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The taxonomic implications of cranial shape variation in *Homo erectus*

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Abstract

The taxonomic status of *Homo erectus* sensu lato has been a source of debate since the early 1980s, when a series of publications suggested that the early African fossils may represent a separate species, *H. ergaster*. To gain further resolution regarding this debate, 3D geometric morphometric data were used to quantify overall shape variation in the cranial vault within *H. erectus* using a new metric, the sum of squared pairwise Procrustes distances (SSD). Bootstrapping methods were used to compare the *H. erectus* SSD to a broad range of human and nonhuman primate samples in order to ascertain whether variation in *H. erectus* most clearly resembles that seen in one or more species. The reference taxa included relevant phylogenetic, ecological, and temporal analogs including humans, apes, and both extant and extinct papionin monkeys. The mean cranial shapes of different temporogeographic subsets of *H. erectus* fossils were then tested for significance using exact randomization tests and compared to the distances between regional groups of modern humans and subspecies/species of the ape and papionin monkey taxa. To gauge the influence of sexual dimorphism on levels of variation, comparisons were also made between the mean cranial shapes of single-sex samples for the reference taxa. Results indicate that variation in *H. erectus* is most comparable to single species of papionin monkeys and the genus *Pan*, which included two species. However, *H. erectus* encompasses a limited range of variation given its extensive geographic and temporal range, leading to the conclusion that only one species should be recognized. In addition, there are significant differences between the African/Georgian and Asian *H. erectus* samples, but not between *H. ergaster* (Georgia + Africa, excluding OH 9 and Daka) and *H. erectus* sensu stricto. This finding is in line with expectations for intraspecific variation in a long-lived species with a wide, but probably discontinuous, geographic distribution.
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Introduction

The past twenty years have seen a significant expansion in the sample of fossil hominins assigned to *Homo erectus* sensu lato (s.l.). These more recent discoveries from the Caucasus, East Africa, and Asia (Sartono, 1990; Gabunia et al., 1999, 2000; Widianto and Grimaud-Hervé, 2000; Delson et al., 2001; Vekua et al., 2002; Asfaw et al., 2002; Baba et al., 2003; Leakey et al., 2003; Potts et al., 2004; Arif et al., 2005; Lordkipanidze et al., 2005; Suwa et al., 2007), in addition to newly revised chronologies for other sites (Swisher et al., 1994, 1996; Shen et al., 1996, 2001; Larick et al., 2001; Zhao et al., 2001; Gathogo and Brown, 2006), have increased the known geographic and temporal range of *H. erectus*, while

also raising doubts about the taxonomic cohesiveness of this species (Schwartz and Tattersall, 1999, 2003; Schwartz, 2000, 2004; Gabounia et al., 2002; de Lumley et al., 2006). The debate concerning whether a single *H. erectus* species or multiple species should be recognized has implications for our understanding of diversity in fossil hominins and further informs interpretations of the evolutionary history of Plio-Pleistocene *Homo*.

A single-species interpretation for *H. erectus* recognizes a broad geographic distribution of this species from eastern and possibly southern and northern Africa in the west, to the Caucasus in the north, and China and Java in the east (Rightmire, 1984, 1990, 1998; Bräuer, 1990, 1994; Bräuer and Mbua, 1992; Asfaw et al., 2002; Antón, 2002, 2003; Potts et al., 2004). It also implies that this group of hominins did not undergo speciation throughout its nearly 1.8 Myr of documented existence, although a certain degree of diachronic

change and geographic differentiation is commonly acknowledged (e.g., Wolpoff, 1999; Antón, 2003; Kidder and Durband, 2004). At its most extreme, *H. erectus* has been viewed as an evolutionary grade within *H. sapiens* (Thorne and Wolpoff, 1981; Jelínek, 1982; Frayer et al., 1993; Wolpoff et al., 1994; Wolpoff, 1999). Alternatively, a two-species interpretation subdivides these same fossils into two distinct but closely related species. An earlier and less derived species, *H. ergaster*, is recognized for the fossils from East Turkana and possibly Dmanisi vs. *H. erectus* sensu stricto (s.s.), which is generally restricted to the Asian fossils and OH 9 or sometimes to only the Asian specimens (Groves and Mazák, 1975; Tattersall, 1986; Groves, 1989; Clarke, 1990, 2000; Wood, 1991, 1994; Wood and Richmond, 2000; Manzi et al., 2003; Bermúdez de Castro et al., 2004). Additional species have also been proposed, including *H. georgicus* for the Dmanisi sample (Gabounia et al., 2002; de Lumley et al., 2006), and a few researchers have suggested that multiple discrete morphs are recognizable even within restricted geographic regions (Schwartz, 2000, 2004; Schwartz and Tattersall, 2003; Cameron et al., 2004; Tattersall, 2007).

Much of this debate has centered on the distribution of discrete traits such as the presence of an angular torus, mastoid fissure, and sagittal keeling (Andrews, 1984; Stringer, 1984; Wood, 1984, 1991, 1994); a higher frequency of these traits in the Asian specimens has been used as support for the two-species model. However, there has been considerable criticism of the use of discrete traits in this context (Hublin, 1986; Turner and Chamberlain, 1989; Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992), resulting in an impasse.

A quantitative approach to testing the species question involves the comparison of metric variation in the fossil sample to that seen in known species. This method was originally applied to traditional morphometric data (e.g., Simpson, 1961; Simons and Pilbeam, 1965; Kay and Simons, 1983; Kimbel and White, 1988; Shea et al., 1993; Wood, 1993; Cope, 1993; Kramer, 1993; Teaford et al., 1993; Kramer et al., 1995; Richmond and Jungers, 1995; Lockwood et al., 1996; Schillaci and Froehlich, 2001) and has more recently been used in the context of 3D geometric morphometrics (Harvati, 2003; Harvati et al., 2004; Terhune et al., 2007). The analyses of Harvati and colleagues suggest that Neandertals should be recognized as a distinct species because the distance between the mean 3D cranial shape of Neandertals and modern humans was similar to the distances seen between species of African apes and Old World monkeys. While utilizing a similar landmark set, this study will take a slightly different approach by focusing on measures of both distance and variation.

This study addresses the question of *H. erectus* taxonomic diversity by comparing the degree of 3D neurocranial shape variation present in a representative *H. erectus* sample to a range of extant hominoid and papionin taxa at different taxonomic levels. Distances between mean cranial shapes of different subsets of the fossil *H. erectus* s.l. specimens were then tested for statistical significance and compared to those seen between regional groups, species, and genera of the comparative taxa.

The distribution of Homo erectus in space and time

Traditionally, *H. erectus* fossils are known from East Africa (East and West Turkana and Olduvai Gorge), China (particularly Zhoukoudian), and Java (Trinil, Perning, Sangiran dome, Ngandong, and Sambungmacan). In the past ten years, additional sites have been identified in all of these regions and in the Caucasus. Particularly relevant to this study are the series of crania and postcranial elements from the 1.77-Myr-old Georgian site of Dmanisi (Gabunia, 1992; Gabunia et al., 1999, 2000; Vekua et al., 2002; Lordkipanidze et al., 2005; Rightmire et al., 2006) and the ∼1.0-Myr-old cranium from Daka in the Middle Awash region of Ethiopia (Asfaw et al., 2002). Previous 3D analysis confirmed the affinities of the Dmanisi and Daka specimens with *H. erectus* (Baab, 2007), extending the taxon's known size and geographic range. *Homo erectus* sites extend from ∼1.8 Ma (or ∼1.9 Ma if cranial fragments KNM-ER 2598 and 2592 and/or the partial innominate KNM-ER 3228 are attributed to *H. erectus*) in Africa and Georgia (Feibel et al., 1989; Vekua et al., 2002), through the middle Pleistocene in China (Shen et al., 2001), to as recently as ∼50 ka in Java (Swisher et al., 1996; but see Grün and Thorne, 1997; Westaway et al., 2003).

Diversity in Homo erectus

Examinations of both cranial morphometrics and discrete characters have highlighted variation within *H. erectus* (Wood, 1984, 1991, 1994; Andrews, 1984; Stringer, 1984; Rightmire, 1990; Bräuer, 1990, 1994; Antón, 2002, 2003; Villmoare, 2005; Skinner et al., 2006; Rightmire et al., 2006; Terhune et al., 2007), which is often, but not always, interpreted within the framework of intraspecific variation. In particular, analyses of cranial metrics have generally supported a single-species model for *H. erectus* (Bräuer, 1994; Kidder and Durband, 2000, 2004; Antón, 2002), but only a few studies have explicitly tested this hypothesis (Kramer, 1993; Bilsborough, 2000; Villmoare, 2005). The only exception to this pattern was the recent 3D geometric morphometric analysis of the temporal bone by Terhune et al. (2007), which found higher levels of variation in their *H. erectus* sample than in extant hominine species. In contrast, so-called "cladistic" approaches to the question of *H. erectus* taxonomy, which utilized discrete character data, have generally supported the division of *H. erectus* s.l. into two or more species (Wood, 1984, 1991; Andrews, 1984; Stringer, 1984; Villmoare, 2005). However, other studies have demonstrated that individual characters used to support a *H. ergaster*/*H. erectus* s.s. distinction are present outside of Asian *H. erectus* (Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992), leading to continued debate about *H. erectus* alpha taxonomy.

Materials

Three-dimensional landmarks that reflect the overall shape of the neurocranium were captured with a Microscribe 3DX (or G2) digitizer (Immersion Corp., San Jose, CA) on a large

sample of *H. erectus* fossils, of which 15 were complete enough to be used in this analysis (Table 1). Certain specimens, such as Trinil and the majority of the Sangiran fossils, were missing key landmarks and could not be analyzed. A few fossils (e.g., Sm 4) were not accessible for data collection. This sample was representative of the known geographic, temporal, and size range of *H. erectus*. All specimens were adult individuals. While the age of Zkd 3 is unclear (cf. Black, 1929, 1931; Weidenreich, 1943; Mann, 1971; Antón, 2001), previous 3D analysis has indicated that Zkd 3 fits well within the range of cranial shape variation for adult Zhoukoudian specimens (Baab, 2007).

The same landmark data were collected from a large sample (n = 1270) of humans, apes, and papionin monkeys, as tabulated in Table 2. The data for all members of Hominini were collected by the author. Three-dimensional data from comparative nonhuman primates were generously provided by other members of the NYCEP Morphometrics Group (www.nycep.org/nmg), especially Kieran McNulty (hominoids) and Stephen Frost (cercopithecines). Although there were minor variations in the phrasing of landmark definitions (e.g., Frost et al., 2003; McNulty et al., 2006), the operational definitions were identical among sources. These data were acquired from adult specimens; the comparative samples are approximately evenly distributed between males and females, but with a male bias in the baboon sample (Table 2).

The recent human sample consisted of 392 individuals from 11 regions that could be divided into three geographic/genetic groups: (1) Africa, (2) Europe/West Asia, and (3) East Asia/Oceania/North America (Tishkoff and Kidd, 2004). In addition to being geographically diverse, this sample was designed to cover a wide climatic range and a variety of subsistence patterns in order to create a maximally variable sample. In order to introduce at least a small amount of time depth to this sample, Skhul 5 and Qafzeh 6 (135−100 ka; Grün et al., 2005)

were included, as were the late Pleistocene specimens from Abri Pataud, France, and Fish Hoek, South Africa. Data were collected from the original Skhul 5 and Fish Hoek specimens and from casts of Qafzeh 6 and Abri Pataud.

