

CRANIAL SHAPE VARIATION IN *HOMO ERECTUS*

by

KAREN L. BAAB

A dissertation submitted to the Graduate Faculty in Anthropology in
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Abstract

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by

Karen L. Baab

Advisor: Professor Eric Delson

The fossil hominin species *Homo erectus* spanned nearly the entire Pleistocene epoch and is known from sites in East Africa, South Africa, Georgia, China and Java. *H. erectus* represents the oldest occurrences of hominins outside of Africa and is associated with novel technological and behavioral adaptations.

I addressed several unanswered questions pertaining to the taxonomy and evolutionary history of *H. erectus* using 3D geometric morphometric techniques. Despite the relatively extensive temporal and geographic range of *H. erectus*, the relative degree of cranial shape variation in this taxon did not exceed that seen in several subspecies and species of non-human primates, and was comparable to the variation seen in a recent, geographically disperse *H. sapiens* sample. This observation was most comparable with a single species interpretation for *H. erectus*. A combination of primitive (e.g., a low midline cranial profile), derived (e.g., relatively wide anterior vault), and unique (e.g., the great width of the occipital bone) shape features served to diagnose *H. erectus* relative to *H. habilis*, mid-Pleistocene *Homo*, Neanderthals and *H. sapiens*. The affinities of several newly described fossils were assessed against this definition. For example, the Dmanisi hominins fit well within the range of variation expressed by other *H. erectus* individuals, while ER 42700 from Ileret did not. While there was a strong intraspecific geographic

signal within *H. erectus*, cranial shape also changed over time within more limited regions of the Old World. The Asian populations of *H. erectus* were autapomorphic in certain aspects of their cranial shape (e.g., the occipital bone) relative to later *Homo* species, and were most likely an evolutionary dead end. There appears to have been greater variation within the earlier populations of Indonesian hominins from Sangiran than in later Javanese populations.

This dissertation also described patterns of cranial shape evolution along several proposed phylogenetic trees for the genus *Homo*, highlighting a general increase in cranial height and breadth and a decrease in constriction across frontotemporale, changes likely related to increases in brain size. By examining the relationship between cranial shape and size, it was demonstrated that the cranial shape of Liang Bua 1 (LB1) is comparable to a scaled down *H. erectus* individual.

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Chapter 1: Overview of *H. erectus* and Introduction to Dissertation

Overview

This dissertation will address cranial shape variation in *Homo erectus* and its implications for the taxonomy, phylogeny and evolutionary history of the species. This project represents the first attempt to answer these questions about *H. erectus* using three dimensional geometric morphometric data. In this first chapter I will review previous research on *H. erectus*, starting with a historical overview of fossil discoveries of the ‘core’ *H. erectus* sample: specimens from the Javanese sites of Sangiran, Trinil and Mojokerto, from Zhoukoudian, China and the large OH 9 calotte from Olduvai Gorge, Tanzania. Additional specimens which are frequently assigned to *H. erectus* will also be discussed from sites such as Koobi Fora, Kenya; Ngandong and Sambungmacan, Indonesia; and Dmanisi, Georgia. This historical overview will also incorporate information about the geology and chronology of *H. erectus* sites. In addition to fossil discoveries, I will also discuss the morphology of *H. erectus*, focusing mainly on the cranium. An assessment of variation within the hypodigm will be presented in terms of geographic, temporal and size-related variation. The implications of the patterning of variation for *H. erectus* taxonomy, evolutionary history and phylogeny will be reviewed. Finally, I will describe the main subjects addressed in this dissertation and its layout.

