and chronological groupings. It should be noted, however, that several of these scenarios are not mutually exclusive; for instance, the specimens included in the two species (A) and geographical groupings are identical. This pattern is an artifact of the paucity of later African specimens available for analysis, but is also reflective of the primary division of variation within the *H. erectus* sample.

The fossil sample was also analyzed *a posteriori* through unweighted pair group average (UPGMA) cluster analysis using the individual Procrustes distances between fossil specimens, specifically to examine how individual fossil specimens group with one another phenetically. This was done

Table 4
A priori fossil groups tested in this analysis as discussed in the literature (Andrews, 1984; Stringer, 1984; Wood, 1984, 1994; Braüer, 1994; Antón, 2002a, 2003; Kidder and Durband, 2004; etc.)

Scenario			Specimens included	
Single Species	*H. erectus*		All specimens	
Two species	A	*H. ergaster*	KNM-WT 15000	KNM-ER 3733
			KNM-ER 3883	D2280
			OH 9	
		H. erectus	Sangiran 4	Sangiran 17
			Ngandong 6	Ngandong 7
			Ngandong 12	Sambungmacan 3
			Sambungmacan 1	Zhoukoudian III
			Zhoukoudian XI	Zhoukoudian XII
	B	*H. ergaster*	KNM-WT 15000	KNM-ER 3883
			KNM-ER 3733	D2280
		H. erectus	OH 9	Sangiran 4
			Sangiran 17	Ngandong 6
			Ngandong 7	Ngandong 12
			Sambungmacan 1	Sambungmacan 3
			Zhoukoudian III	Zhoukoudian XI
			Zhoukoudian XII	
Geographical*	African/European		KNM-WT 15000	KNM-ER 3733
			KNM-ER 3883	D2280
			OH 9	
	Asian	Chinese	Zhoukoudian III	Zhoukoudian XI
			Zhoukoudian XII	
		Indonesian	Sangiran 4	Sangiran 17
			Ngandong 6	Ngandong 7
			Ngandong 12	Sambungmacan 1
			Sambungmacan 3	
Temporal	Early		KNM-WT 15000	KNM-ER 3733
			KNM-ER 3883	D2280
			OH 9	Sangiran 4
			Sangiran 17	
	Late		Zhoukoudian III	Zhoukoudian XI
			Zhoukoudian XII	Ngandong 6
			Ngandong 7	Ngandong 12
			Sambungmacan 1	Sambungmacan 3

* Although specimens are divided into African/European, Chinese, and Indonesian groupings, only the division between the African/European and Asian samples is examined here.

primarily to examine the integrity of the *a priori* groups and to compare how the fossil specimens clustered on the basis of their morphology to expected groupings from the literature.

Generalized Procrustes Analysis, PCA, and thin plate spline analyses were carried out using Morphologika (O'Higgins and Jones, 1998). Procrustes distances between individuals and between groups were calculated using software provided by W. Harcourt-Smith and created by P. O'Higgins. Cluster analyses, plots of intra- and intertaxonomic Procrustes distances, and the Kruskal-Wallis test were conducted and visualized using Statistica (Release 6.1, Statsoft, Inc.).

Hypotheses

As stated above, the goal of the analysis was to evaluate taxonomic explanations for the observed variation within *H. erectus* (*sensu lato*). To do so, we frame statistical hypotheses within the broader context of the taxonomic hypotheses. Procrustes distances between individuals and between groups of specimens are compared to distributions of Procrustes distances within and between extant species. In each comparison, the statistical null hypothesis is that variation in *H. erectus* approximates variation in extant species, whether constituting one or two species. In other words, we are not simply asking whether variation in *H. erectus* is "too great" when compared to the most variable of the extant taxa; we are also testing whether this variation is consistent with multiple-species groups and whether previously suggested groupings of fossils within *H. erectus* show differences consistent with those seen among our samples of extant species.

Support for a multiple-species classification of *H. erectus* (*sensu lato*) would come from the following results:

1) Procrustes distances among all individuals within the fossil sample are statistically significantly distinguishable from, and greater than, distributions of intraspecific Procrustes distances for the extant taxa.
2) Procrustes distances between the means of any fossil groups (i.e., between African and Asian or *H. ergaster* and *H. erectus* specimens) are statistically significant and are consistent with the observed ranges of distances between our samples of extant species.

Failing to obtain these results would support the null taxonomic hypothesis of this study: that *Homo erectus* should be considered a single polytypic species. Variation within this taxon would then be inferred to be due to within-species geographical and/or chronological variation.

A more complicated pattern would emerge if levels of variation are generally high, but previously suggested multiple-species scenarios do not produce significantly different groups or reduce levels of variation within each group to the level seen in our samples of extant species. For that reason, high levels of variation could potentially be explained by sampling: 1) an anagenetically evolving lineage; 2) a single, highly sexually dimorphic taxon (i.e., a higher level of sexual dimorphism than observed in extant hominids); or 3) populations that are more divergent than populations represented by the comparative samples. In discussing the results, these potential explanations will be taken into account.

Error testing

Because the data from the samples of extant taxa examined here were primarily collected by two researchers (C.E.T. and C.A.L.), a test of interobserver error was conducted to ensure that all of the data were comparable. To gauge this error, C.E.T. re-digitized 23 modern human specimens from the Hamann-Todd Osteological Collection (Cleveland Museum of Natural History) that were digitized by C.A.L. in 1999. Procrustes distances were calculated between repeated trials of the same individuals and between different individuals and the distribution of these distances were compared (Fig. 2). Except for one individual, the Procrustes distances calculated

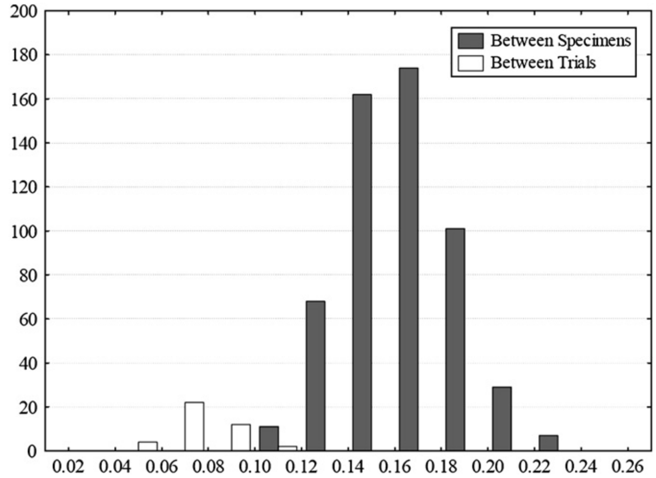

Fig. 2. Interobserver error analysis. Black columns represent the frequency distribution of Procrustes distances between individual *H. sapiens* specimens ($n = 24$). White columns represent the distribution of Procrustes distances between repeated trials by C.E.T. and C.A.L. of the same individuals. The frequency values are exaggerated for better visualization.

between trials of the same specimen were smaller than for those calculated between specimens, suggesting that interobserver error was low (i.e., different trials of the same specimen were more similar to one another than to other specimens). This analysis therefore suggests that any influence of interobserver error is negligible in comparison to distributions of Procrustes distances among groups.

Intraobserver error for C.E.T. was also evaluated (error estimates for C.A.L. can be found in Lockwood et al., 2002). To measure this error, all fossil specimens and a subset of the extant human specimens were digitized twice during data collection, and Euclidean distances between landmarks for each trial were calculated. Error was acceptable if the distances between landmarks for each trial were 3 mm or less (~1.5 mm error for each landmark); specimens were re-digitized if the maximum error was found to be above 3 mm. For the most part, error was below 1 mm. No specific landmarks were found to be more prone to error than any other.