Both species of chimpanzees were represented in this study, including all three widely recognized subspecies of *Pan troglodytes*. Within *Gorilla*, two species and two subspecies were sampled (Groves, 2003), as were both subspecies of *Pongo*. The baboon taxonomy here follows Szalay and Delson (1979) and Frost et al. (2003) in recognizing the traditional five varieties (Guinea, chacma, yellow, anubis, and hamadryas) as subspecies of *Papio hamadryas* and also according full subspecies status to the Kinda baboon. All species of the *Macaca fascicularis* species group (*M. fascicularis*, *M. cyclopis*, *M. fuscata*, and *M. mulatta*) are represented here. In addition, the three chronological subspecies of *Theropithecus oswaldi* were included in this analysis.

The choice of comparative taxa should reflect those sources of variation expected to influence the degree of differentiation in *H. erectus*. Modern humans and *Pan* are the closest relatives and thus the most appropriate phylogenetic models for *H. erectus*, while *Gorilla* and *Pongo* provide more conservative tests of the single-species hypothesis due to the fact that they are highly sexually dimorphic. However, the apes all inhabit very limited geographic ranges in contrast to *H. erectus*. Modern humans are at least as geographically diverse as the fossil hominin taxon, but they exhibit low levels of intergroup variation and have a very limited time depth relative to the ∼1.8 Myr spanned by *H. erectus*. Due to the limitations of the available phylogenetic models, it was deemed important to include other ecological and geographic models (Shea et al., 1993; Jolly, 2001; Harvati et al., 2004).

Papionins are appropriate ecological analogs for early hominins (Jolly, 1970, 2001; Delson, 1978; Elton, 2006), and both the *Macaca fascicularis* species group and *Papio hamadryas* share similarly extensive geographic ranges with *H. erectus*. Both *M. cyclopis* and *M. fuscata*, the Taiwanese and Japanese macaques, respectively, are currently isolated from mainland Asia by bodies of water and likely have been since the middle Pleistocene (Delson, 1980; Fooden, 1995, 2006; Morales and Melnick, 1998; Fooden and Wu, 2001; Marmi et al., 2004; Fooden and Aimi, 2005). Thus, stochastic variation resulting from geographic isolation that may be contained within the *H. erectus* sample could also be modeled using the *M. fascicularis* species group. Moreover, the papionin taxa consist of closely related species and subspecies, respectively, which may mirror the population structure found in *H. erectus*.

One approach to modeling variation due to anagenetic processes is to view "geographic variation today [as] broadly comparable to past spatio-temporal variation" (Delson, 1997: 446), in which case temporal variation can be modeled through the inclusion of multiple subspecies or demes within comparative species samples (Richmond and Jungers, 1995; Lockwood et al., 1996; Lockwood, 1999; Terhune et al., 2007). From this perspective, *P. troglodytes*, *H. sapiens*, and *P. hamadryas* would all be excellent models of temporal variation because they each include several large regional samples (modern

Table 1
Homo erectus sample

Specimens by site	Age (in Myr)[1]	Original/cast
East Turkana		
KNM-ER 3733 and 3883	1.78−1.58	Original
Olduvai Gorge		
OH 9	1.30	Original
Bouri		
Daka	1.00	Original
Dmanisi		
D2280	1.77	Cast
Sangiran		
S 17	1.30	Cast
Ngandong		
Ng 6, 10, 11, 12	0.10−0.03	Original
Sambungmacan		
Sm 3	1.00−0.03	Original
Zhoukoudian		
Zkd 3, 5, 11, 12	0.80−0.45	Cast

[1] Ages based on Bartstra et al. (1988), Feibel et al. (1989), Swisher et al. (1996), Delson and Van Couvering (2000), Gabunia et al. (2000), Zhao et al. (2001), Delson et al. (2001), Larick et al. (2001), Shen et al. (2001), Asfaw et al. (2002), and Vekua et al. (2002).

Table 2
Samples, sample sizes, and sex

Taxon	Sample size for 16-landmark set (female, male, unknown)	Sample size for 32-landmark set (female, male, unknown)
Total *H. erectus*	13	13
African/Georgian	5	4
KNM-ER 3733, 3883, Daka, D2280	4	4
OH 9	1	—
Asian	8	9
S 17, Sm 3, Ng 6, 11, 12, Zkd 11, 12	7	7
Ng 10	1	—
Zkd 3, 5	—	2
Modern *H. sapiens*	379	392
Africa	85	86
Afalou/Taforalt	21 (7, 10, 4)	27 (10, 11, 6)
Khoe-San, S. Africa	32 (15, 11, 6)	31 (15, 11, 5)
Teita, Kenya	31 (13, 17, 1)	28 (11, 16, 1)
Fish Hoek (UP)[1]	1	—
Europe/West Asia	79	82
Greifenberg, Austria	49 (21, 26, 2)	49 (20, 27, 2)
Lachish, Palestine	27 (13, 12, 2)	32 (16, 14, 2)
Skhul 5 (EAMH)	1	1
Qafzeh 6 (EAMH)	1	—
Abri Pataud (UP)	1	—
EA/OC/NA[2]	215	224
Andamanese	32 (16, 15, 1)	31 (16, 14, 1)
Aboriginal Australian	45 (22, 22, 1)	45 (22, 22, 1)
East Asian	27 (9, 12, 6)	33 (12, 15, 6)
Grand Gulch, Utah	45 (17, 26, 2)	48 (18, 28, 2)
Ipiutak, Alaska	47 (17, 20, 10)	47 (16, 21, 10)
Mongolians	19 (7, 12)	20 (7, 13)
Pan	161	
P. paniscus	44 (22, 19, 3)	
P. troglodytes	117	
P. t. troglodytes	82 (53, 28, 1)	
P. t. schweinfurthii	13 (3, 10)	
P. t. verus	22 (12, 10)	
Gorilla	98	
G. gorilla	74	
G. g. gorilla	74 (31, 43)	
G. beringei	24	
G. b. beringei	22 (10, 12)	
G. b. graueri	2 (1, 1)	
Pongo pygmaeus	56	
P. p. pygmaeus	36 (20, 16)	
P. p. abelii	20 (10, 10)	
Papio hamadryas	437	
P. h. anubis	155 (49, 106)	
P. h. cynocephalus	32 (9, 25)	
P. h. hamadryas	31 (4, 27)	
P. h. kindae	26 (13, 13)	
P. h. papio	17 (1, 16)	
P. h. ursinus	176 (74, 102)	
Macaca fascicularis species group	99	
M. fascicularis	54 (22, 32)	
M. fuscata	12 (3, 9)	

Table 2 (*continued*)

Taxon	Sample size for 16-landmark set (female, male, unknown)	Sample size for 32-landmark set (female, male, unknown)
M. cyclopis	2 (0, 2)	
M. mulatta	31 (18, 13)	
Theropithecus oswaldi	13	
T. o. oswaldi	5 (2, 3)	
T. o. darti	5 (4, 1)	
T. o. leakeyi	3 (1, 2)	
Total	1256	405

[1] UP = Upper Paleolithic.
[2] EA/OC/NA = East Asia/Oceania/North America.

humans) or multiple subspecies (*P. troglodytes* and baboons). However, the equivalence of geographic variation in neontological species and spatiotemporal variation in fossil species has not yet been widely accepted. For this reason, the fossil species *Theropithecus oswaldi* was included as a comparative species. Although this species spans a greater time interval than *H. erectus* (~3 Myr), the three chronological subspecies (*T. o. darti*, *T. o. oswaldi*, and *T. o. leakeyi*; Leakey, 1993) each have a duration of between 0.8 and 1.25 Myr (see Table 6; Delson, 1984; Frost, 2001).

An additional complication is that many of the taxa listed above also incorporate a high degree of sexual dimorphism, which may increase morphological variation in these groups, particularly *P. hamadryas*, *Pongo*, and *Gorilla* (cf. Terhune et al., 2007). The extent of sexual dimorphism in *H. erectus* is currently unknown, due in part to the complexities involved in assigning sex to fossils (Armelagos and Van Gerven, 1980). Although there is a large size range within *H. erectus*, this variation is more easily attributed to temporogeographic or taxonomic differences than to sexual variation (but see Gunz et al., 2007). The large size variation in the Dmanisi mandibles may indicate higher-than-expected levels of sexual dimorphism, at least in early *H. erectus*, unless multiple hominin taxa are represented in the same levels from this site (Skinner et al., 2006; Rightmire et al., 2006). The recent description of KNM-ER 42700 from Ileret, Kenya, also indicates that African *H. erectus* displayed marked sexual dimorphism around 1.5 Ma (Spoor et al., 2007), although the attribution of KNM-ER 42700 to *H. erectus* is uncertain (Baab, 2007).

The issue of sexual dimorphism is mediated somewhat by analyzing the cranial vault rather than the face, as levels of dimorphism are generally lower in the neurocranium than in the facial skeleton and dentition in anthropoid primates (Ravosa, 1991; Masterson and Hartwig, 1998; Plavcan, 2002). However, regions of muscle attachment are influenced by sex (Plavcan, 2002), and the location of some landmarks (i.e., bregma and inion) on the sagittal and compound temporonuchal crests has the potential to increase sex-related variation in certain groups in this analysis, particularly the apes and monkeys. The issue of sexual dimorphism was addressed explicitly by comparing the distance between the mean cranial

shapes of large and small *H. erectus* individuals to distances between single sex samples in the reference taxa (discussed below).

Methods

Geometric morphometrics

Two landmark sets were used for this study, consisting of 16 and 32 landmarks, respectively (Fig. 1; Table 3). The landmark protocols were chosen to represent the basic shape of the cranial vault rather than focusing on discrete characters thought to distinguish between *H. ergaster* and *H. erectus* s.s. because several studies have shown that these traits are more widely distributed across Plio-Pleistocene *Homo* species (Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992). Secondly, traits that are particularly variable in fossil hominins may not be as variable in the reference taxa and would therefore bias the analysis in favor of a multiple-species model (Harvati et al., 2004). Finally, the vault has been shown to preserve

a strong phylogenetic signal in modern humans (Harvati and Weaver, 2006), and is thus an appropriate region of the skull to address the taxonomic question outlined above. Both landmark sets captured information about the midline profile, supraorbital torus, and breadth at the midvault. The 32-landmark set provided a denser sampling of cranial landmarks, reflecting additional information about the cranial breadth at the anterior and posterior vault, the temporal base, and the height of the temporal squama, but was available only for the hominins (fossil and extant). Two slightly different samples of 13 *H. erectus* specimens were used for the 16- and 32-landmark protocols based on differential preservation as outlined in Table 2.

In order to maximize sample sizes, missing bilateral landmarks were reconstructed by reflection of their antimeres across the midsagittal plane (e.g., McNulty et al., 2006; Gunz and Harvati, 2006). Landmark configurations for all individuals were then superimposed using generalized Procrustes analysis (GPA) in order to remove the effects of location, orientation, and scale (Rohlf, 1990; Rohlf and Marcus, 1993; O'Higgins, 2000; Adams et al., 2004). Generalized Procrustes analysis works by first superimposing specimens' centroids (the geometric center of a landmark configuration) at the origin, scaling configurations to a unit centroid size (the square root of the sum of squared distances from all landmarks to the centroid), and then rotating them until the residual sum-of-squares across all landmarks and specimens falls below a set tolerance level (Gower, 1975; Rohlf and Slice, 1990). The superimposed landmarks were then treated as shape variables in standard multivariate statistical analyses (Kent, 1994). In all cases, the landmarks were averaged with their reflected equivalents in order to minimize the effects of bilateral asymmetry, especially in fossil specimens (Bookstein, 1996). Morpheus et al. (Slice, 1998) was used for GPA and for visualization purposes, and statistical analysis was performed in SAS 8 (SAS Institute, 1999–2001).