The second chapter deals with the magnitude of variation present within the *H. erectus* sample and its taxonomic implications. In order to establish whether the amount of variation in *H. erectus* is outside that expected for a single species, variation will be quantified and assessed relative to other hominins and non-hominin primates. In chapter

3, I will examine the relative uniqueness of *H. erectus* cranial shape compared to a range of modern and fossil *Homo* species, including *H. heidelbergensis*, *H. neanderthalensis* and early anatomically modern *H. sapiens*, all of which potentially overlap temporally with *H. erectus* and some of which (e.g. *H. heidelbergensis*) share aspects of cranial shape with *H. erectus*. While phylogeny reconstruction is outside the scope of this analysis, geometric morphometric analysis of 3D shape data can address the nature of shape change across evolutionary transitions involving *H. erectus*. In chapter 3, I will also evaluate competing phylogenetic scenarios, particularly whether *H. erectus* in the far east contributed significantly to the ancestry of modern humans from this region. In chapter 4, I focus exclusively on intraspecific variation in cranial shape within *H. erectus*, elucidating the extent to which various factors (geography, time and sex / allometry) influence cranial form within *H. erectus*. Analyses in chapter 4 will also address hypotheses concerning the taxonomy and evolutionary history of *H. erectus*. The final chapter (chapter 5) will synthesize the results of the three data analysis chapters and place the results and conclusions within the broader context of hominin evolution. This chapter will also provide a detailed comparison of my results with previous work, identifying areas of agreement and disagreement and addressing possible reasons for the latter.

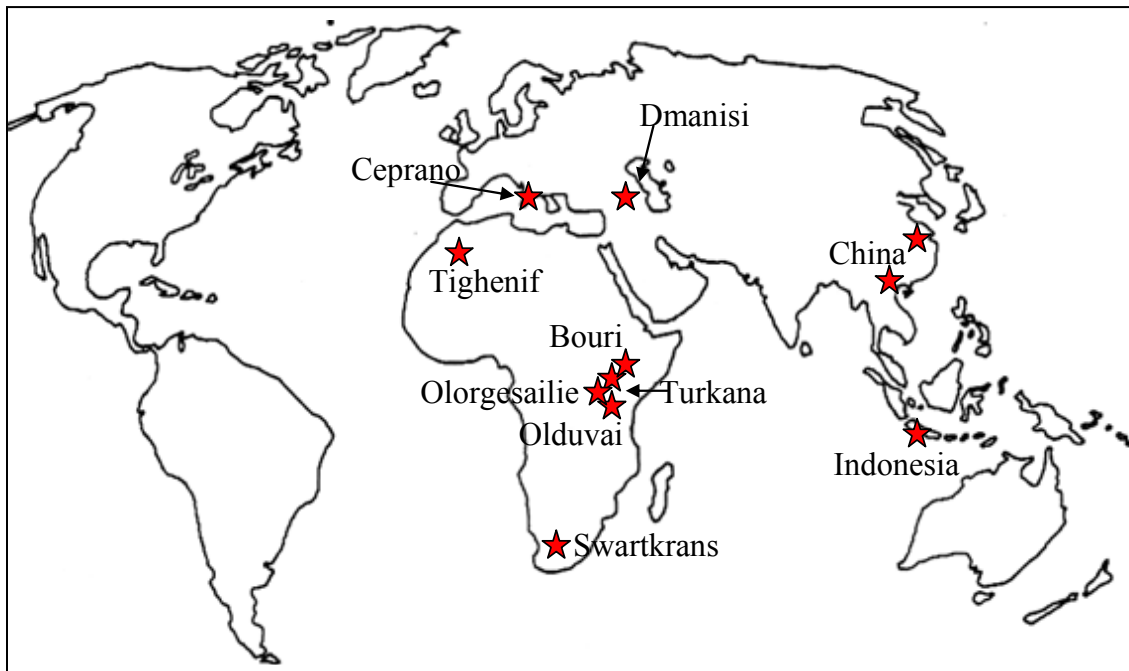
Introduction

The taxonomic status and phylogenetic position of *Homo erectus* is currently in flux. Much of this uncertainty can be attributed to an incomplete understanding of variation within *H. erectus*. However, several characteristics of *H. erectus* make this an