Results

Principal components analysis

To examine how fossils fell in morphospace relative to the extant taxa, all of the extant and fossil specimens were analyzed together via GPA and PCA. The results of this analysis (Fig. 3) were, as expected, comparable to those of Lockwood et al. (2002); this is unsurprising given that the extant great ape dataset is the same. PC 1 explained the largest percentage of variance (52.2%) and separated apes and humans. PC 2 differentiated orangutans and gorillas from *Pan* (9% of the variation), and PC 3 separated *Pongo* from all other taxa, and, to a lesser extent, gorillas from *Pan* (4.5%). Differentiation along these PC axes reflects variation in the depth of the mandibular fossa, form of the articular eminence, and configuration of the tympanic and petrous elements—Lockwood et al. (2002) provide further description of the morphological differences among the extant taxa.

The fossil sample generally clustered together along PC 1, overlapping the modern human distribution. Within the fossils, the Koobi Fora specimens (KNM-ER 3733, KNM-ER 3883) and Dmanisi cranium D2280 are farthest from the human mean, whereas Zhoukoudian III, Sangiran 4, and Ngandong 12 are the most humanlike.

When the fossil sample was subjected to a principal components analysis separate from the modern hominid sample, variation along the PC axes was driven by numerous aspects of temporal bone shape (Fig. 4; Table 5). PC 1, which explained 23.1% of the variance in the sample, separated specimens primarily on the basis of postglenoid process size and position; size of the preglenoid plane; depth, size and position of the mandibular fossa; anteroposterior (AP) angulation of the tympanic plate (in lateral view); size and placement of the supramastoid crest; and AP width of the tympanic element. PC 2, which explained 20.1% of the variance, was influenced by the size of the preglenoid plane; placement of the supramastoid crest; depth and posterior extension of the mandibular fossa; and overall mediolateral (ML) compression of the temporal bone. Fewer features contributed to the variation along PC3, although this axis still explained a relatively large amount of variation (17.5%). Features heavily influencing this axis were the placement and size of the mandibular fossa; supramastoid crest placement (anterior or posterior); size of the glenoid region[2]; and the angle of the preglenoid plane.

Although the GPA analysis scales all specimens to centroid size, this standardization does not entirely remove size-related shape changes (i.e., allometry). Therefore, in order to evaluate the influence of allometry within the fossil sample, the PC axes were regressed on centroid size. Only one of these axes was found to be significantly correlated with centroid size, and this axis (PC 9) only explained approximately 3% of the variation in the sample. Additionally, when a size matrix of fossil specimens (i.e., a matrix of the absolute values of the difference in centroid size between two specimens) was compared to the fossil Procrustes distance matrix using a Mantel test (Mantel, 1976; Smouse et al., 1986), the correlation was found to be very small ($r = -0.003$) and was not significant ($p = 0.5$). As a result, groupings of fossil specimens along the PC axes are largely unrelated to size variation, and the influence of allometry in the calculation of Procrustes distances is not statistically significant.

Perhaps the most striking result of the principal components analysis is that there is no clear division between either the African or Asian specimens, nor between the specimens that have been traditionally attributed to *H. ergaster* or *H. erectus*. However, KNM-ER 3883, KNM-ER 3733, and KNM-WT 15000 do appear to group together along the negative loadings of PC 1 and PC 2 to the exclusion of all other specimens, including OH 9 and Dmanisi 2280. The position

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[2] Following Kimbel et al. (2004), the terms glenoid and glenoid region refer generally to the cranial component of the temporomandibular joint.

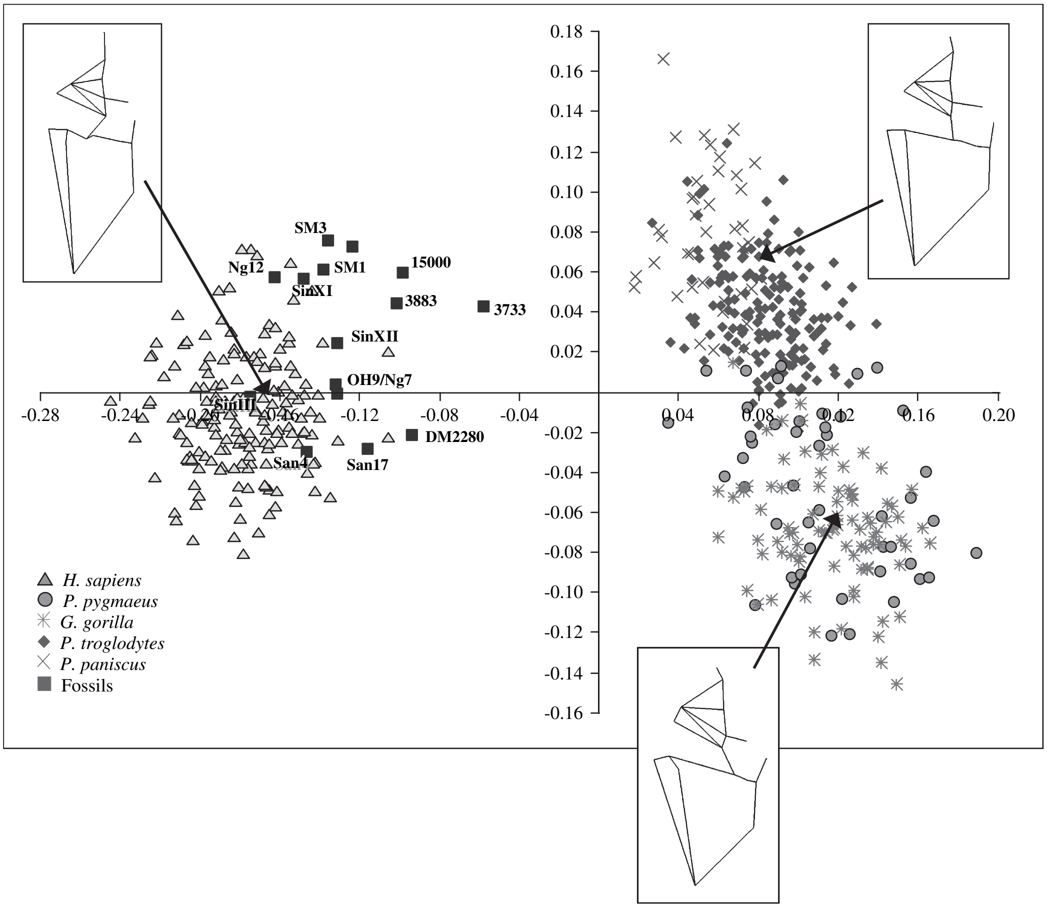

Fig. 3. PCA results for all hominids showing the relative locations of the extant and fossil samples. PC 1 (x-axis) accounts for 52.2% of the total variance in the sample, while PC 2 (y-axis) accounts for 9% of the total variance. The wireframe diagrams shown (which represent an inferior view of a left temporal bone) illustrate the variation along these two PC axes. Abbreviations for the fossil specimens are provided in Table 2.

of D2280 is especially interesting given its previous comparisons to some of the early African fossils (e.g., KNM-ER 3883, KNM-ER 3733, and KNM-WT 15000; Gabunia et al., 2000; Rightmire et al., 2006; but see Schwartz and Tattersall, 2002). The position of OH 9 on these PC axes is less surprising, although still striking, since it consistently clusters with the Ngandong and Sambungmacan fossils.

Within the Asian sample, the Ngandong and Sambungmacan specimens fall close to one another, as do the *Sinanthropus* Zhoukoudian specimens. The two Sangiran specimens, however, separate out along PC 1, although they are not as distinct on PC 2. These results are noteworthy, especially as these two individuals are probably the oldest Asian specimens in the sample examined here, and are separated in time from one another by perhaps 400 kyr (Swisher et al., 1994, 1996; Antón, 2003). Sangiran 4, in particular, is separated from the rest of the fossil specimens primarily on the basis of its extremely laterally placed postglenoid process, small glenoid region, and deep mandibular fossa.