In the case of OH 9, the frontal squama is broken just anterior to bregma. However, as part of the standard data-collection protocol, a "curve" (a collection of closely spaced semilandmarks) was recorded from glabella to bregma; in OH 9 this curve ends just short of bregma. I determined through visual inspection in Morpheus that KNM-ER 3733 and 3883, D2700, Ng 5, S 17, and Zkd 3 share a similar trajectory of the midsagittal profile with OH 9. The mean position of bregma in these specimens was taken as the best available estimate for bregma and was added to the original OH 9 landmark configuration. Casts of OH 9 frequently reconstruct the missing portions of the superior vault, so I also collected landmark data from a cast of OH 9. The reconstructed bregma is located at the same height as, but about a centimeter (11.1 mm) posterior to, the position of bregma indicated by the cast. The exact anteroposterior position of bregma in OH 9 is unknown, but these two estimates confirm the relative height of bregma in this specimen. As a further test of this landmark-reconstruction method, the same procedure was performed on KNM-ER 3733, which is not missing bregma. Results indicate that the position of the estimated bregma was
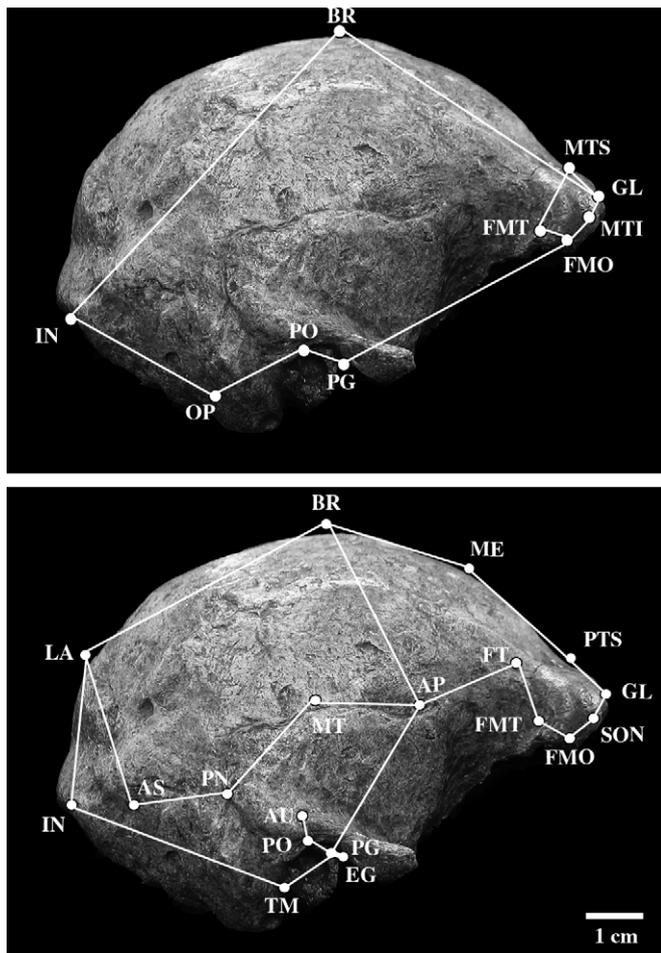

Fig. 1. Landmarks illustrated on Ngandong 12, right lateral view: the 16-landmark set is shown on the top and the 32-landmark set is shown on the bottom. Abbreviations refer to Table 3. The approximate positions of opisthion (OP) and the entoglenoid process (EG) are indicated but are not actually visible in this view. The white wireframes are for visualization purposes only and do not represent actual data.

Table 3
Landmark definitions, abbreviations, and inclusion in 16- and 32-landmark sets

Landmark	Definition[1]	Abbreviation[2]	Analyses[3]
Opisthion	Midline point at the posterior margin of the foramen magnum	OP	16
Inion	Point at which the superior nuchal lines merge in sagittal plane	IN	16, 32
Lambda	The apex of the occipital bone at its junction with the parietals, in the midline	LA	32
Bregma	Posterior border of the frontal bone in the sagittal plane	BR	16, 32
Metopion	Point midway between glabella and bregma in the midline, calculated a postieriori	ME	32
Post-toral sulcus	Point of maximum concavity behind supraorbital torus in the midline	PTS	16, 32
Glabella	Most anterior midline point on the frontal bone, usually above the frontonasal suture	GL	16, 32
Supraorbital notch	Point of greatest projection of notch into the orbital space, taken on medial side of notch	SON	32
Midtorus inferior	Point on inferior margin of supraorbital torus directly above the center of the orbit	MTI	16
Midtorus superior	Point on superior aspect of the anterior surface of the supraorbital torus, directly above midtorus inferior	MTS	16
Frontomalareorbitale	Point where the frontozygomatic suture crosses the inner orbital rim	FMO	16, 32
Frontomalaretemporale	Point where the frontozygomatic suture crosses the temporal line (or outer orbital rim)	FMT	16, 32
Anterior pterion	Point where coronal suture intersects sphenofrontal or sphenoparietal suture	AP	32
Midtemporal squama	Point midway along temporal squamal suture between infratemporal crest and parietal notch, calculated a posteriori	MT	32
Porion	Uppermost point on the margin of the external auditory meatus	PO	16, 32
Auriculare	A point vertically above the center of the external auditory meatus at the root of the zygomatic process	AU	32
Frontotemporale	Point where the temporal line reaches its most anteromedial position on the frontal	FT	32
Asterion	Point where occipitomastoid and lamboid sutures intersect	AS	32
Parietal notch	Point on posterosuperior border of the temporal where the squamosal and parietomastoid sutures meet	PN	32
Tympanomastoid junction	Point where tympanic tube and mastoid fissure meet laterally	TM	32
Postglenoid process	Most inferolateral point posterior to glenoid fossa and anterior to ectotympanic tube (corresponds to postglenoid tuberosity or postglenoid crest)	PG	16, 32
Entoglenoid	Most inferior point on the entoglenoid pyramid	EG	32

[1] Landmark definitions are derived from the following sources: Howells (1973), White (2000), Frost (2001), Harvati (2001), and McNulty (2003). Crania were oriented in Frankfurt horizontal.
[2] The abbreviations refer to Fig. 1.
[3] The 16 and 32 refer to the 16- and 32-landmark analyses, respectively.

nearly identical to the original bregma, falling slightly posterior (1.8 mm) to the original landmark. End points of linear measurements are commonly estimated for fossil hominins and a measurement error of less than 2 mm is very reasonable. Based on these results, OH 9 (with a reconstructed bregma) was included in the 16-landmark analysis.

Analysis

Principal components analysis. A principal components analysis (PCA) was performed on both the 16- and 32-landmark sets for just the *H. erectus* sample in order to explore neurocranial shape variation in this taxon. The cranial shapes associated with the negative and positive ends of each of the principal components were visualized. In addition, multivariate analysis of variance (MANOVA) was used to examine significant differences among the major geographic groups and between the *H. ergaster* and *H. erectus* s.s. subdivisions using the scores for principal component 1 (PC 1) and PC 2.

Intrataxic variation. A new metric, the sum of squared distances, was developed in order to evaluate the overall variance in *H. erectus* cranial vault shape relative to the comparative taxa. The Procrustes distance is the distance between two specimens in Kendall's shape space (the shape space occupied by Procrustes-aligned shape configurations), measured here as an angle in radians. By summing the squared pairwise

Procrustes distances (SSD) among *H. erectus* individuals, it was possible to quantify the dispersion of these specimens in shape space (e.g., the variation *within* this taxon); the resulting value is the *H. erectus* SSD. Bootstrapping methods were then used to determine empirical distributions of SSDs in the reference taxa (Lockwood et al., 1996, 2000; Arsuaga et al., 1997; Lorenzo et al., 1998; Bermúdez de Castro et al., 2001), against which the *H. erectus* value was evaluated.

The bootstrapping procedure used in this analysis worked as follows: 13 individuals (equal to the size of the *H. erectus* sample) were selected randomly from a reference taxon, and the SSD was recorded for this sample. This sampling-calculation step was performed 10,000 times for each analysis in order to create an empirical distribution of SSDs for each comparative taxon. The probability of obtaining the *H. erectus* SSD was determined by comparing that value directly to the distribution of resampled SSDs for a given taxon. The number of SSDs in each reference taxon smaller than the *H. erectus* SSD is reported, along with the single SSD value for *H. erectus* and the mean SSD for each reference sample. As the primary question addressed here is to which taxonomic level *H. erectus* compares most closely, the results are also presented in terms of whether the *H. erectus* SSD falls within the 50%, 75%, or 95% confidence interval (CI) of each reference taxon. Variation in *H. erectus* was considered most comparable to the taxonomic level of the reference taxon if its SSD

fell within the 50% CI, somewhat less comparable at the 75% CI level, and so forth.

When sampling at a taxonomic level that incorporated one or more lower taxonomic levels, the 13 individuals were drawn from approximately even numbers of each of the lower taxonomic levels so that larger sample sizes for some taxa did not unduly bias the resampling. For example, when looking at variation within all of *Papio hamadryas*, the sample size for the chacma baboon is very large compared to the Guinea baboon sample (176 vs. 17 specimens, respectively). In this case, since 17 was the smallest sample size of the six samples, each of the other five forms of baboons was randomly resampled to 17 individuals, and then 13 were chosen (again, randomly) from the resulting 102 specimens. This two-step resampling procedure was repeated for each of the 10,000 calculations per sample. Taxa with sample sizes smaller than 13 were not directly compared to the *H. erectus* sample but were included in larger taxonomic comparisons. In the case of the fossil cercopithecine *T. oswaldi*, which had a sample size equal to *H. erectus*, analysis of variance (ANOVA) was used to test for differences in average Procrustes distance between the two fossil taxa. Differences in mean Procrustes distance between *H. erectus* and the chronologically ordered pairs of subspecies (*T. o. darti−T. o. oswaldi* and *T. o. oswaldi−T. o. leakeyi*) were also examined, as they span time intervals more similar to that of *H. erectus* (1.93 and 2.38 Myr, respectively).

Distance between mean shapes. The second approach focused on the Procrustes distance between the average cranial shapes found in different subsets of the *H. erectus* sample. These subsets were designed to reflect geographic, size, and possible species divisions within *H. erectus* s.l. (Table 4). The distances between mean shapes were also calculated for

regional groups of modern humans and for subspecies and species pairs within each genus of the reference taxa. In this way, the analysis also served as a test of whether the landmark sets did indeed reflect differences in cranial vault shape attributable to taxonomic distinctions in the reference taxa. While the degree of sexual dimorphism (both size and shape) in *H. erectus* is unknown, a division based on size (centroid size) may correspond roughly to male-female differences (Rightmire, 1990). The distance between the average small and large *H. erectus* (Table 4) shapes was compared to the distances between the average male and female landmark configurations within single species (and subspecies of *P. hamadryas*) of the nonhuman comparative taxa. For all pairwise comparisons, the probability of obtaining the observed distances by chance was determined using permutation tests (Kramer, 1993; Richmond and Jungers, 1995; McNulty et al., 2006); if the distance exceeded that seen in 95% of cases, then the null hypothesis was rejected. In order to maintain an overall error rate of $\alpha = 0.05$, a Bonferroni−Holm (also known as a sequential or step-down Bonferroni) adjustment for multiple comparisons was performed (Holm, 1979).