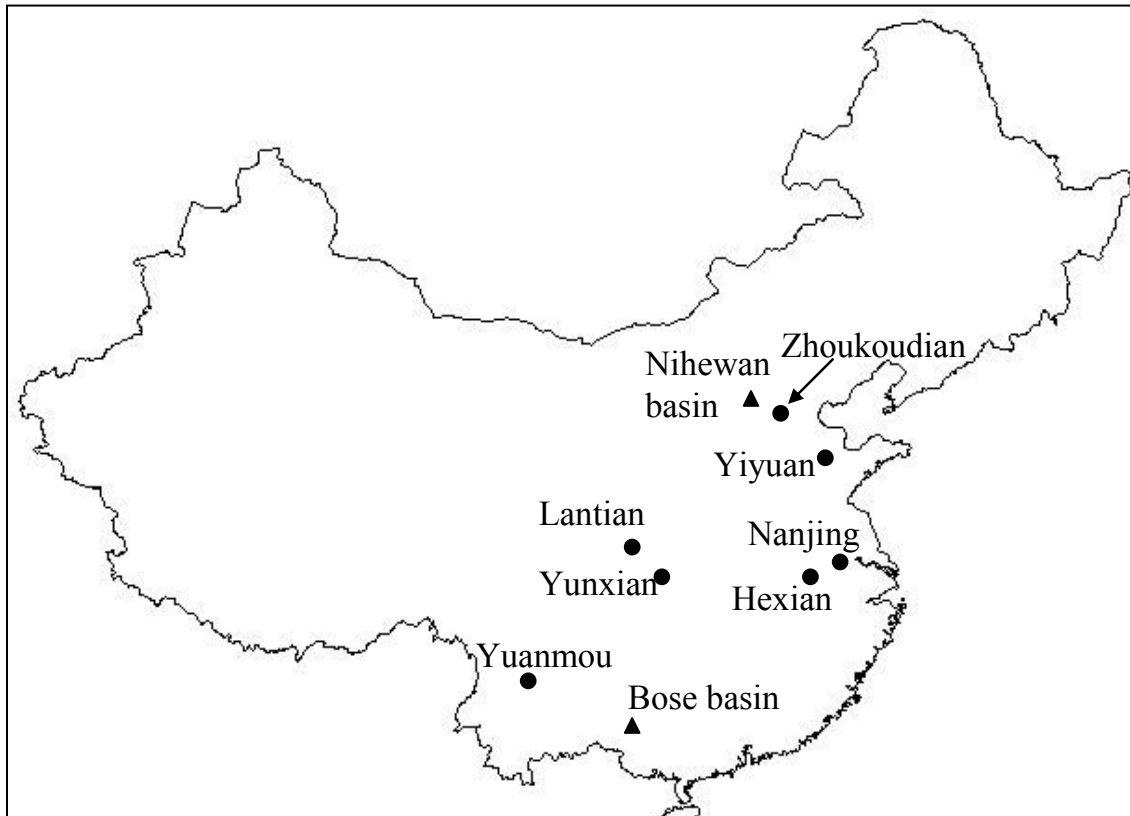
ideal species in which to investigate variation. First, there is a relatively large sample of cranial specimens from geographically widespread sites in China, Indonesia, Africa and Europe that have all been attributed to *H. erectus*, as illustrated in Figure 1.1a. In addition to the wide geographic range inhabited by *H. erectus*, there is also evidence of this species from the late Pliocene through much of the Pleistocene, a time range of potentially ~1.8 Ma. The range of cranial capacities from under 700 cc to over 1200 cc reflects the high degree of size variation present within the *H. erectus* hypodigm. Finally, evidence from the Republic of Georgia also suggests that *H. erectus* was the first hominin to inhabit temperate climates.

Figure 1.1: Map showing distribution of *H. erectus* sites across the Old World (a). The red stars in (a) represent the approximate location of *H. erectus* fossil sites. More detailed maps of China (b) and Indonesia (c) are also provided below. The circles are the locations of *H. erectus* fossils sites and the triangles are archaeological sites.