The Kenyan specimens also appear to be morphologically diverse, given the wide separation between KNM-ER 3733, KNM-ER 3883, and KNM-WT 15000. Moreover, KNM-ER 3883 is more similar to the Asian fossils than is KNM-ER 3733. When the separation of these three specimens along PC 1 and PC 2 is examined, KNM-WT 15000 is seen to have a smaller postglenoid process; a more extensive preglenoid plane; a shallower mandibular fossa; a lower and more anterior placement of the supramastoid crest; and some mediolateral compression of the temporal bone overall.

The major morphological differences between the consensus configuration of KNM-ER 3733 and KNM-ER 3883 and the morphologies in the Asian (plus OH 9) group (Fig. 5) include lateral placement of the postglenoid process, increased depth of the mandibular fossa and increased height of the articular eminence, reduction of the preglenoid plane, medial placement and reduced size of the glenoid region, and a more anteriorly angled tympanic plate in the Asian specimens. It should be noted, however, that the expression of features among the Asian specimens is variable, and that the results of the PCA and TPSA do not support clear morphological groupings of fossil specimens.

Individual Procrustes distances

Procrustes distances between individuals within the extant sample were calculated in order to examine the variation within and between taxa. Figure 6 is a box plot of these distances within and among species. In this plot, the higher the

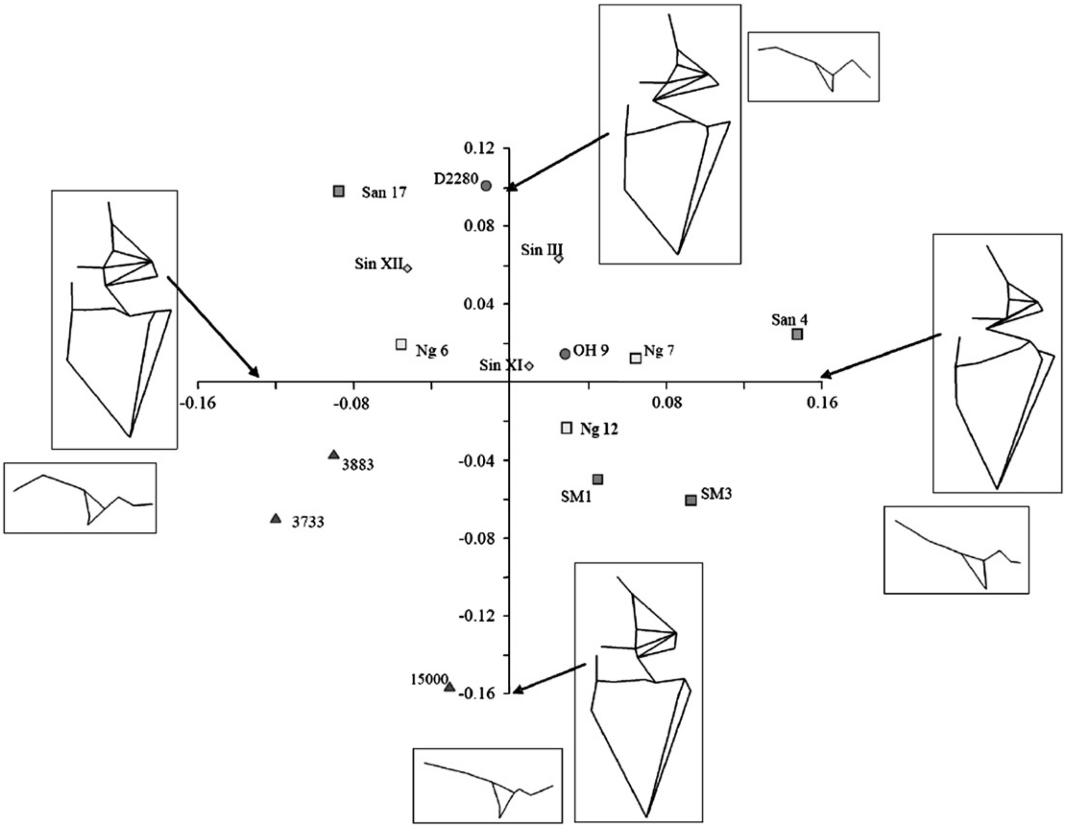

Fig. 4. PCA results for the fossil sample. PC 1 (x-axis) represents approximately 23.1% of the variance within the fossil specimens, while PC 2 (y-axis) accounts for 20.1% of the total variance. The wireframe diagrams (inferior and lateral views of a right temporal bone) are shown to illustrate the morphological variation along these two PC axes. Specimen abbreviations are provided in Table 2.

median value for a group and the wider the range of Procrustes distances between individuals, the greater the variation within the sample; the more dissimilar the two groups being compared, the higher the median value of Procrustes distances.

Figure 6 illustrates the high degree of variation in temporal bone morphology within the samples examined here. There is a relatively small amount of variation within *P. troglodytes*, with larger amounts of variation (and higher median values) in all of the other hominid taxa sampled. The highest intraspecific variation observed was in *P. pygmaeus*; this appears to be a result of both a high degree of variation among populations and a large degree of sexual dimorphism within this taxon. Procrustes distances observed within species were, on average, slightly higher than those observed within subspecies (not shown).

As would be expected, distributions of Procrustes distances for comparisons between species were found to be higher than intraspecific distances, although there is a large degree of overlap. Such overlap has been illustrated by Lockwood et al. (2005) for temporal bone data and by Aiello et al. (2000) for cranial metrics generally. The comparisons between humans and apes are an exception, with the median values and distributions considerably higher than any of the observed intraspecific or interspecific comparisons of the ape samples. These results emphasize the highly autapomorphic state of the human temporal bone in relation to the general ape condition, since the distinct morphology of the human temporal bone drives the large Procrustes distances in these comparisons.

A priori *fossil groupings*

When the distribution of distances among all of the specimens within the fossil sample is compared to intra- and interspecific distances in the sample of extant species (Fig. 6, single species), it is clear that the average variation within the fossils is greater than that observed within any of the hominid comparative taxa, although there is some overlap between the fossil distribution and several of the extant intraspecific distributions (particularly for *P. pygmaeus*). The distribution of Procrustes distances among all individuals within the fossil sample is most similar to the distribution of Procrustes distances in the interspecific and intergeneric comparisons among ape taxa, and is less similar to the intraspecific distributions for all of the extant hominids, with the exception of *P. pygmaeus* (Table 6). Differences among the fossils are substantially smaller than differences between apes and humans, as expected.

When the fossil specimens were separated into *a priori* groups, in all cases the *H. ergaster* or African groups were more variable (i.e., have a higher median value) than the *H. erectus* or Asian samples (Fig. 6). This result is particularly interesting since the *H. ergaster*/African group spans a shorter

Table 5
Expression of morphological variation in the fossil sample along PC axes 1–4. Features are defined in relation to the centroid shape, and are not intended to infer phylogeny or primitive versus derived character states. Signs indicate the loading coefficients of eigenvectors. Many features are likely correlated

Feature	PC1 (23.1%)		PC2 (20.1%)		PC3 (17.5%)		PC4 (9%)	
	−	+	−	+	−	+	−	+
Articular eminence inclination	shallow	steep	shallow	steep	X	X	steep	steeper
Articular eminence width	wide	narrow	wide	narrow	narrow	wide	wide	narrow
External auditory meatus orientation	posterior	anterior	posterior	anterior	X	X	X	X
External auditory meatus size	small	large	large	small	X	X	large	small
Jugular fossa placement	anterior	posterior	posterior	anterior	anterior	posterior	anterior	posterior
Mandibular fossa depth	shallow	deep	shallow	deep	deeper	deep	X	X
Mandibular fossa placement	X	X	medial	lateral	antero-lateral	postero-medial	anterior	posterior
Postglenoid process placement	medial	lateral	medial	lateral	lateral	medial	X	X
Postglenoid process size (inferior projection)	large	small	small	large	X	X	large	small
Preglenoid plane angle (direction plane is facing)	X	X	anterior	posterior	posterior	anterior	anterior	posterior
Preglenoid plane size	large	small	large	small	small	large	large	small
Supramastoid crest placement	superior	inferior	anterior	posterior	anterior	posterior	inferior	superior
Supramastoid crest size	large	small	X	X	X	X	small	large
Suprameatal crest size	X	X	X	X	small	large	X	X
Temporal length (AP)	short	long	long	short	long	short	X	X
Temporal width (ML)	wide	narrow	narrow	wide	narrow	wide	X	X
Glenoid size	large	small	large	small	small	large	large	small
Tympanic length (AP)	short	long	short	long	X	X	X	X
Tympanic orientation/inclination	horizontal	vertical	horizontal	vertical	X	X	X	X
Tympanic projection/extension*	lateral	medial	lateral	medial	lateral	medial	X	X
Zygomatic root size	large	small	X	X	X	X	large	small

X: little to no effect on PC.