The significance of the distance between mean shapes was evaluated through permutation (randomization) tests. First, the Procrustes distance between the mean shapes of two paired (a priori assigned) subsets of *H. erectus* was calculated (Table 4), such as between early and late *H. erectus* ($n = 5$ and $n = 10$, respectively). This distance was then compared to the empirical distribution of distances between all possible permutations of group membership, maintaining sample sizes equal to the original groups ($n = 5$ and 10). Because the sample size of *H. erectus* was relatively small, an exact randomization test (where all permutations are examined) was utilized. The same procedure was used for *T. oswaldi*. For the extant taxa, exact randomization tests were not feasible due to the larger sample sizes, so the empirical distributions were based on 10,000 permutations of group membership. Because of the great discrepancies in sample sizes among the extant taxa, it was deemed necessary to base the empirical distributions on equal sample sizes in order to avoid biasing the comparisons in favor of the taxon with the larger sample size. Hence, for each pair of taxa analyzed, the one with the larger sample size was randomly resampled to the same size as that of the smaller sample at the beginning of each of the 10,000 repetitions. Within the extant taxa, exact randomization tests (testing all possible permutations) were only used for those comparisons that included either *M. cyclopis* or *Gorilla beringei graueri*, due to the small sample sizes of $n = 2$ for these taxa. In common with the other extant taxa, the empirical distributions were based on equal sample sizes, constrained by the smaller samples ($n = 2$).

Hypothesis testing

The two alternative hypotheses being examined in this study are that *H. erectus* represents one or more than one species. While neither hypothesis can be falsified per se, the available evidence may lend stronger support to one or the other

Table 4
The mean shapes of the following subsets of *H. erectus* were tested using permutation tests of the Procrustes distance between the group means

Subset 1	Subset 2
African/Georgian KNM-ER 3733, 3883, Daka, OH 9[1], D2280	**Asian** Ng 6, 10[1], 11, 12, Sm 3, S 17, Zkd 3[2], 5[2], 11, 12
Original *H. ergaster*[3] KNM-ER 3733, 3883	**Original *H. erectus* s.s.[3]** S 17, Zkd 3[2], 5[2], 11, 12, OH 9
Expanded *H. ergaster* KMN-ER 3733, 3883, D2280	**Expanded *H. erectus* s.s.** Ng 6, 10[1], 11, 12, Sm 3, S 17, Zkd 3[2], 5[2], 11, 12, OH 9[1]
Early *H. erectus* (>1 Ma) KNM-ER 3733, 3883, OH 9[1], D2280, S 17	**Late *H. erectus* (≤1 Ma)** Ng 6, 10[1], 11, 12, Sm 3, Zkd 3[2], 5[2], 11, 12, Daka
Small *H. erectus* s.l. KNM-ER 3733, 3883, D 2280, Daka, Sm 3, Zkd 3[2], 11	**Large *H. erectus* s.l.** Ng 6, 10[1], 11, 12, S 17, Zkd 5[2], 12, OH 9[1]

[1] OH 9 and Ng 10 were only included in the 16-landmark analyses.
[2] Zkd 3 and 5 were only included in the 32-landmark analyses.
[3] *H. ergaster* (=*H. leakeyi*) and *H. erectus* s.s. are sensu Clarke (1990, 2000) and Wood (1991, 1994).

formulation. Although an oversimplification, the hypothesis that *H. erectus* represents multiple species would be supported if variation in the *H. erectus* sample is greater than that in the reference species and if the distance between the mean shapes of *H. erectus* subsets is greater than the range of intraspecific distances seen in the comparative taxa. Conversely, if variation in *H. erectus* is more comparable to single neontological species, particularly given the extensive geographic and temporal range of this hominin taxon, then this would support a single-species model. An additional complication is that the use of many reference taxa may not result in such a straightforward interpretation (Harvati et al., 2004), because variation may not be constant across taxa for a given taxonomic rank (Plavcan and Cope, 2001), such that *H. erectus* could resemble a single species in some comparisons and multiple species in others. Ultimately, the determination of whether *H. erectus* represents one or more species will be based on both the degree and the pattern of variation within the sample.

Results

Principal components analysis

The PC plots for the 16- and 32-landmark sets are illustrated in Figs. 2 and 3. The smaller landmark set separates the African and Asian fossils along PC 1 (34.6% of the total variation), although the East Turkana specimens score similarly to Ng 10 and Sm 3. Specimen D2280 is intermediate between the two groups on this axis. The Indonesian fossils and Daka score high on PC 2 (18.4%), while KNM-ER 3733 and Zkd 11 score much lower. Taken together, the Indonesian fossils form a cluster toward the upper right corner of the graph; the Chinese fossils occupy the lower right; and the African fossils align at the left with negative scores on PC 1. The sole Dmanisi specimen plots nearest KNM-ER 3883 but is
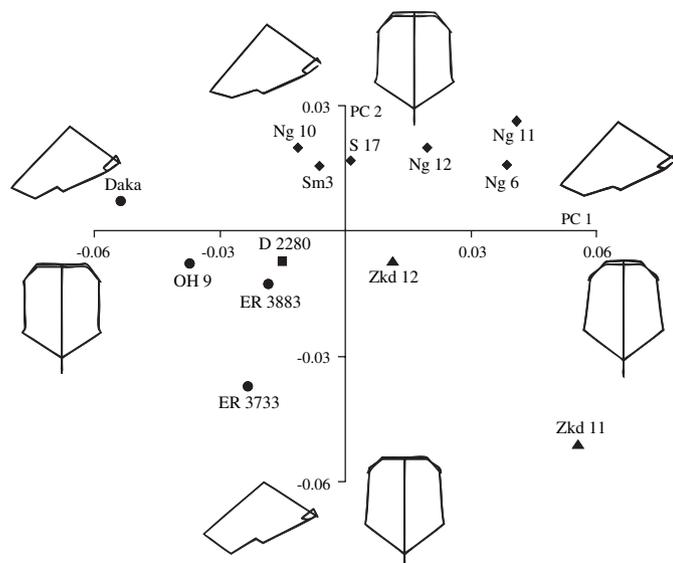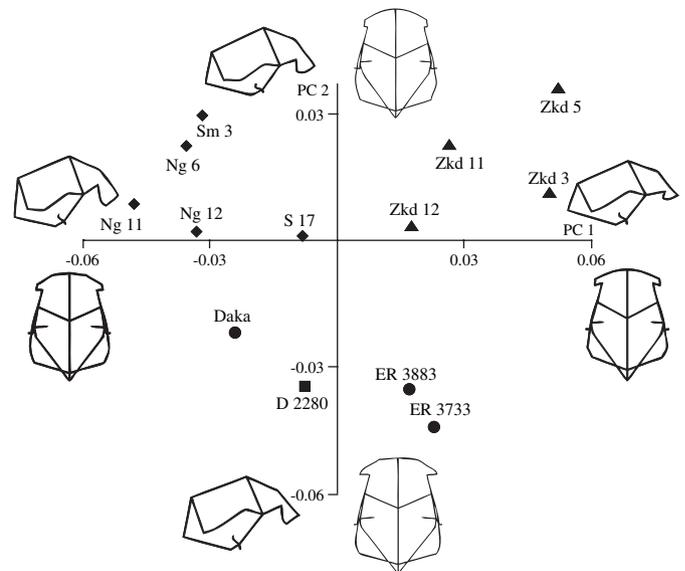

Fig. 3. Principal components analysis of *H. erectus* using 32-landmark protocol: PC 1 (30%) vs. PC 2 (18%).

roughly equidistant from other nearby African, Indonesian, and Chinese specimens.

In the PCA of the more complete landmark set, the most variable aspects of cranial shape (PC 1, 30.0%) separate the Indonesian and Zhoukoudian fossils, whereas the African/Georgian fossils are separated from the Asian specimens on PC 2 (18.4%). Again, there are three clear clusters, but here Dmanisi falls definitely with the African fossils, intermediate between the early and later specimens. The 32-landmark PCA illustrates that the most geographically and temporally circumscribed samples (e.g., East Turkana, Zhoukoudian, later Indonesian) are also the most coherent in terms of their cranial shape, but there is overlap among all geographic regions.

Variation in landmark and sample compositions, such as the absence of OH 9 and the addition of Zkd 3 and 5 to the 32-landmark PCA, both contribute to differences in the PC ordinations. However, both PC plots reveal similar aspects of cranial shape that separate the major geographic groups: the Asian specimens generally have greater height at bregma, relatively narrower supraorbital tori, and greater posterior projection of the vault. In the 16-landmark PCA, the African specimens have more arched supraorbital tori (the supraorbital notches are more superiorly positioned relative to glabella), while the Indonesian fossils have more anteriorly projecting supraorbital tori at glabella and the supraorbital notches. In the 32-landmark PCA, the African specimens have, relative to Asian *H. erectus*, a shorter parietomastoid suture, a higher temporal squama, greater postorbital constriction, a more projecting and posteriorly positioned entoglenoid process, and a more posteriorly positioned postglenoid process and auriculare. Within the Asian group, the Indonesian fossils are distinguished by a more vertical orientation of the occipital plane, greater outward expansion at metopion, lack of a midline post-toral sulcus, and posterosuperiorly positioned frontotemporale (see also Baab, in press).

Fig. 2. Principal components analysis of *H. erectus* using 16-landmark protocol: PC 1 (35% of the variance) vs. PC 2 (18%).

Although Ng 6 is considerably longer in the midsagittal plane (glabella–opisthocranion) than Sm 3, these specimens plot quite close to one another on the first two PCs. This seeming incongruity is explained partially by the fact that the superimposition process removes scale so that the PCA reflects only differences in shape, not size. Secondly, the PCA reflects the patterns of covariation among the landmarks, rather than differences in a single dimension. The shape differences seen between Ng 6 and Sm 3 are not the same as those captured by the first two components. Rather, these two specimens share several aspects of cranial shape on PCs 1 and 2 that together differentiate all of the Indonesian fossils in the analysis; they share a higher neurocranium, wider frontal squamae with reduced postorbital constriction, vertical occipital plane, long parietomastoid suture, and virtually no post-toral sulcus in the midsagittal plane. The shorter, rounder vault of Sm 3 (and Daka) is contrasted with the longer, lower shape of Ng 6 on PC 3 (not shown). It is also worth noting that the most posterior landmark analyzed, inion, was taken where the superior nuchal lines meet in the midline, which was generally just inferior and anterior to opisthocranion, located on the transverse occipital torus. The large occipital torus of Ng 6 contributes significantly to the overall anteroposterior length of this specimen compared to Sm 3, which presents a more gracile occipital torus.