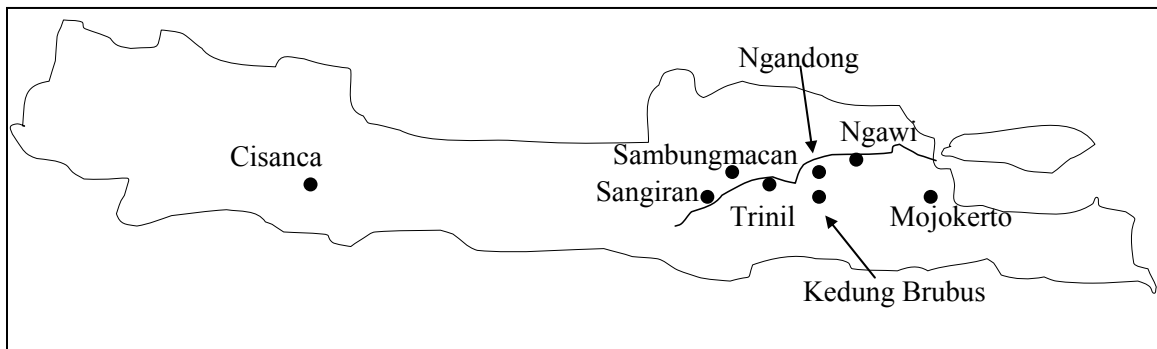
a)



b)



c)



The long time span and wide geographic range of *H. erectus* across the Old World is testimony to the success of this taxon in adapting to life outside of Africa, an adaptation also seen in modern humans. The close evolutionary relationship and similarities in adaptations between *H. erectus* and modern humans makes this a key species in hominin evolution. Despite the (relatively) large fossil sample available for *H.*

erectus, many questions remain to be answered. In terms of the taxonomic status of this group, three major hypotheses have been put forward (1) *H. erectus* represents an early grade within a greatly expanded *H. sapiens*, (2) the entire hypodigm can be described as a single polytypic species or (3) multiple species can be identified within this fossil sample. If either the first or second options are accepted, then another point of disagreement concerns the presence and relative importance of geographic, diachronic and size-related (both sexual and allometric) variation within this sample. While some studies have highlighted a lack of evolutionary change (stasis) within *H. erectus* (Bilsborough, 2000), others have found evidence of directional change from early to later members of this taxon (Wolpoff, 1999). A number of studies have emphasized geographic variation within this taxon, both between African and Asian representatives (Andrews, 1984; Stringer, 1984) and within the Asian sample (Antón, 2002; Liu *et al.*, 2005), though certain similarities appear to cut across geographic boundaries (Rightmire, 1990). There is also some evidence that larger crania are more comparable across space and time, as are smaller crania (Rightmire, 1990), though how individual characters are related to size is not well-understood (Spoor *et al.*, 2005). When Antón (2003, p. 162) reviewed the state of *H. erectus* research, she identified a need for “systematic assessment of the covariance and significance of characters related to time and geography, but also most critically to size, sex, and ... age variables.” This work can be viewed as a first step in addressing this gap in our understanding of *H. erectus* evolutionary history.

Similar ambiguities surround the phylogenetic position of *H. erectus*. It is possible that some of the populations represented by Africa *H. erectus* fossils were on the lineage leading to *H. sapiens* (via *H. heidelbergensis*) (Rightmire, 1990), but it is less

clear whether Asian *H. erectus* contributed to this lineage (Hublin, 1986; Lieberman, 2001) or represented an evolutionary side branch (Andrews, 1984; Wood, 1984). An alternative viewpoint is that regional variants of *H. erectus* or other archaic *Homo* give rise to modern humans in their respective geographic regions (e.g., Australasia or China) (Thorne and Wolpoff, 1981; Wolpoff, 1999; Frayer *et al.*, 1993). Additional fossil discoveries attributed to *H. erectus* from Africa, Europe and the Caucasus have incurred further questions. Do the fossils from Dmanisi, Georgia represent the first migration of *H. erectus* from Africa (Gabunia *et al.*, 2000b; Vekua *et al.*, 2002, Rightmire *et al.*, 2006) or a pre-*erectus* migration (Gabounia *et al.*, 2002; de Lumley *et al.*, 2006)? This latter possibility raises the question of whether *H. erectus* evolved inside Africa (Bilsborough and Wood, 1986; Antón *et al.*, 2002a) or outside of Africa (Clarke, 1990; 2000a; Asfaw *et al.*, 2002; Wang and Tobias, 2001).