* This feature, while variable in the sample, is evaluated in relation to the postglenoid process, which, in some specimens, is extremely laterally placed.

interval of time (~400 kyr) than the *H. erectus*/Asian sample (~1.5 myr). Statistically, the *H. ergaster* groupings are indistinguishable from all of the extant distributions, whereas the *H. erectus* samples are significantly different from the variation observed in the two most extreme ape-human comparisons (Table 6). Within the Asian sample, however, the distribution for the Zhoukoudian sample (which contains only three specimens and is drawn from a relatively restricted period of time) is extremely small, and falls well within the extant intraspecific distributions. The distribution for the Indonesian sample, in contrast, is considerably wider. Statistically, both of these Asian groups are significantly different only from the *Gorilla-Homo* and *Pongo-Homo* distributions. Correspondingly, when the specimens are separated on the basis of time, the "early" group is markedly more diverse than the "late" group; the "early" distribution is significantly more variable than the *P. troglodytes* and *P. paniscus* samples, whereas the "late" group differs only from the great ape-*Homo* comparisons.

A posteriori *fossil groupings*

To investigate the phenetic relationships between specimens within the sample *a posteriori*, the matrix of Procrustes distances between fossil specimens (Table 7) was subjected to UPGMA cluster analysis (Fig. 7). Two major groups of specimens were identified: one joined KNM-ER 3733, KNM-ER 3883, and KNM-WT 15000, and the second group included all other specimens. Both of these groups show relatively large linkage distances between specimens. This cluster analysis therefore suggests that any groups present within the fossil sample are not purely geographically or chronologically based. It is notable, though, that the Kenyan specimens span a maximum time of only 270 kyr (Antón, 2003) while the two remaining African/European specimens, D2280 and OH 9, which have been dated to the same general time period as the Kenyan specimens, are relatively distinct and cluster instead with the Zhoukoudian specimens (D2280) and Ngandong 7 and 12 (OH 9) in the UPGMA phenogram. Also of note is the distinctiveness of Sangiran 4 from all of the other Asian specimens. Examination of the individual Procrustes distances between specimens (Table 7) indicates that Sangiran 4 is most similar to Zhoukoudian III (0.1814) and Sambungmacan 3 (0.1973). Conversely, Sangiran 4 is least similar to Sangiran 17 (0.2900).

Procrustes distances between group means

Permutation tests for the significance of the Procrustes distances between the means of the extant groups reveal that these distances are highly statistically significant at the Bonferroni-corrected p-value of 0.0004 (0.05/105), except for Southeast Asian to Australian Aborigine extant human populations. In fact, all groups are significantly different at the $p < 0.0001$ level, except for the measured distance between the means of *P. p. pygmaeus* and *P. p. abelli* ($p = 0.0019$)

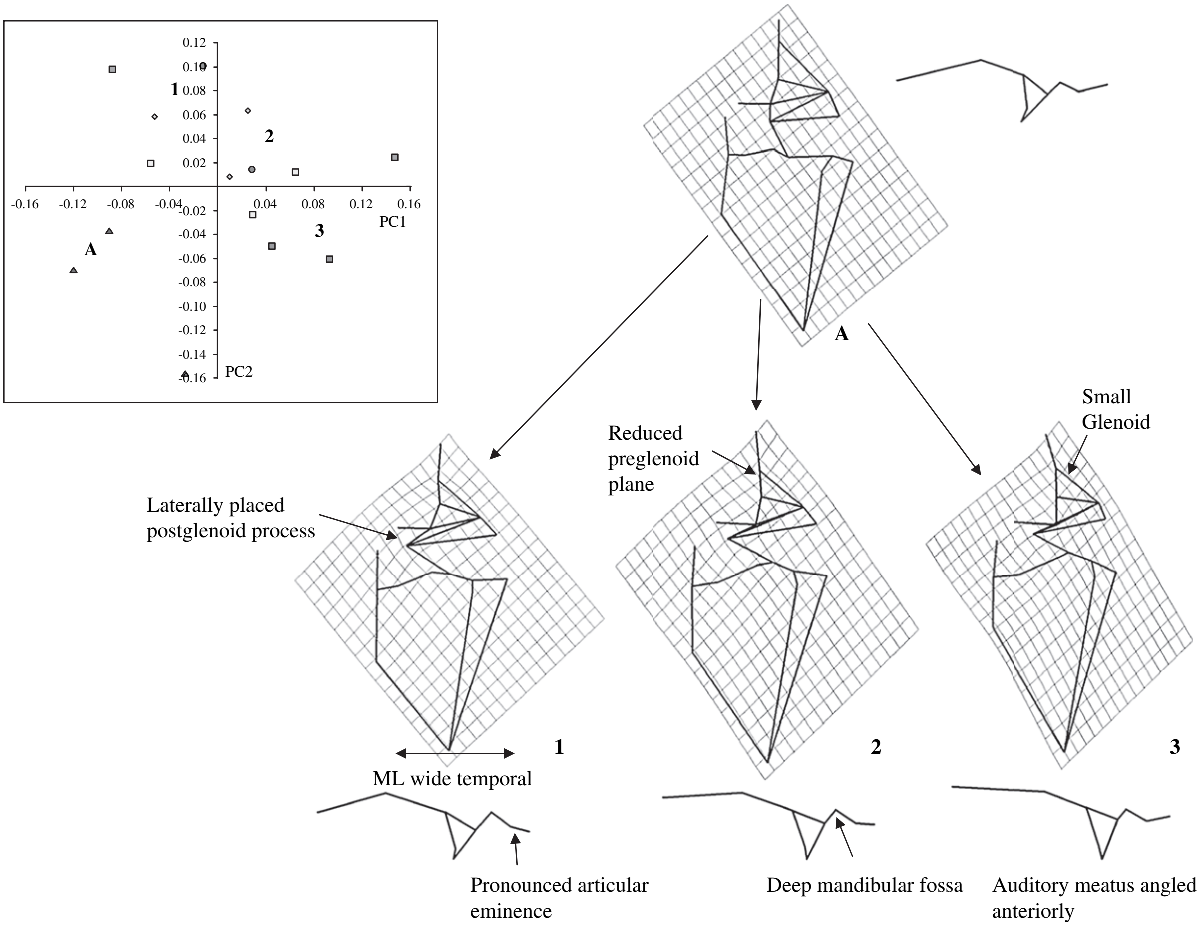

Fig. 5. TPSA showing the transformation from a consensus configuration of ER 3733, 3883, and WT 15000 (A) to three hypothetical landmark configurations in morphospace along PCs 1 and 2 (1–3). Inferior and lateral view wireframes of a right temporal bone are shown. Labeled characters distinguish shapes 1–3 from shape A. Comparisons are not meant to imply ancestor-descendent relationships, but are instead used to illustrate general changes in temporal bone morphology between regions along PC 1 and PC 2.

and between the Southeast Asian and Australian Aborigine human populations ($p = 0.0165$). The Procrustes distances between geographical groups within species range from 0.0417 (*P. t. schweinfurthii* to *P. t. troglodytes*) to 0.0851 (Nubians to Southeast Asians). Distances between species range from 0.0869 (*P. troglodytes* to *P. paniscus*) to 0.3059 (*P. p. abelli* to *H. sapiens*). Cluster analysis of the distance matrix between the extant hominid groups (Fig. 8) matches that published by Lockwood et al. (2002). Examination of these Procrustes distances allows for the delineation of ranges for intra- and interspecific distances (Fig. 8), as the lowest interspecific distance measured (between *P. troglodytes* and *P. paniscus*) was approximately 0.09.