Multivariate analysis of variance of the PC 1 and 2 scores indicates that the African/Georgian and Asian *H. erectus* subsets (Table 4) are significantly different for both landmark configurations (16-landmark set: $p = 0.0011$; 32-landmark set: $p = 0.0012$). The expanded *H. ergaster* and *H. erectus* s.s. samples are not significantly different on PCs 1 and 2 for the 16-landmark set but are for the 32-landmark set ($p = 0.0006$). This discrepancy is due to the fact that OH 9 was not included in *H. erectus* s.s. in the more complete landmark set due to insufficient preservation. As the neurocranial vault shape of OH 9 clearly aligns this specimen with the other African fossils on PC 1 (Fig. 2) based on its wider supraorbital torus that is taller at midorbit, lower position of bregma, less posteriorly projecting inion, and more medially positioned postglenoid process, its inclusion in *H. erectus* s.s. serves to reduce the distinctiveness of the two taxa. The association of OH 9 with other African fossils is not an artifact of only using 16 landmarks, however, as the same pattern was revealed by a larger number of landmarks (see Baab, 2007).

The PCA ordinations demonstrate that both the 16- and the 32-landmark GPAs recover geographic groups and distinguish among them as well as do nonmetric traits, as reported by Andrews (1984), Stringer (1984), and Wood (1984). The following sections investigate the magnitude and pattern of morphological variation in *H. erectus* s.l. relative to the reference taxa.

Bootstrapping analysis of SSDs: 16-landmark set

The average SSD in multispecies configurations (e.g., the *M. fascicularis* species group) is higher than in single species of the same group, confirming that the SSD metric reflects the expected relative variation at the species rank and above

(Table 5). In a few cases, the variation in subspecies (or regional groups of modern humans) is higher than that seen in the species as a whole (e.g., African modern humans vs. all *H. sapiens*), but this likely reflects the underlying population substructure within each species.

Variation in *H. erectus* is most comparable to that seen in *M. fascicularis*, some single subspecies of baboons (*P. h. anubis* and *P. h. cynocephalus*), and the genus *Pan*, as summarized in Table 5 and illustrated in Figs. 4 and 5. The *H. erectus* SSD (0.46) falls within the central 50% of the range for these taxa and is very similar to the mean values for these taxa (0.43–0.49). Variation in the *H. erectus* sample falls at the high end of the distributions for *P. paniscus*, *P. troglodytes*, *P. t. verus*, and the geographically diverse *H. sapiens* sample, as well as the three broad geographic groups of modern humans, as nearly all (95–100%) SSDs for these taxa are smaller than the *H. erectus* SSD. In contrast, variation in single species and subspecies of both gorillas and orangutans exceeds that observed for *H. erectus* (only 0–9% of SSDs are smaller than the *H. erectus* value). The variation seen in the *H. erectus* sample falls at the high end of intrasubspecific variation, but at

Table 5
Comparison of the *H. erectus* sum of squared Procrustes distance (SSD) with empirical distributions generated for modern humans, apes, and monkeys using the 16-landmark set

Reference taxon	Percentage smaller than *H. erectus* SSD	Mean SSD
Homo erectus		0.46
Modern humans		
East Asian/Oceanian/North American	99.90	0.33
European/West Asian	99.17	0.32
All *H. sapiens*	96.83[3]	0.37
African *H. sapiens*	95.86[3]	0.38
Apes		
P. paniscus	100.00	0.29
P. t. verus	100.00	0.30
P. troglodytes	95.48[3]	0.38
P. t. troglodytes	89.39[3]	0.39
Pan	**60.79[1]**	**0.45**
G. b. beringei	9.35[3]	0.57
G. gorilla	1.44[3]	0.66
Gorilla	0.96	0.66
P. p. pygmaeus	0.00	0.84
P. pygmaeus	0.00	0.95
P. p. abelii	0.00	1.06
Monkeys		
P. h. hamadryas	98.18	0.38
P. h. kindae	96.93[3]	0.40
P. h. ursinus	77.30[2]	0.43
M. mulatta	77.08[2]	0.42
P. h. anubis	**74.03[1]**	**0.43**
M. fascicularis	**45.85[1]**	**0.47**
P. h. cynocephalus	**30.11[1]**	**0.49**
Macaca fascicularis species group	19.00[2]	0.52
Papio hamadryas	9.72[3]	0.56

[1] *H. erectus* SSD falls within 50% confidence interval (CI) of reference taxon (bold).

[2] *H. erectus* SSD falls within 75% CI of reference taxon.

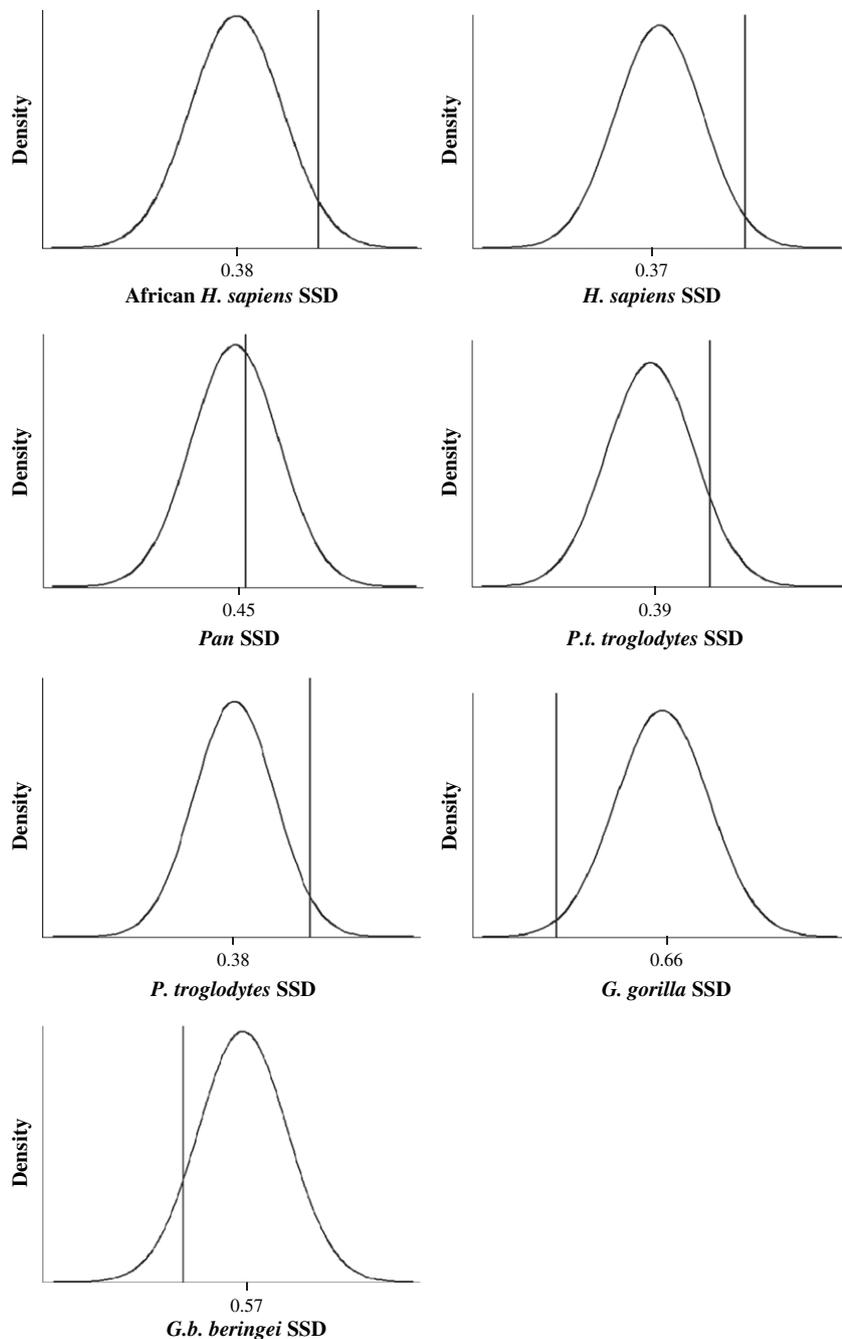[3] *H. erectus* SSD falls within 95% CI of reference taxon.

Fig. 4. Empirical distributions of the 10,000 bootstrapped SSDs (based on the 16-landmark set) for each hominoid taxon in which the *H. erectus* value (vertical line) falls within the 95% CI. Mean SSD is labeled for each distribution. Distributions are fit to a parametric normal density function for illustration purposes.

the low end of intraspecific variation for *P. hamadryas*, and is comparable to that found in either single species of *Macaca* or (to a lesser degree) the *M. fascicularis* species group as a whole.

Because of the small sample size for fossil *Theropithecus*, no bootstrapping was performed, but an ANOVA indicates that the average Procrustes distance in *H. erectus* is statistically significantly smaller than that seen in *T. oswaldi* (Table 6). *Homo erectus* is also less variable than the two pairs of consecutive subspecies (*T. o. darti–T. o. oswaldi* and *T. o. oswaldi–T. o. leakeyi*, which span 1.9 and 2.39 Myr, respectively).

Bootstrapping analysis of SSDs: 32-landmark set (Homo only)

Using the more extensive set of 32 landmarks, *H. erectus* variation falls within the 50% CI for the African regional sample (Table 7; Fig. 6) and within the 75% CI for European/W. Asian modern humans and *H. sapiens*, as a whole. Variation in *H. erectus* is generally greater than that seen in the East Asian/Oceanian/North American *H. sapiens*, as 94% of the SSDs for this regional group are smaller than the *H. erectus* value. These results are similar to those found using the 16-landmark set,
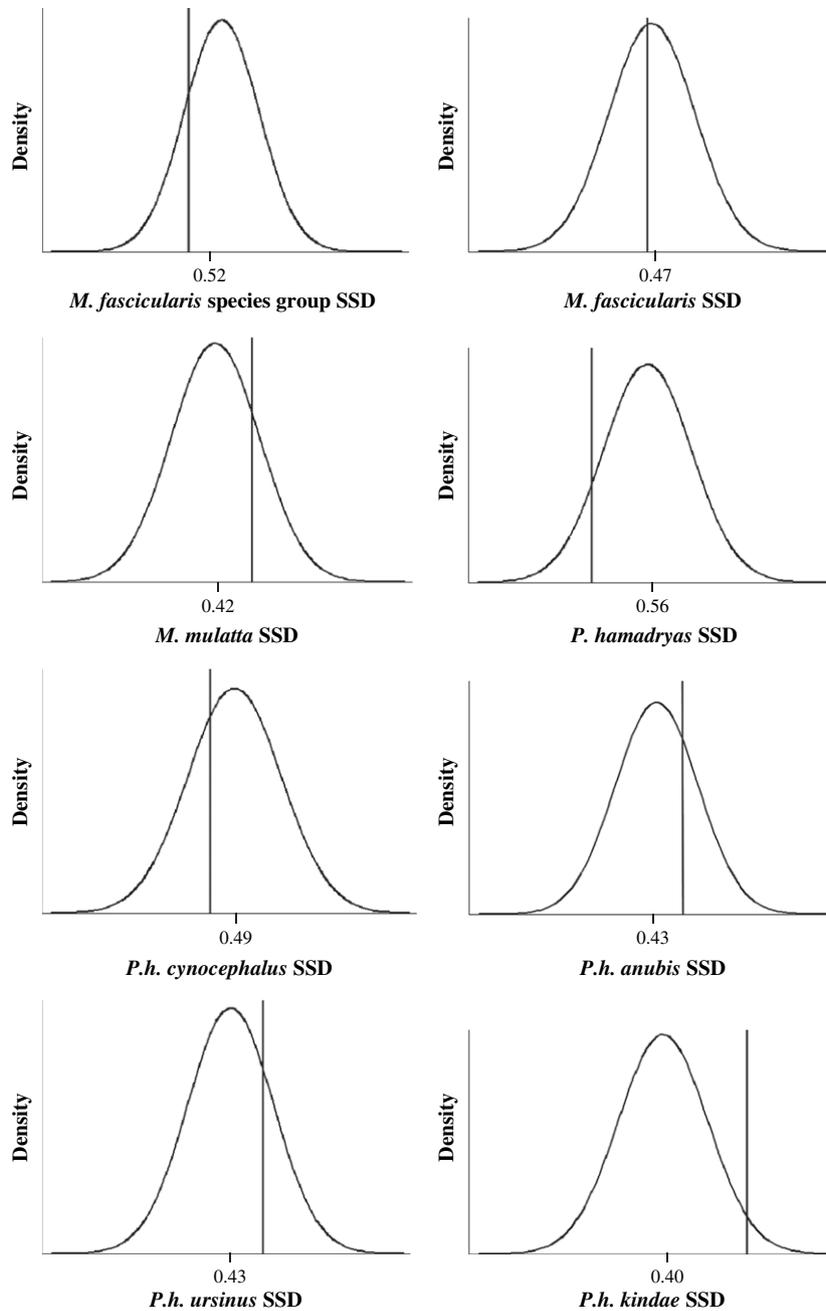
Fig. 5. Empirical distributions of the 10,000 bootstrapped SSDs (based on the 16-landmark set) for each papionin taxon in which the *H. erectus* value (vertical line) falls within the 95% CI. Mean SSD is labeled for each distribution. Distributions are fit to a parametric normal density function for illustration purposes.

although the *H. erectus* SSD is smaller compared to *H. sapiens* when 32 landmarks are used. This result may be related to landmark choice, but it also likely reflects differences in the composition of the *H. erectus* samples (Table 2).