An exploration of variation within *H. erectus* must be limited to the skull because of the dearth of postcranial elements securely assigned to this species. Previous analyses have focused on either the distribution of discrete characters within *H. erectus* (e.g., Andrews, 1984; Stringer 1984; Wood, 1984, 1991, 1994; Villmoare, 2005) or metric variation within this taxon (e.g., Bilsborough and Wood, 1986; Rightmire, 1984, 1990; Bilsborough, 2000; Antón, 2002; Antón, *et al.*, 2002b). While both types of data provide important information about intra- and inter- specific variation, concerns have been raised over the definition, homology and relevancy of many discrete characters (Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992; Brown, 1994). Additionally, morphometric data are preferable for addressing questions of alpha taxonomy (Harrison, 1993) and have proven useful in discriminating among a variety of hominin and non-hominin primate

taxa at the specific, subspecific and demic levels (Howells, 1973, 1989; Albrecht and Miller, 1993; Shea *et al.*, 1993; Frost *et al.*, 2003; Hennessy and Stringer, 2002; Guy *et al.*, 2003; Harvati *et al.*, 2004; McNulty, 2005). The extension of standard morphometrics to two- and three- dimensional geometric morphometrics provides a powerful tool kit that can be used to quantify and visualize variation in shape.

‘Core’ Homo erectus sample

Among those researchers who accept *H. erectus* as a distinct species, there is almost universal agreement that the fossils from Trinil, Sangiran, Modjokerto and Zhoukoudian are part of this hypodigm (see maps in Figure 1.1). OH 9 is also generally included in *H. erectus*, even when other East African fossils are not (e.g., Wood, 1991), although this is not always the case. It is also considered part of the ‘core’ sample because traditionally OH 9 has been included in descriptions of *H. erectus* morphology (e.g., Le Gros Clark, 1964; Howell, 1978).

Indonesia: In 1891 Eugène Dubois discovered the ‘missing link’ at Trinil on the Indonesian island of Java and named it *Pithecanthropus erectus* (Dubois, 1894). Dubois recognized *Pithecanthropus* as an intermediate between apes and humans. A calotte was recovered in addition to a number of teeth and postcranial fragments, mainly femoral. Trinil 2 was notable for being long and low with a straight transverse supraorbital torus. Many more cranial remains have been recovered from sites in the Sangiran dome, Central Java since the time of Dubois. Through the 1930s a series of partial crania (S 2, 3 and 4)

were recovered from the Sangiran dome by local inhabitants during cultivation of the land. A site in East Java produced a juvenile cranium usually considered to be a young *H. erectus* (Mo[d]jokerto or Peking 1) (von Koenigswald, 1950; Storm, 1994; Antón, 1997). G.H.R. von Koenigswald was involved in many of these discoveries. The Sangiran remains were considered further examples of *Pithecanthropus*, similar to Dubois' Trinil specimen. S 10, which consists of part of the posterior neurocranium, was recovered in 1963 and described by Jacob (1964; 1967a). Only two years later another fragmentary cranium, S 12, was collected near the village of Tanjung. Sartono described the most complete *H. erectus* specimen from Asia found six years later, a well-preserved cranium named S 17 (Sartono, 1971). Additional dentognathic fossils, smaller cranial and postcranial fragments, and one endocast (S 23) discovered from the mid-1930s through the late-1970s round out the Sangiran sample (Indriati, 2004).