The distances among the *a priori* fossil groups are also variable (Fig. 8), with the smallest Procrustes distances between the chronological groupings of specimens at 0.0896, a value that is not statistically significant ($p = 0.2501$). The largest distances were found in the two-species (and geographic) model. In configuration A (which is identical to the African/European vs. Asian model), where OH 9 is considered to represent *H. ergaster*, the Procrustes distance between taxa was 0.1116, with a p-value of 0.027. In configuration B, in which OH 9 is included in *H. erectus*, the Procrustes distance is slightly higher, at 0.1339 ($p = 0.0011$). Although both of the p-values for the two-species scenarios are significant at the $p < 0.05$ level, after Bonferroni correction ($p < 0.0125$), only the p-value for the two-species scenario B is statistically significant. Similarly, the distance between the Indonesian and Chinese specimens (0.1112) was very similar to the Procrustes distance between the African and Asian specimens, but was not statistically significant ($p = 0.2299$), perhaps because of small sample sizes. With the exception of the Procrustes distance between the early and late groups, all distances fell within the range of extant interspecific distances and are larger than distances between human populations or between great ape subspecies.

Discussion

The results of the analyses presented here indicate a high level of diversity within the fossil sample. Principal components and cluster analyses tentatively separate the fossils into two groups: the first is composed of the Kenyan specimens KNM-ER 3733, ER-3883, and KNM-WT 15000, while the other includes all of the Asian specimens, as well as OH 9

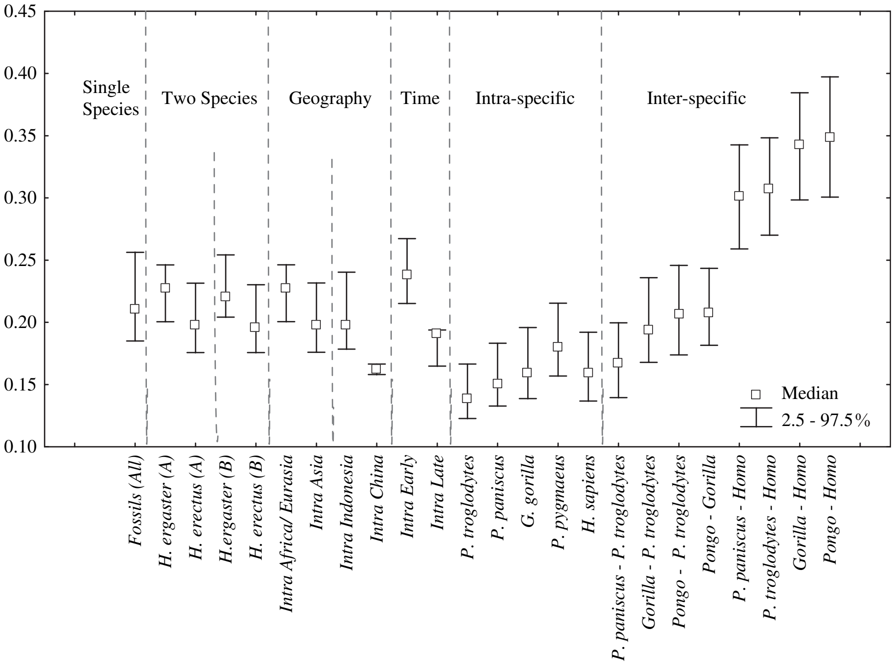

Fig. 6. Range plot of Procrustes distances among all individuals within the extant sample as compared to the distribution of Procrustes distances within the *a priori* fossil groups. Distributions shown for a single group or taxon (e.g., *P. troglodytes*) represent values among all individuals within that group, whereas distributions comparing two taxa (e.g., *P. troglodytes* and *P. paniscus*) represent Procrustes distances between individuals within each of these taxa (i.e., these values do not include Procrustes distances among individuals within the same group). Ranges shown represent the median and 95% confidence interval for each group.

and Dmanisi 2280. Morphologically, these groups are distinguished primarily by changes in the size and depth of the mandibular fossa, position of the postglenoid process, and size of the preglenoid plane.

When the distribution of Procrustes distances between individuals in the *a priori* fossil groups are compared to distributions of intra- and interspecific variation in the samples of extant taxa, the range of distances within the fossil samples are, on average, higher and the distribution of distances between all the specimens is significantly different statistically from all of the extant intraspecific distances, except those within *P. pygmaeus*. High levels of variation are also seen within each of the *a priori* fossil groups, particularly in the Asian sample. In general, differences among the fossil specimens studied here are similar to those seen among fossil temporal bones normally assigned to different species, as shown by Lockwood et al. (2005). That said, the same study illustrated that Procrustes distances among intraspecific fossil pairs may also be relatively high.

Analysis of the Procrustes distances between the means of the *a priori* fossil groups reveals that the morphological distance between *H. ergaster* and *H. erectus* is statistically significant when OH 9 is included in the *H. erectus* sample. All Procrustes distances between groups fall within the range of

Table 6
Matrix of corrected *p*-values for the Kruskal-Wallis test of significance between groups. Significant *p*-values are in bold

	Fossils (All)	*H. ergaster* (A)	*H. erectus* (A)	*H. ergaster* (B)	*H. erectus* (B)	Intra Africa/Eurasia	Intra Asia	Intra China	Intra Indonesia	Intra Early	Intra Late
P. troglodytes	**0.00002**	0.1155	0.0621	0.5255	0.0619	0.1125	0.0578	1.0000	0.2527	**0.0020**	1.0000
P. paniscus	**0.0055**	0.6741	0.9237	1.0000	1.0000	0.6592	0.8750	1.0000	1.0000	**0.0357**	1.0000
G. gorilla	**0.0269**	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.1401	1.0000
P. pygmaeus	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
H. sapiens	**0.0148**	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.1099	1.0000
P. paniscus - P. trog	0.1717	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.5303	1.0000
Gorilla - P. trog	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Pongo - P. trog	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Pongo - Gorilla	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
P. paniscus - Homo	1.0000	1.0000	0.5443	1.0000	0.1813	1.0000	0.5788	0.5429	1.0000	1.0000	0.0838
P. trog - Homo	0.3588	1.0000	0.1629	1.0000	**0.0452**	1.0000	0.1744	0.2891	1.0000	1.0000	**0.0245**
Gorilla - Homo	**0.0001**	1.0000	**0.0002**	1.0000	**0.00002**	1.0000	**0.0002**	**0.0101**	**0.0197**	1.0000	**0.00003**
Pongo - Homo	**0.00003**	1.0000	**0.00006**	1.0000	**0.000006**	1.0000	**0.00007**	**0.0058**	**0.0088**	0.7924	**0.00001**

Table 7
Matrix of Procrustes distances between fossil specimens

	3883	3733	15000	SM1	SM3	San17	San4	Ng12	Ng7	Ng6	SinXI	SinIII	SinXII	D2280	OH9
3883	-														
3733	0.1661	-													
15000	0.2155	0.2039	-												
SM1	0.2384	0.2300	0.2612	-											
SM3	0.2446	0.2520	0.2341	0.1477	-										
San17	0.2089	0.2243	0.3066	0.2419	0.2677	-									
San4	0.2800	0.3073	0.2753	0.2455	0.1973	0.2900	-								
Ng12	0.1876	0.2278	0.2366	0.1646	0.1607	0.2122	0.2208	-							
Ng7	0.2173	0.2554	0.2712	0.1967	0.1923	0.2264	0.2077	0.1514	-						
Ng6	0.1747	0.2056	0.2769	0.1874	0.2092	0.1617	0.2798	0.1602	0.1949	-					
SinXI	0.1900	0.2102	0.2348	0.1757	0.1598	0.2006	0.2169	0.1680	0.1826	0.1625	-				
SinIII	0.2217	0.2447	0.2471	0.2325	0.2151	0.1991	0.1814	0.2021	0.1967	0.2082	0.1538	-			
SinXII	0.2011	0.2052	0.2581	0.2295	0.2261	0.1624	0.2445	0.1919	0.2352	0.1731	0.1622	0.1706	-		
D2280	0.2321	0.2427	0.2878	0.2645	0.2586	0.2160	0.2325	0.2390	0.2335	0.2456	0.1949	0.1621	0.1836	-	
OH9	0.1881	0.2237	0.2776	0.1902	0.1802	0.2094	0.2186	0.1427	0.1432	0.1851	0.1759	0.2199	0.1987	0.2192	-

interspecific variation for the comparative samples, with the exception of the distance between the "early" and "late" specimen groupings. The latter finding indicates that chronological variation is not the primary source of variation in the *H. erectus* (*sensu lato*) sample.