Distances between average shapes: 16-landmark set

Geographic/taxonomic groupings. Of the five different subdivisions of *H. erectus* specimens examined here (outlined in Table 4), only the distance between the average shapes of the African/Georgian and Asian *H. erectus* is greater than that expected by chance, as summarized in Table 8. The *p*-value associated with this distance ($p = 0.002$) falls just below the

Table 6
Results of ANOVA comparing average pairwise Procrustes distances in *H. erectus* and *T. oswaldi*

H. erectus vs.	Probability associated with ANOVA *F*-value	Time span of *Theropithecus* taxa in Myr[1]
T. oswaldi	<0.0001*	3.00
T. o. darti–T. o. oswaldi	0.0002*	1.93
T. o. oswaldi–T. o. leakeyi	<0.0001*	2.38

* Significant after the Bonferroni–Holm adjustment for multiple tests.
[1] Dates following Frost (2001).

Table 7
Comparison of the *H. erectus* sum of squared Procrustes distance (SSD) with empirical distributions generated for modern humans for the 32-landmark set

Reference taxon	Percentage smaller than *H. erectus* SSD	Mean SSD
H. erectus	—	0.59
East Asian/Oceanian/North American *H. sapiens*	94.72[3]	0.49
European/West Asian *H. sapiens*	76.09[2]	0.53
All *H. sapiens*	76.18[2]	0.55
African *H. sapiens*	72.85[1]	0.55

[1] *H. erectus* SSD falls within 50% confidence interval (CI) of reference taxon.
[2] *H. erectus* SSD falls within 75% CI of reference taxon.
[3] *H. erectus* SSD falls within 95% CI of reference taxon.

Bonferroni–Holm adjusted *p*-value of 0.003 (corrected from the standard alpha of 0.05). The *p*-values for the distances among subdivisions that are not strictly geographic, such as when OH 9 is grouped with Asian specimens in *H. erectus* s.s., did not even approach statistical significance.

All comparisons among geographic/genetic groups of modern humans are statistically significant, as seen in Table 8. The majority of comparisons between pairs of species within a single genus are also significant, as are many of the subspecies comparisons. The only species contrasts that are not significantly different are between *M. cyclopis* and other *Macaca* species. Most ape subspecies comparisons are not significant, with the exception of *P. t. troglodytes* vs. *P. t. verus*, whereas all pairs of *P. hamadryas* subspecies differ significantly in their average shapes. While two of the subspecies comparisons in the fossil papionin *T. oswaldi* are significant before the Bonferroni–Holm correction, none of them are significant after

this correction. It is worth noting that none of the comparisons where a species or subspecies is represented by only two individuals (*M. cyclopis* and *G. b. graueri*) are significant. Because the comparisons were constrained to sample sizes of only $n = 2$, there is higher variance than in the other comparisons; thus it was more difficult to get a statistically significant result.

As illustrated in Fig. 7, the shape differences between African/Georgian and Asian *H. erectus* include a higher neurocranial profile, more superiorly positioned opisthion, narrower supraorbital torus, and more projecting glabella in the latter group. These differences are similar to those seen in the PC plot in Fig. 2. The distance (Table 8) between the average African/Georgian and Asian *H. erectus* cranial shapes (0.053) is greater than that between regional/genetic groups of modern humans (0.019–0.027). Compared to the hominoids, the distance between the geographic groups of *H. erectus* is similar to or higher than that seen between species (0.037–0.058) and higher than that seen between subspecies (0.032). The *H. erectus* value is also within the range of interspecific distances for members of the *M. fascicularis* species group (0.050–0.061) and toward the high end of the range of intersubspecies comparisons for *P. hamadryas* (0.032–0.072). Although not significant after the Bonferroni–Holm correction, the distance between *T. o. darti* and *T. o. oswaldi* (0.052) is nearly identical to that seen between *H. erectus* geographic groups.

Female-male/size comparisons. Eight of the 14 male-female contrasts are statistically significant after the Bonferroni–Holm correction (Table 9). Not surprisingly, the greatest male-female distances are in *G. gorilla* and in subspecies of *P. hamadryas*, while the smallest distances are in chimpanzees and macaques. Although not significant after the Bonferroni–Holm correction, the distance between male and female *T. oswaldi* specimens is similar to that seen in *G. gorilla*.
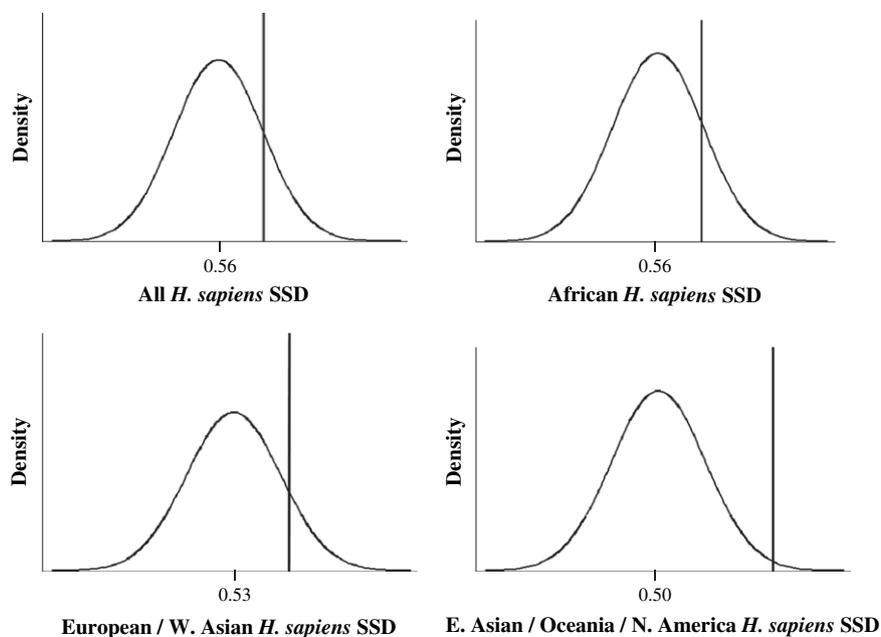

Fig. 6. Empirical distributions of the 10,000 bootstrapped SSDs (based on the 32-landmark set) for the modern humans in which the *H. erectus* value (vertical line) falls within the 95% CI. Mean SSD is labeled for each distribution.

Table 8

Results of permutation tests of the Procrustes distances between the mean cranial shape of regional/taxonomic groups in both *H. erectus* and the reference taxa using the 16-landmark set (*H. erectus* groupings defined in Table 4)

Comparison	Procrustes distance between group means	Probability that there is no difference in group means[1]	Number of pairwise comparisons for exact randomizations
Homo erectus			
African/Georgian vs. Asian	0.053	0.002*	1287
Original *H. ergaster* vs. original *H. erectus* s.s.	0.045	0.667	15
Expanded *H. ergaster* vs. expanded *H. erectus* s.s.	0.044	0.082	220
Early *H. erectus* vs. late *H. erectus*	0.043	0.040	286
Small *H. erectus* vs. large *H. erectus*	0.038	0.097	1716
Modern humans			
Africa vs. EU/WA[2]	0.025	<0.001*	
Africa vs. EA/OC/NA[3]	0.027	<0.001*	
EU/WA vs. EA/OC/NA	0.019	<0.001*	
Apes			
P. troglodytes vs. *P. paniscus*	0.058	<0.001*	
P. t. schweinfurthii vs. *P. t. troglodytes*	0.019	0.472	
P. t. schweinfurthii vs. *P. t. verus*	0.026	0.032	
P. t. troglodytes vs. *P. t. verus*	0.032	<0.001*	
G. gorilla vs. *G. beringei*	0.037	<0.001*	
G. b. beringei vs. *G. b. graueri*	0.029	0.984	693
P. p. pygmaeus vs. *P. p. abelii*	0.026	0.330	
Monkeys			
M. cyclopis vs. *M. fascicularis*	0.056	0.386	4293
M. cyclopis vs. *M. fuscata*	0.073	0.242	198
M. cyclopis vs. *M. mulatta*	0.061	0.325	1395
M. fascicularis vs. *M. fuscata*	0.050	<0.001*	
M. fascicularis vs. *M. mulatta*	0.046	<0.001*	
M. fuscata vs. *M. mulatta*	0.061	<0.001*	
P. h. anubis vs. *P. h. cynocephalus*	0.032	<0.001*	
P. h. anubis vs. *P. h. hamadryas*	0.041	<0.001*	
P. h. anubis vs. *P. h. kindae*	0.066	<0.001*	
P. h. anubis vs. *P. h. papio*	0.035	0.001*	
P. h. anubis vs. *P. h. ursinus*	0.039	<0.001*	
P. h. cynocephalus vs. *P. h. hamadryas*	0.052	<0.001*	
P. h. cynocephalus vs. *P. h. kindae*	0.048	<0.001*	
P. h. cynocephalus vs. *P. h. papio*	0.039	<0.001*	

Table 8 (*continued*)

Comparison	Procrustes distance between group means	Probability that there is no difference in group means[1]	Number of pairwise comparisons for exact randomizations
P. h. cynocephalus vs. *P. h. ursinus*	0.032	<0.001*	
P. h. hamadryas vs. *P. h. kindae*	0.072	<0.001*	
P. h. hamadryas vs. *P. h. papio*	0.042	<0.001*	
P. h. hamadryas vs. *P. h. ursinus*	0.049	<0.001*	
P. h. kindae vs. *P. h. papio*	0.068	<0.001*	
P. h. kindae vs. *P. h. ursinus*	0.071	<0.001*	
P. h. papio vs. *P. h. ursinus*	0.038	0.001*	
Theropithecus oswaldi			
T. o. darti vs. *T. o. leakeyi*	0.081	0.018	56
T. o. darti vs. *T. o. oswaldi*	0.052	0.032	252
T. o. leakeyi vs. *T. o. oswaldi*	0.062	0.054	56

* Significant after the Bonferroni–Holm adjustment for multiple tests.
[1] Alpha = 0.05.
[2] EU/WA = Europe/West Asia.
[3] EA/OC/NA = East Asia/Oceania/North America.