The Trinil and Sangiran crania present sagittal profiles which are short supero-inferiorly and elongated antero-posteriorly. The maximum cranial breadth occurs low down on the vault, often at the level of the supramastoid crests. The frontal bone is receding, there is marked postorbital constriction and the supraorbital torus is straight across with no supratotal sulcus. A sharp angle is formed between the occipital and nuchal planes with a transverse occipital torus which is usually thickest medially. An angular torus, bregmatic eminence and midline keeling on the frontal, parietals or both are common. The average endocranial volume for several Sangiran hominins is 930 ml (according to values from Holloway, 2000). More details concerning *H. erectus* morphology can be found in the 'Cranial Morphology' section below.

The Sangiran dome localities have yielded the majority of *H. erectus* specimens in Indonesia. The Sangiran dome is found within the Solo basin in Central Java. Hominins have been found in both the younger Bapang (Kabuh) and the upper layers of the Sangiran (Pucangan) Formations. The specimens found in the upper Sangiran layers are too fragmentary and distorted to be included in most metric analyses, and are composed mostly of dentognathic material (but also some cranial remains: S 27, S 31 and an occipital from the Bukuran locality). The most notable exception is the S 4 partial cranium, which consists of a well-preserved palate and posterior vault. The Bapang layers are a series of fluvial cycles (C1-C5, bottom to top) composed of volcanic and carbonate/silicate sediments (Larick *et al.*, 2001). Within the Bapang Formation, the fluvial energy decreases throughout time so that the younger fossils are better preserved than the older ones.

The Bapang layers overlie the Sangiran Formation, composed of the upper hominin-bearing ‘black clays’ and the Lower Lahar Unit which is a non-hominin-bearing volcanic mudflow. The “Grenzbank” layer is the bottom most layer of the Bapang sediments and marks the boundary between the two formations. Most fossils derive from the Grenzbank and Bapang layers. *H. erectus* was also recovered from the uppermost layers of the Sangiran Formation, but the lack of pumice in the upper two layers of the Sangiran Formation precludes argon dating.

It has been suggested previously that hominins in Java are either less than 1 Ma or between 1 and 0.7 Ma based on faunal, fission-track, paleomagnetic and tektite analyses (Sémah *et al.*, 1981; Pope, 1983, 1984; Suzuki *et al.*, 1985; Hyodo *et al.*, 1993, 2002; Itihara *et al.*, 1994; van den Bergh *et al.*, 1996; Langbroek and Roebroeks, 2000). More

recent dating work took advantage of the presence of hornblende in the Bapang Formation. Larick *et al.* (2001) reported a series of hornblende $^{40}\text{Ar} / ^{39}\text{Ar}$ dates from the southeast region of the Bapang Formation between 1.5 and 1 Ma, dates which are considerably older than the generally accepted Middle Pleistocene dates. However, these older dates are in agreement with other potassium-argon and argon-argon dates published by Swisher (1997), Curtis (1981) and Obradovich and Naeser (1982). This radiometric chronology assigns the Sangiran fossils from the Bapang Formation ages between 1.5 and 1 Ma and a date of >1.5 Ma for some more fragmentary material that derived from the upper Sangiran layers (the 'black clays'). The Lower Lahar was deposited between 1.7 and 1.9 Ma, providing a maximum age for the settlement of Java by terrestrial species like *H. erectus* (Sémah *et al.*, 2000; Bettis *et al.*, 2004).

Discordance with fission-track, paleomagnetic and tekite dating evidence may be explained by technical problems with the fission-track dates (Bettis *et al.*, 2004), magnetic overprinting in the paleomagnetic record (Antón, 2003) and the lack of widespread evidence for tektites in the lithostratigraphy of Java (Bettis *et al.*, 2004). However, studies of the preserved fauna have generally supported the later dates (e.g., de Vos, 1985; van den Bergh *et al.*, 2001) and while a few microfaunal studies have supported a longer chronology (e.g., Ninkovich and Burckle, 1978), this discrepancy has not been fully explained (de Vos and Sondaar, 1994; Corvinus, 2004).