Diagnostic features in Homo erectus

Although it is difficult to equate landmark configurations to discrete character-states, landmarks do reflect morphology accurately enough to infer the size or placement of some features. For instance, continuously variable features, such as the size of the postglenoid process, are easily reflected via 3D geometric morphometrics. Conversely, nonmetric characters, such as the presence or absence of the squamotympanic fissure—a fissure between the entoglenoid process and the tympanic plate (Weidenreich, 1943; Andrews, 1984; Rightmire, 1984, 1990)—are difficult to capture, although other landmarks may be indirectly influenced by the presence or absence of any such features.

A number of nonmetric features of the temporal bone have been identified by previous researchers as being associated with one or more sample divisions of *H. erectus*. These features include a mastoid fissure; angular torus; a preglenoid tubercle; prominent petrosal spine; an anteriorly open digastric groove; and an entoglenoid composed entirely of squamous temporal rather than sphenoid (Weidenreich, 1943; Clark, 1964; Tobias, 1967; Macintosh and Larnach, 1972; Heim, 1974, 1976; Santa Luca, 1980; Andrews, 1984; Rightmire, 1984, 1990; Stringer, 1984; Braüer and Leakey, 1986; Condemi, 1989; Clarke, 1990; Picq, 1990; Pope, 1992; Etler, 1994; Martinez and Arsuaga, 1997; Zeitoun, 2003). The states

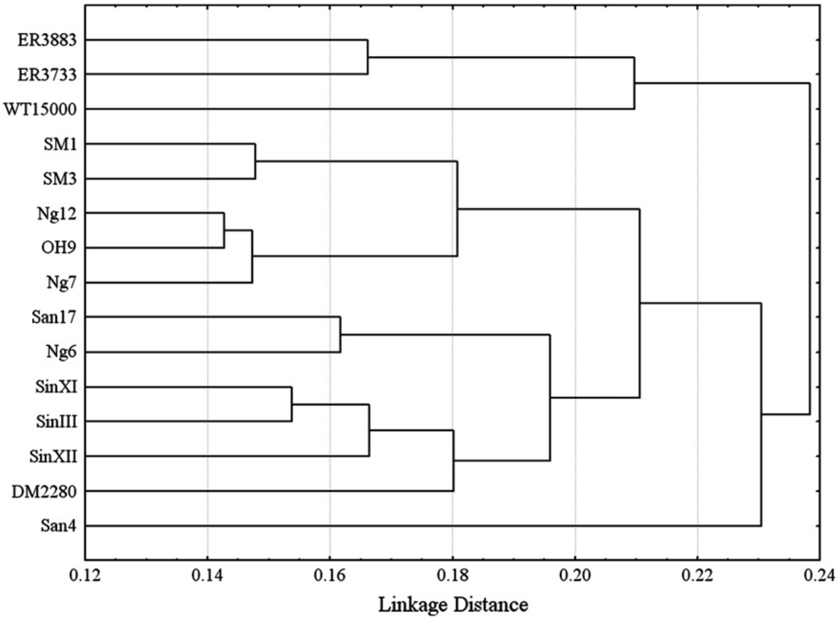

Fig. 7. UPGMA cluster analysis of Procrustes distances between fossil specimens. Specimen abbreviations are provided in Table 2.

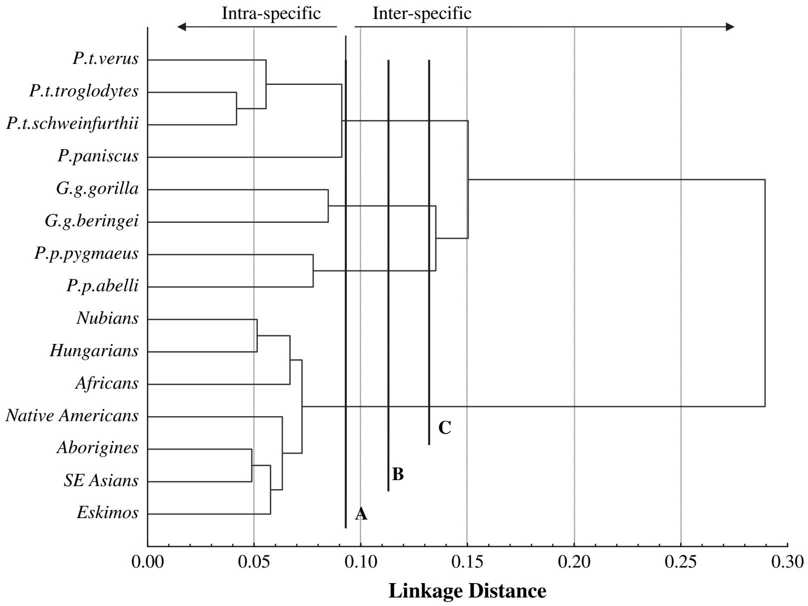

Fig. 8. UPGMA cluster analysis of mean Procrustes distances between extant taxa examined in this study, with the ranges for intraspecfic and interspecific variation identified using the extant sample denoted. Vertical lines indicate the mean Procrustes distances (mPd) between *a priori* fossil groups. A: "early" vs. "late" specimens (mPd = 0.0896, $p = 0.2501$); B: China vs. Indonesia (mPd = 0.1112, $p = 0.2299$) and *H. ergaster* (A) vs. *H. erectus* (A)/Africa/Eurasia vs. Asia (mPd = 0.1116, $p = 0.027$): and C: *H. ergaster* (B) vs. *H. erectus* (B) (mPd = 0.1339, $p = 0.0011$).

of these features were not directly evaluated in this study, although such features may still impact the overall analysis.

The results of this analysis do, however, show direct links between particular landmark configurations (as indicated in the PCA, wireframe diagrams, and thin-plate splines above) and several aspects of temporal bone morphology that have previously been identified as unique in *H. erectus*, such as strongly developed supramastoid crests (Weidenreich, 1943; Santa Luca, 1980; Rightmire, 1984); the absence of a raised articular eminence (Weidenreich, 1943; Rightmire, 1984, 1990); and reduction of the postglenoid process (Weidenreich, 1943; Howells, 1980; Condemi, 1989; Picq, 1990; Rightmire, 1990; Etler, 1994). In addition, in the Asian sample the tympanic plate is angled anteriorly (in lateral view), which results in the long axis of the external auditory meatus running posterosuperiorly to anteroinferiorly. This feature may be associated with the presence of the tympanomastoid fissure (Andrews, 1984; Stringer, 1984; Antón, 2002a), even though the morphology of the mastoid is not represented in this analysis due to poor preservation of this region in the fossil sample.