The distance between the average neurocranial shape of the smallest and largest *H. erectus* fossils (0.032), used as a proxy for intersexual distance, is comparable to that seen in the macaques and well below the distance found in the most dimorphic taxa.

Distances between average shapes: 32-landmark set

Using the 32-landmark set, all distances between regional groups of modern humans are significant (Table 10). More importantly, there is a significant difference only between the original *H. ergaster* and *H. erectus* s.s. subsets. This result is different from the 16-landmark analysis, in which the African/Georgian and Asian subsets are significantly different. This result may be due to the additional landmarks, but it also reflects the slightly different sets of original *H. erectus* s.s. specimens used in the two analyses (see below). The shape differences between the average original *H. ergaster* and *H. erectus* s.s. configurations are illustrated in Fig. 7 (similar to the shape differences seen in Fig. 3). *Homo erectus* s.s. has a longer and slightly higher vault with a wider midvault, narrower supraorbital torus, and more outward expansion at metopion. The Chinese specimens share a distinct cranial morphometric pattern (Antón, 2002; Kidder and Durband, 2004; Durband et al., 2005; Baab, in press), corresponding to that described above for *H. erectus* s.s. (a wider midvault relative to the frontal and occipital regions), which probably reflects the strong influence of the four Zhoukoudian specimens in the original *H. erectus* s.s. subset for this analysis. The homogeneous nature of this sample (see Fig. 3) probably inflates this distance even though this unique shape is not found in the other *H. erectus* s.s. specimens from Sangiran.
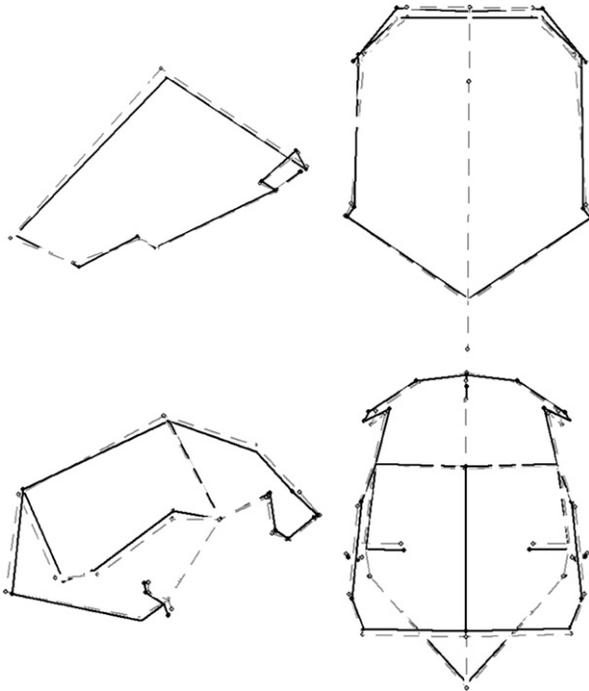
Fig. 7. Differences between the mean cranial vault shapes of the African/Georgian (black) vs. Asian (dashed gray) *H. erectus* subsets using the 16-landmark set (**top**) and *H. ergaster* (black) vs. *H. erectus* s.s. (dashed gray) using the 32-landmark set (**bottom**). Wireframes correspond to those shown in Fig. 1.

Table 9
Results of permutation tests of the Procrustes distances between the mean cranial shape of males and females in the reference taxa using the 16-landmark set

Taxon	Procrustes distance between single-sex means	Probability that there is no difference in single-sex means[1]	Number of pairwise comparisons for exact randomizations
Pan			
P. troglodytes	0.017	0.003*	
P. paniscus	0.021	0.020	
Gorilla			
G. gorilla	0.053	<0.001*	
G. beringei	0.038	0.027	
Pongo			
P. pygmaeus	0.045	0.002*	
Macaca fascicularis species group			
M. fascicularis	0.040	<0.001*	
M. fuscata	0.039	0.132	
M. mulatta	0.030	0.021	
Papio hamadryas			
P. h. anubis	0.050	<0.001*	
P. h. cynocephalus	0.059	<0.001*	
P. h. hamadryas	0.060	0.024	
P. h. kindae	0.045	<0.001*	
P. h. ursinus	0.056	<0.001*	
Theropithecus			
T. oswaldi	0.054	0.028	462

* Significant after the Bonferroni–Holm adjustment for multiple tests.
[1] Alpha = 0.05.

Table 10
Results of permutation tests of the Procrustes distances between the mean cranial shape of regional/taxonomic groups in both *H. erectus* and modern humans using the 32-landmark set (*H. erectus* groupings defined in Table 4)

Comparison	Procrustes distance between group means	Probability that there is no difference in group means[1]	Number of pairwise comparisons for exact randomizations
Homo erectus			
African/Georgian vs. Asian	0.050	0.028	715
Original *H. ergaster* vs. *H. erectus* s.s.	0.062	<0.001*	21
Expanded *H. ergaster* vs. expanded *H. erectus* s.s.	0.056	0.032	220
Early *H. erectus* vs. late *H. erectus*	0.048	0.050	715
Small *H. erectus* vs. large *H. erectus*	0.035	0.337	1716
Homo sapiens			
Africa vs. EU/WA[2]	0.032	<0.001*	
Africa vs. EA/OC/NA[3]	0.029	<0.001*	
EU/WA vs. EA/OC/NA	0.031	<0.001*	

* Significant after the Bonferroni–Holm adjustment for multiple tests.
[1] Alpha = 0.05.
[2] EU/WA = Europe/West Asia.
[3] EA/OC/NA = East Asia/Oceania/North America.

Discussion

The interpretation of variation in the fossil record is of fundamental importance in paleontology, and comparison to extant taxa with the purpose of determining how many extinct species to recognize in a sample has a long tradition within paleoanthropology (e.g., Simons and Pilbeam, 1965; Kay and Simons, 1983; Kimbel and White, 1988; Wood, 1993; Kramer, 1993; Teaford et al., 1993; Richmond and Jungers, 1995; Lockwood et al., 1996; Harvati et al., 2004). While *H. erectus* s.l. is clearly distinct from modern humans in its longer and lower neurocranium, prominent supraorbital torus, angulated occipital in the midsagittal plane, wide posterior neurocranium, and robust cranial superstructures (Weidenreich, 1935, 1943; Le Gros Clark, 1964; Howell, 1978; Howells, 1980; Rightmire, 1990; Antón, 2003; Baab, 2007), it is less clear whether multiple species are included in this taxon. Although most claims for multiple species within *H. erectus* s.l. have been based on the distribution of discrete traits (e.g., Wood, 1991; Villmoore, 2005), individual characters said to delineate *H. erectus* s.s. from other species have also been identified in *H. ergaster* and other non–*H. erectus* hominin fossils (Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992; Kimbel and Rak, 1993). Moreover, a cladistic approach to species identification may be philosophically unsound (Manzi et al., 2003), as a higher frequency of certain nonmetric features in the Asian fossils could also correspond to intraspecific patterns of variation in a long-lived and spatially dispersed species such as *H. erectus* (Turner and Chamberlain, 1989; Harrison, 1993; Walker, 1993).

In contrast to character-based investigations, a few studies have used traditional linear measurements to quantify metric variation in *H. erectus* with the explicit aim of addressing

taxonomic diversity in this taxon (Kramer, 1993; Bräuer, 1994; Bilsborough, 2000; Villmoore, 2005). This study extends those traditional morphometric approaches by the application of an explicitly 3D methodology that measures variation in the shape of the cranial vault while retaining information about the original geometric relationships among landmarks. The primary aim of this study was to bring a new perspective to bear on the question of *H. erectus* taxonomy. Both inter- and intraspecific variation would result in shape differences among temporal/spatial subsets of *H. erectus*. Only by quantifying the magnitude of variation in *H. erectus* relative to better-sampled primate taxa is it possible to differentiate between these two possibilities. Perhaps the greatest challenge to this approach is distinguishing between two species with the same cranial shape that differed only in size or in nonmetric traits vs. a single species that varied in size and discrete character expression. Hence, the results of this study should be interpreted alongside previous research on the size and discrete cranial features of *H. erectus*.

The two sets of landmarks used here capture significant differences among most species and subspecies of the reference taxa, as well as differences between males and females in many taxa. In addition, the 16-landmark set captures statistically significant temporogeographic variation within the *H. erectus* sample. Compared to modern humans, variation in *H. erectus* is greater when the 16-landmark set is utilized, confirming that these landmarks provide a conservative test of the species question in *H. erectus*. Although the distance between the mean shapes of the original *H. ergaster* and *H. erectus* s.s. subsets is significant using the 32-landmark set, as discussed above, this contrast mostly highlights the unique cranial metric pattern in the Zhoukoudian sample (Antón, 2002; Kidder and Durband, 2004; Durband et al., 2005; Baab, in press).

Including multiple reference taxa provides a greater context for the variation observed in *H. erectus* because the degree of variation is not constant across a given taxonomic rank (e.g., species; Shea et al., 1993; Plavcan and Cope, 2001), and the most relevant phylogenetic, ecogeographic, and temporal models are not one and the same. This approach recognizes the difficulty of species delineation in the fossil record (and even among extant groups) and may not allow for a simple black-and-white assessment of how many species are present in the *H. erectus* sample. One challenge is identifying the most appropriate taxonomic comparators for *H. erectus*. This discussion will first evaluate the null hypothesis that *H. erectus* represents a single species relative to the different reference taxa. The discussion will then synthesize these various results and compare them with previous studies.

Variation in Homo erectus *compared to the hominoids*

Relative to modern humans and chimpanzees, the standard phylogenetic comparators, the variation in *H. erectus* is greater than expected for a single neontological species. Although the *H. erectus* SSD is within the 50% CI for *H. sapiens* using the expanded landmark set, this probably reflects a less variable *H. erectus* sample for the 32-landmark analyses. The results

based on 16 landmarks are therefore a more conservative test because they utilized a more variable *H. erectus* sample. While it is possible to compare variation in *H. erectus* to ranges of both intrasubspecific and intraspecific variation in chimpanzees, their limited ecogeographic range may decrease morphological variation within this taxon. In this regard, humans are a more appropriate reference species. *Homo erectus* variance falls at the high end of the *H. sapiens* range (cf. Figs. 4 and 6); if greater spatial diversity in the modern humans is viewed as a proxy for temporogeographic variation in the fossil hominin (sensu Delson, 1997), then *H. erectus* should probably be viewed as multiple species.