Several very early $^{40}\text{Ar} / ^{39}\text{Ar}$ dates have been proposed by Swisher and colleagues, but have received a fair amount of criticism. Swisher *et al.* (1994) reported a date of 1.66 Ma for a horizon 2 meters above S 27 and S31. However, because there is no pumice in the top two layers of the Sangiran Formation, the layer sampled was either

Bapang or Lower Lahar (the bottom layer of the Sangiran Formation) (Larick *et al.*, 2001). The date appears too old to be from the Bapang Formation and is in accord with other $^{40}\text{Ar} / ^{39}\text{Ar}$ dates from the Lower Lahar (Sémah *et al.*, 2000; Bettis *et al.*, 2004). This date is therefore not associated with S 27 and 31.

In addition to the debate concerning an earlier or later settlement of Java, there is disagreement concerning the relative positioning of the hominins within the Sangiran dome deposits. While there is general agreement that S 4, as well as some of the more fragmentary dentognathic fossils are from below the Grenzbank layer (the boundary between the Sangiran and Bapang Formations) and that S 17 is from between the Middle and Upper Tuffs of the Bapang Formation, there is not consensus regarding the relative ordering of S 2, 3, 10 and 12 within the sequence (Sartono, 1975; Pope, 1988; Rightmire, 1988; Itihara *et al.*, 1994; Larick *et al.*, 2002). There is, however, very little (or no) discussion as to how these positions within the stratigraphy were determined. Larick *et al.*, (2002) also assigned stratigraphic positions and ages (1.3-1.24 Ma) to more recently described fossils from Grogol Wetan, Tanjung and Bukuran, though at least one contradicts a previous $^{39}\text{Ar}/^{40}\text{Ar}$ date of 0.78 from the Grogol Wetan site (Saleki, 1997).

The Trinil fossils are generally assigned ages based on correlation with the Sangiran dome deposits although there is some uncertainty regarding the faunal correlation between these sites (de Vos *et al.*, 1982; Sondaar, 1984; Bartstra, 1983; Pope, 1983; Theunissen *et al.*, 1990). Contra von Koenigswald (1934; 1935), it has been suggested that the Trinil fauna (associated with Trinil 2) may be older than the 'Djetis' ('Jetis') fauna which has commonly been associated with the Sangiran Formation (de Vos *et al.*, 1982; Sondaar, 1984). As a result, Trinil 2 has been assigned both Middle and

Early Pleistocene ages. It seems clear that the faunal types recognized by von Koenigswald are too simplistic (Pope, 1983) and more recent studies have recognized additional faunal types (e.g., van den Bergh *et al.*, 2001). The current consensus seems to be a stratigraphic position of Trinil 2 near the base of the Bapang Formation, with an age around ~1 or ~1.5 Ma depending upon what set of dates are used (Swisher *et al.*, 1994; Rightmire, 2004; van den Bergh *et al.*, 2001).

Further east, a juvenile calvaria was discovered in East Java near Perning in 1936. The Mojokerto child (Perning 1) was found by Andoyo, a fieldworker for the Geological Survey of the colonial Netherlands East Indies Bureau of Mining. Von Koenigswald initially named the Modjokerto child *H. modjokertensis* (von Koenigswald, 1936) though he and Weidenreich later referred to it as a young *Pithecanthropus* (von Koenigswald and Weidenreich, 1939). Historical debate over the exact provenance (and hence age) of the Mojokerto fossil have been thoroughly documented by Huffman and colleagues (Huffman, 2001; Huffman *et al.*, 2005, 2006). These workers conclude based on historical and geological evidence that the specimen was found in situ in a conglomerate sandstone within a layer equivalent to the Sangiran (Pucangan) Formation of the Sangiran dome. Swisher *et al.* (1994) propose a very early date of 1.8 Ma for this fossil. However, it now appears that the date reported for Mojokerto is not associated with the stratigraphic layer from which the fossil was derived, casting this early date into doubt as well (Huffman *et al.*, 2005, 2006).