Results of this study are consistent with interpretations from analyses of variation in qualitative features. In a recent analysis, Villmoare (2005) concluded that craniometric variation in *H. erectus* was not significantly greater than in modern human populations. In contrast, analysis of nonmetric characters suggested levels of variation above that seen in geographically distant populations of modern humans. Similarity between our results and the nonmetric analysis by Villmoare (2005) suggests that at least some of the qualitative features are captured by the geometric morphometric analysis, although clearly the impact of these discrete characters on 3D landmark configurations needs to be evaluated in further detail.

On the whole, these results indicate that the variation observed here can be used to identify traditionally recognized features of *H. erectus* and to distinguish between fossil groups. The majority of these differences have previously been noted (e.g., Stringer, 1984; Braüer, 1994; Martinez and Arsuaga, 1997; Antón, 2002a). The early African fossils (specifically including KNM-WT 15000, KNM-ER 3733, and KNM-ER 3883) are characterized by large glenoids; a shallow mandibular fossa with a poorly developed articular eminence; a relatively large postglenoid process; a large preglenoid plane; and a posteriorly angled tympanic plate. Conversely, "classic" *H. erectus* is characterized by a small glenoid; a reduced preglenoid plane; laterally placed postglenoid process; a deep mandibular fossa with a well developed articular eminence; and an anteriorly angled tympanic plate.

Taxonomic composition of H. erectus (sensu lato)

If the Asian and African samples of *H. erectus* represent a single species, we would expect variation in the combined fossil sample to be consistent with that seen within extant species. Our results suggest that the total sample variation in *H. erectus* is, however, mostly inconsistent with variation seen within extant species, based on the two criteria outlined in the hypothesis-testing section above. First, on average, levels of variation within the fossil sample are statistically significantly higher than distributions of intraspecific Procrustes distances for extant hominid taxa. Secondly, Procrustes distances between the means of *a priori* fossil groups (i.e., between African and Asian, or *H. ergaster* and *H. erectus* samples) are statistically significant, and are consistent with the observed ranges of distances between extant species.

However, the large overlap of the fossil sample and the individual Procrustes distance distributions for extant taxa (particularly the orangutan distribution), as well as the lack of statistical significance for most of the Procrustes distances between groups in the fossil sample, indicates that we cannot completely discount a single-species explanation for the observed variation. Finally, and perhaps most importantly, examination of the alternative taxonomic, geographic, and chronological divisions of the fossil sample demonstrate that these divisions do not reduce within-group variation to levels consistent with intraspecific comparisons of extant hominid taxa.

Suggestions of multiple species within *Homo erectus* have generally been confined to the recognition of two species: *H. ergaster* and *H. erectus*. While *H. erectus* is recognized as primarily Asian, and therefore has traditionally encompassed all of the Chinese and Javanese specimens, and *H. ergaster* has primarily included the early African specimens, most researchers place OH 9 in *H. erectus* (e.g., Wood, 1994; Antón, 2003). The data presented here suggest that OH 9 is most similar to the Ngandong specimens. Morphologically, OH resembles the Ngandong specimens by having a relatively smaller glenoid region; deeper mandibular fossa; more laterally placed postglenoid process; and a slightly anteriorly angled tympanic plate. This resemblance therefore suggests that OH 9 is more appropriately attributable to *H. erectus* (i.e., the two-species model B is most appropriate). Similarly, previous descriptions of the Dmanisi cranial materials have tended to ally these specimens with the Koobi Fora *H. ergaster* crania (Gabunia et al., 2000, 2001; Rightmire et al., 2006), although some features of the dentition and mandible have been compared more favorably to the Javan and Zhoukoudian materials (Rosas and Bermúdez de Castro, 1998; Gabunia et al., 2001). Our analysis indicates strong affinity of D2280 temporal bone morphology to that of the Zhoukoudian specimens, although these sites are widely separated from one another in both space and time ($\sim$1.2 myr). The most marked morphological similarities between Dmanisi 2280 and the Zhoukoudian specimens include a mediolaterally wide temporal bone with a posteriorly placed supramastoid crest, and a relatively small glenoid region with a deep mandibular fossa. This finding is consistent with recent descriptions of the Dmanisi crania (Rightmire et al., 2006), in which a number of features of the cranial base of Dmanisi 2280 were described as being similar to those first discussed by Weidenreich (1943) in reference to the *Sinanthropus* crania.

Both OH 9 and Dmanisi 2280 are generally similar in size to the Asian assemblages (Ngandong and Zhoukoudian, respectively) which they resemble. This is particularly true for OH 9, which has a cranial capacity (1,067 cc) that exceeds that of all of the other African specimens and is more consistent with the Asian sample (Antón, 2003). Dmanisi 2280, although different from the Zhoukoudian sample in cranial capacity—D2280 = 780 cc vs. Zhoukoudian average = 986 cc (Antón, 2003)—has a centroid size comparable to that of the Zhoukoudian specimens. Therefore, the similarity of OH 9 to the Ngandong specimens and of Dmanisi 2280 to the Zhoukoudian assemblage suggests that allometric variation might be present within the fossil sample. Although Generalized Procrustes Analysis scales all specimens to the same unit centroid size (which effectively removes isometric size from any subsequent analyses of the coordinate data), allometric effects are not removed. The results reported here, however, indicate that shape differences between the fossil specimens are uncorrelated with size differences, and therefore the role of allometry in the fossil sample is probably minimal. Given this finding, and the fact that fossil specimens are difficult to attribute to sex, there is no reason to assume that pronounced levels of sexual dimorphism underlie the observed variation in *H. erectus*, even though features of the temporal bone (e.g., size of the mastoid process) are frequently used to assign sex to humans (e.g., Buikstra and Ubelaker, 1994). As another example, orangutans show high levels of sexual dimorphism in shape and, therefore, high levels of shape variation. However, male and female orangutans are also very different in size. If sexual dimorphism was the major factor in explaining *H. erectus* shape variation, then a greater size influence would be expected.

The variation observed within the Kenyan fossil sample is striking, particularly the differentiation of KNM-WT 15000 from KNM-ER 3733 and KNM-ER 3883. Several lines of evidence suggest that the differences in temporal bone shape between KNM-WT 15000 and KNM-ER 3733 and KNM-ER 3883 are not entirely a result of ontogenetic variation. Studies quantifying temporal bone growth in humans indicate that many changes in temporal bone shape are completed relatively early. Thus, as KNM-WT 15000 is an older subadult, the majority of changes in temporal bone shape would have been completed before this individual's death, although some changes may still have occurred in cranial superstructures had KNM-WT 15000 survived into adulthood. Notably, Antón (2002b) considers Zhoukoudian III to be an older subadult or young adult in which the size of the brain is fully adult, even though some of the secondary cranial characters may not be completely developed. That these two subadult specimens do not appear more similar to one another than other specimens recovered from the same geological age or region lends further credence to the suggestion that the temporal bones of these specimens contain important diagnostic features and are (for the most part) adult in morphology.

Of course, dependence upon the existing ontogenetic data for the temporal bone relies on the assumption that *H. erectus* and *H. sapiens* share a common pattern of ontogenetic development in the temporal bone. Such an assumption is difficult to test with the existing sample of *H. erectus* crania. Clearly, further analyses of temporal bone growth in both great apes and humans are warranted in order to fully evaluate the impact of ontogenetic variation on this morphology. However, while the data presented here do indicate that KNM-WT 15000 is more morphologically distinct from KNM-ER 3733 and 3883 than might be expected given previous descriptions, KNM-WT 15000, KNM-ER 3733, and ER 3883 are more similar to one another (as indicated by the cluster analysis and Procrustes distance matrix of the fossil specimens presented above) than they are to the Eurasian, Chinese, or Indonesian specimens, despite the potential influence of ontogeny.