If gorillas and orangutans are used as reference taxa, then variation in *H. erectus* is less than that expected for a single species, or in the case of *Pongo*, for a single subspecies. These taxa provide more conservative tests than chimpanzees and humans (Lieberman et al., 1988; Wood et al., 1991; Wood, 1993) because the high level of sexual dimorphism in the shape of the cranial vault, particularly in gorillas (Table 9), may have resulted in higher levels of intrasubspecies and intraspecies variation in these taxa. Although there is some evidence that early *H. erectus* from Georgia was highly dimorphic (Skinner et al., 2006; Rightmire et al., 2006; see also Spoor et al., 2007), later populations do not exhibit such marked size differences, and a comparison of small and large specimens here did not uncover strong size-shape dimorphism. At the same time, subspecies of *Pongo* are more variable than subspecies of *Gorilla*, despite the greater sexual dimorphism in cranial shape in the latter genus. Similarly, the baboon subspecies, while also exhibiting elevated levels of sexual dimorphism, are not as variable as either gorillas or orangutans, suggesting that other factors are also responsible for the inflated variation in the gorillas and orangutans. Overall, gorillas and especially orangutans, are more distantly related to *H. erectus* than chimpanzees (or modern humans) and likely exhibit greater sexual dimorphism in body mass, craniofacial dimensions, and cranial shape than *H. erectus*. In addition, both occupy more tropical environs and less extensive geographic ranges than *H. erectus*. For this reason, gorillas and orangutans are not the most relevant analogs for *H. erectus*.

Variation in Homo erectus *relative to papionins*

Variation in the *H. erectus* sample fits comfortably within the range of single species or subspecies of monkeys. The *H. erectus* SSD also falls within the 95% CI of *P. hamadryas* (including all six subspecies) and the *M. fascicularis* species group. While the magnitude of variation exhibited by *H. erectus* is therefore within the range of these multispecies configurations, it is at the extreme (low) end of expected variation. Both *P. hamadryas* and the *M. fascicularis* species group incorporate greater geographic diversity than do the ape taxa, making them relevant reference taxa for the geographically widespread *H. erectus*. Although the six forms of baboons are assigned here to subspecies of a single *P. hamadryas* species on the basis of the clinal nature of their cranial anatomy (Frost et al., 2003) and their tendency to interbreed at their

borders (Jolly, 1993, 2003), at least five of them are often elevated to full species rank (*P. hamadryas*, *P. papio*, *P. ursinus*, *P. anubis*, and *P. cynocephalus*; Hill, 1970; Groves, 2001; Wildman et al., 2004). Therefore, while the assignment of the baboon forms to subspecies rank is consistent with the biological species concept, a cogent argument can be made that levels of variation in each subspecies would mirror intraspecific variation in other taxa. Indeed, the baboon subspecies, particularly those with larger geographic ranges (*P. anubis*, *P. ursinus*, and *P. cynocephalus*; see Jolly, 1993), are at least as variable as macaque species (see Table 5). In this context, it is clear that *H. erectus* variation falls well within the range of single Old World monkey species, and at the low end of multiple-species configurations (see Fig. 5). While these results could support either a single- or multiple-species interpretation, the fact that this geographically and temporally diverse *H. erectus* sample is not more variable than the majority of species suggests that the single-species model for *H. erectus* cannot be ruled out.

In the final set of comparisons, it is clear that *H. erectus* is less variable than the fossil species *T. oswaldi*, which spanned a longer time interval, as well as the *T. o. darti*–*T. o. oswaldi* set of chronologically ordered subspecies, which spanned a similar time interval as *H. erectus*. At least some of the variation in the *T. o. darti*–*T. o. oswaldi* set is likely to be due to anagenetic changes that occurred over the ∼1.9-Myr lifespan of these two subspecies, although shape differences attributable to sexual dimorphism (see Table 9) may also have influenced overall levels of variation in *T. oswaldi*.

Synthesis of results

If variation at each rung of the taxonomic hierarchy was strongly canalized along primate lineages, such that more closely related species had more similar levels of variation than more distant relatives, then the phylogenetic models would always be the most relevant analogs for fossil hominins. However, the results of this analysis indicate that intraspecific variation is not consistent among hominoids. *Homo sapiens* and species of *Pan* are among the least variable species, whereas the gorilla and orangutan species and subspecies are the most variable of the reference taxa included in this study. On these grounds, as well as for reasons outlined above, the apes are probably not the most relevant analogs for *H. erectus*. Modern humans and the papionin monkeys are better reference taxa due to their more generalized ecologies and broader geographic ranges. Also, *H. erectus* s.l. was likely either a single, polytypic species (Rightmire, 1986, 1990; Turner and Chamberlain, 1989; Antón, 2003), several temporogeographically circumscribed subspecies (Campbell, 1965, 1972; Howells, 1980; Howell, 1994; Antón, 2003), or several closely related but geographically dispersed species (Wood, 1991; Clarke, 2000; Schwartz and Tattersall, 2003; Manzi et al., 2003). These different population structures are mirrored in *H. sapiens*, *P. hamadryas*, and the *M. fascicularis* species group, respectively. Although not entirely unambiguous, given the extensive geographic and temporal range of this fossil hominin taxon, I prefer a single-species

interpretation for *H. erectus*, as it did not exceed variability in many single neontological species, despite its greater geographic range and temporal depth. The fact that this sample exhibits such a consistent cranial form through nearly 1.8 Myr and across thousands of kilometers is itself an interesting observation regarding the evolutionary history of *H. erectus*. The overlap of *H. erectus* with the *M. fascicularis* species group and with the entire *P. hamadryas* species may indicate that there was population structure within this species, possibly related to the temporogeographic groupings present in the sample (e.g., East Turkana, Zhoukoudian, Ngandong) (see Fig. 3). According to this model, certain cranial superstructures are expressed more frequently in the Asian populations (e.g., an angular torus, suprameatal crest, midline keeling) as a result of drift and isolation (Antón, 2007). Although not explicitly addressed in this study, endocranial volume in *H. erectus* appears to have increased gradually over its time span (Leigh, 1992; Antón and Swisher, 2001; Rightmire, 2004), a pattern that could easily be interpreted within a framework of anagenetic change within this species. Indeed, several of the morphological differences observed between African/Georgian and Asian *H. erectus* samples may be attributable to this well-documented increase in cranial capacity (i.e., greater height at bregma, outward expansion at metopion, wider frontal and temporal squamae and reduced postorbital constriction).

This finding is consistent with many previous studies based on both metric (Kramer, 1993; Antón, 2002; Kidder and Durband, 2004; Villmoare, 2005) and nonmetric (Rightmire, 1990; Bräuer and Mbua, 1992; Antón, 2002, 2003) variation in *H. erectus*, but contrary to others (Andrews, 1984; Stringer, 1984; Wood, 1984, 1991; Villmoare, 2005; Tattersall, 2007). The only other 3D geometric morphometric approach to this question (Terhune et al., 2007) reported very different findings: variation in the shape of the *H. erectus* temporal bone was greater than that seen in neontological species. The discrepancy between the latter study and this one may be due to their use of only hominoid reference taxa as well as their more restricted temporal-bone landmark set. Perhaps details of temporal-bone morphology are more variable than the shape of the neurocranium. The observation that levels of variation in different subsets of *H. erectus* were also higher than expected for single species (Terhune et al., 2007) confirms the presence of high interindividual variation in temporal-bone shape rather than multiple taxa in this sample.

In another recent study, Villmoare (2005) found that, while linear measurements supported a single-species model for *H. erectus*, statistical analysis of discrete characters indicated the presence of more than one species. This could reflect multiple species that maintained a similar cranial bauplan, while varying more in nonmetric features. Alternatively, this pattern may signify that *H. erectus* was a single species with some interindividual or spatial/temporal differentiation (cf. Baab, 2007). This second explanation received more support from both the Terhune et al. (2007) study and the analyses here that tested the distance among group means of different *H. erectus* subsets.

When the full *H. erectus* sample is divided into pairs of subsets that correspond to geographic, temporal, size, and

proposed taxonomic subdivisions, the African/Georgian vs. Asian contrast is significant when the 16-landmark set is utilized but not when the more complete 32 landmarks are used (probably due to differences in sample composition). Divisions that place OH 9 with the Asian specimens (*H. erectus* s.s. sensu Clarke, 1990, 2000; Wood, 1991, 1994) vs. the East Turkana (and Dmanisi) fossils are not significant in either case, nor are the contrasts based on time and size. Shape differences between African and Asian specimens include the relatively higher vault, narrower supraorbital torus, reduced constriction across frontotemporale, lower temporal squama, longer parietomastoid suture, anteriorly positioned basal temporal-bone structures, and less-projecting entoglenoid process. This description confirms some earlier observations regarding the large entoglenoid process in the African fossils (Picq, 1990; Rightmire, 1990) and weaker postorbital constriction in some of the Asian fossils (Delson et al., 2001; Baba et al., 2003), while also highlighting some newly described differences between the groups (e.g., a relatively lower position of the temporal squama, narrower supraorbital torus, and anteriorly positioned temporal-base structures in the Asian specimens).

The finding that geographic variation is more marked than that seen between *H. ergaster* and *H. erectus* s.s. is also confirmed by the grouping of OH 9 with other African specimens rather than with the Asian fossils in the PCA. This conclusion differs from some previous studies that found greater affinities between OH 9 and the Asian fossils (Wood, 1991; Clarke, 2000; Terhune et al., 2007), but is in agreement with workers that have not found a particular resemblance between OH 9 and the Asian fossils (Picq, 1990; Rightmire, 1990; Antón, 2002, 2003). Perhaps OH 9 is more similar in its overall cranial vault shape to other African fossils (see also Baab, 2007), while sharing some resemblances to the Asian specimens in more specific aspects of its cranial morphology.

This geographic patterning of variation, also evident in Figs. 2 and 3, is easily accommodated within a single polytypic species under the biological species concept, where anagenetic change, local adaptation, and genetic isolation acted to differentiate the eastern and western portions of the hypodigm. If, on the other hand, the phylogenetic species concept is applied and two species are recognized, then this study supports a strictly geographic criterion for species division that does not combine OH 9 and the Asian specimens in the same species. *Homo erectus* and recent *H. sapiens* are very distinct in their overall neurocranial shape, and combining these two into a single evolutionary species (*H. sapiens*; sensu Thorne and Wolpoff, 1981; Frayer et al, 1993; Wolpoff et al., 1994; Wolpoff, 1999; Hawks et al., 2000) would greatly increase the variation over the level seen in *H. erectus* alone. As the current, more restricted *H. erectus* sample is already comparable in magnitude of variation to several neontological species, it seems probable that a temporally expanded *H. sapiens* species (including *H. erectus* and other fossil *Homo* taxa) would then be considerably more variable than most single species of the reference taxa. This study does not therefore lend support to the interpretation of *H. sapiens* as a single evolutionary species spanning ∼ 1.8 Myr.

Conclusions

The use of different phylogenetic, ecological/geographic, and temporal analogs for comparison with *H. erectus* resulted in a holistic and nuanced view of variation within *H. erectus*. As variation within a species is not directly correlated with phylogeny, the apes are not necessarily the most appropriate reference taxa simply by virtue of their close genetic relatedness to *H. erectus*. Rather, modern humans and papionin monkeys were more relevant analogs due to the greater overlap of their geographic ranges and ecological habitats, as well as potential similarities in population structure between these taxa and *H. erectus*. In common with previous studies that have shown a great deal of overlap in discrete characters across the range of *H. erectus*, the results of this analysis most strongly support a single-species interpretation for *H. erectus*. From this perspective, the variation in cranial shape uncovered in this study should be interpreted within the framework of intraspecific variation, rather than species distinctions. If the phylogenetic species concept is applied, however, then there is limited evidence for a multiple-species model that follows strictly geographic lines rather than linking OH 9 with the Asian fossils in *H. erectus* s.s. Regardless of how many species are recognized, it is interesting that neurocranial shape was conserved across the great temporal depth and spatial range encompassed by the *H. erectus* hypodigm.

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