In comparison to the Kenyan sample, the diversity within the Asian *H. erectus* sample is more complex, as this sample includes more specimens which cover wider geographical and temporal ranges. It is unsurprising that the Zhoukoudian specimens cluster most closely to one another (Santa Luca, 1980; Antón, 2002a, 2003; Kidder and Durband, 2004). The same is true for the Sambungmacan and Ngandong crania, although there is more variation among the Ngandong sample than was originally expected, as this sample is usually considered relatively morphologically homogeneous (Santa Luca, 1980; Antón, 2002a, 2003; Schwartz and Tattersall, 2003). Notably, all three of these assemblages (Zhoukoudian, Sambungmacan, and Ngandong) are from relatively restricted time horizons, and therefore the low levels of variation observed within these three groups may be expected simply on the basis of time. Correspondingly, in the Sangiran sample, which includes the oldest of the Asian specimens, there is a high degree of divergence between Sangiran 4 and Sangiran 17. This may be related to the relatively larger separation of these two specimens in time—approximately 300,000 kyr (Antón, 2003)—in comparison to the Zhoukoudian, Sambungmacan, and Ngandong samples.

The data presented here are consistent with previous research by Antón (2002a) and Kidder and Durband (2004) that assessed metric and nonmetric variation within a range of Asian *H. erectus* specimens and found that the Zhoukoudian sample is easily distinguished from the Indonesian fossils. Furthermore, as noted by Antón (2002a), while the Zhoukoudian specimens are temporally intermediate between the geologically younger Ngandong and Sambungmacan specimens and the earlier Javanese sample (the variation in which encompasses that of the late specimens), the Zhoukoudian crania are not morphologically intermediate. Thus, there does appear to be a geographic component to the observed variation among the Asian specimens, which, as indicated by the results here, is high but not inconsistent with extant intraspecific variation. Consequently, while there may be multiple taxa lurking within the Asian sample, neither time nor geography are sufficient explanations for the observed variation.

Examination of variation within the two broad temporal groups included in this analysis suggests that variation within the sample cannot be easily partitioned into chronologically delimited species. The wide range of Procrustes distances in the "early" time group—specimens in which range from ca. 1.78 (KNM-ER 3733) to 1.3 Ma (Sangiran 17)—indicates a high level of diversity. In contrast, the "late" sample, which spans roughly the same amount of time—580 ka (Zhoukoudian III) to 50 ka (Ngandong)— is less variable, and is consistent with extant intraspecific variation. If evolutionary change within a lineage (anagenesis) was responsible for the observed pattern of variation, we might expect to see variation in morphological features through time. However, the morphological similarity between OH 9 and the Ngandong sample, as well as between Dmanisi 2280 and the Zhoukoudian specimens, indicate that the observed morphologies do not form a temporal morphocline from "early" to "late" samples. Furthermore, one of the morphologically unique specimens in the sample (Sangiran 4) is also one of the oldest, and is morphologically very distinct from its early African counterparts.

Given the extremely wide range of time from which the fossil sample studied here was drawn, it could be argued that relatively high levels of morphological variation in *H. erectus* should be expected, particularly in the context of the temporally restricted extant samples used in the comparative analysis. This lack of temporal variation in the extant comparative samples is a frequently encountered problem in analyses of fossil variation. Here we attempted to control for temporal variation by including extant hominoid samples that are mixed both geographically and taxonomically. Specifically, with the exception of *P. paniscus*, the samples for all of the species used in this analysis include multiple subspecies (e.g., *Pan*, *Gorilla*, *Pongo*) or, as is the case for the modern human sample, multiple geographically diverse populations, which may provide an analogue for chronological variation in the fossil record. For instance, by collapsing distinct subspecies of *Gorilla* and *Pongo*—which are often considered different species (Janczewski et al., 1990; Garner and Ryder, 1996; Rowe, 1996; Xu and Arnason, 1996; Saltonstall et al., 1998; Zhang et al., 2001)—the subspecific samples from each of these genera actually represent a time since divergence of well over 1.0 myr (Ruvolo, 1996; Zhi et al., 1996; Zhang et al., 2001; Steiper, 2006). In this context, the mean of the individual Procrustes distances within the "early" fossil group is appreciably higher than the individual Procrustes distances observed between *P. troglodytes* and *P. paniscus*, as is the mean of the Procrustes distance distribution for the entire fossil sample (Fig. 6). Furthermore, the mean Procrustes distances between the *a priori H. erectus* groups are at or above those observed both between the *Gorilla* and *Pongo* subspecies as well as between *P. troglodytes* and *P. paniscus* (see Fig. 8). Therefore, if the fossil variation is due to time, then this variation exceeds that observed between multiple subspecies and species that may have diverged as early as 2.5 Ma (Ruvolo, 1996; Zhi et al., 1996; Gagneux et al., 1999; Zhang et al., 2001; Stone et al., 2002; Yu et al., 2003; Won and Hey, 2005; Steiper, 2006).

Dividing the sample geographically, while consistent with the Procrustes distance results, is complicated by several issues. In particular, OH 9 and Dmanisi 2280 are more similar morphologically to the Asian sample, and there are no later African *Homo erectus* specimens that are contemporaneous with the late Asian specimens, such as the Ngandong or Zhoukoudian fossils. The interaction between time and geography is likely to have been complex, as has been implied by previous researchers (Andrews, 1984; Stringer, 1984; Wood, 1984; Asfaw et al., 2002). Asfaw et al. (2002) suggested that the early fossil record of *H. erectus* samples a widely distributed single-species or lineage, with a speciation event separating the Asian and African populations approximately one million years ago. In such a model, the later Asian specimens were sufficiently distinct in that they did not bear on later human evolution, while African *H. erectus* led to subsequent species on the human lineage. Such a scenario could therefore account in part for the distinctiveness of OH 9 as observed here, as well as the similarity of this specimen to the Asian materials, and the lack of later African *H. erectus* specimens, which are instead attributed to archaic *H. sapiens* or *H. heidelbergensis* (e.g., Bodo, Buia, Kabwe, etc.).

Another possible explanation for the patterns observed here could be that of multiple migrations of hominins into and out of Africa beginning as early as ~1.8 Ma, as suggested recently by Dennell and Roebroeks (2005). For instance, the early appearance of *H. erectus* in both Georgia and Java could indicate an early migration out of Africa, with a subsequent migration of hominins back into Africa by ~1.45 Ma. This scenario could potentially explain the similarity of the Dmanisi materials to both the African and Asian specimens, as well as the appearance of classic *Homo erectus* morphology (as represented by OH 9 and possibly the Daka cranium) in Africa between 1.5 and 1.0 Ma ago (Asfaw et al., 2002). Finally, the high levels of variation seen even among the early African and Asian specimens may indicate that a speciation event, or multiple speciation events, occurred early in the geographic dispersal of *H. erectus* populations, and population differentiation was pronounced in this group throughout the Pleistocene.

Conclusions

The research presented here indicates that variation within temporal bone morphology of *Homo erectus* tends to be greater than that observed in extant hominid species. Differences between *H. erectus* (including OH 9) and *H. ergaster* are statistically significant and are greater than differences between geographically distinct human populations or subspecies of great apes. However, high levels of within-group variation are seen even when the fossil sample is divided into regional or chronological groups. Thus, the total range of variation cannot easily be partitioned into previously suggested taxonomic, geographic, or chronological groupings of specimens. Instead, it seems likely that geographic and temporal factors combine to create a pattern of population differentiation and variation that is difficult to interpret in the context of variation within extant hominids.

While this study has focused on temporal bone anatomy, it is largely consistent with recent studies of cranial variation in *H. erectus* (e.g., Antón, 2002a; Villmoare, 2005). However, it is inconsistent with the general interpretations of Dmanisi cranial affinities that ally the Dmanisi specimens strongly with the early African remains, but that also recognize similarities with Asian *H. erectus*—a finding that is supported here (Rosas and Bermúdez de Castro, 1998; Gabunia et al., 2000, 2001; Schwartz and Tattersall, 2002; Rightmire et al., 2006). These results suggest that cranial variation within *H. erectus* (*sensu lato*) is clearly complex and that specimens within this taxon cannot easily be grouped on the basis of geography or time. Further analyses will be needed to demonstrate whether other parts of the skull are consistent with the patterns of variation observed here.

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