China: Dubois (1938) did not see much similarity between the Javan remains and the many fossils discovered in cave deposits at Zhoukoudian (Chou-kou-t'ien), China. The

majority of the Zhoukoudian remains were uncovered from Locality 1 between 1921 and 1937 by Swedish, Chinese and Canadian researchers. These fossils, which were originally named *Sinanthropus pekinensis*, are an important part of the fossil hypodigm as there are six relatively complete calottes and numerous other craniodental remains, including some unarticulated facial fragments (Black, 1926, 1927, 1931; Pei, 1930; Weidenreich, 1935, 1937a, b, 1943). The most complete specimens are known as Skulls II, III, V, X, XI and XII. With the exception of Skull III, all specimens are believed to be adults and both sexes are represented (Weidenreich, 1943). Originally Skull V consisted of just a left temporal and fragmentary right temporal bone. However, the addition of frontal and occipital fragments found by a team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in 1966 resulted in a much more complete calvaria (Qiu *et al.*, 1973). Though all the original fossils (with the exception of a few teeth) found pre-World War II were lost during the war, excellent casts are available at the American Museum of Natural History in New York City.

As noted by Weidenreich (1943), the Zhoukoudian remains all have long and low sagittal profiles. The frontal is receding but with marked frontal tuberosities and clear supratrochlear sulci behind the straight supraorbital tori. The occipital and nuchal planes form a sharp angle so that inion and opisthocranium are coincident, and there is a clear transverse occipital torus that is continuous laterally with the angular torus. The calvaria generally have midline keeling on the frontals and parietals, as well as coronal keeling and a bregmatic eminence (cruciate eminence). The maximum cranial breadth occurs low on the vault, and the average cranial capacity is 1075 cc.

The fossil site of Zhoukoudian is a series of karst caves which were systematically excavated beginning in 1921. *H. erectus* fossils derive from the Lower Cave (Locality 1) on Longgushan (Dragon Bone Hill) while more modern humans have been uncovered from the Upper Cave (Shandong) at Zhoukoudian. The lithostratigraphy of Locality 1 is consistent with an open-air cave (Goldberg *et al.*, 2001). The presence of artifacts and burnt bone may support “transient hominid presence in the cave” (Boaz *et al.*, 2004, p 546). Hyenas may also have played a role in accumulating hominins at Locality 1, as there is a great deal of hyena damage on the hominin fossils from the site (Boaz *et al.*, 2004).

Locality 1 consists of many layers, numbered from top to bottom (down to 17) with hominin fossils found in layers 3, 4, 5, 7, 8/9 and 10, though evidence of hominins, including archaeological material, was found in the top 13 layers. The majority of these deposits were “rockfall from the bedrock walls and collapsed fault breccia, and fine-grained silts washed into the cavity from outside” (Goldberg *et al.*, 2001). Of the more complete calvarial remains, Skulls II and III from layer 10 are the oldest while Skulls X, XI and XII from layer 8/9 are slightly younger. The only relatively complete calvarium from higher in the sequence is Skull V which was excavated from layer 3 (Weidenreich, 1935). The Zhoukoudian material has traditionally been dated to the Middle Pleistocene but there is disagreement concerning the exact dates. Skull V from layer 3 has typically been dated to approximately 0.3 Ma or younger (e.g., Huang *et al.*, 1991; Yuan *et al.*, 1991; Grün *et al.*, 1997), but has more recently been dated to slightly older than 0.4 Ma (Shen and Jin, 1993; Shen *et al.*, 2001). Dates for the older layers (8-10) usually fall between .4 and .6 Ma, though U-series dates reported by Shen *et al.* (2001) are older (0.6

- 0.8 Ma). The early Pleistocene dates of Shen *et al.* (2001, p. 681) may be more reliable than past dating efforts because “pure, dense and well-preserved speleothem carbonates are more likely to act as a closed system for U-TH isotopes than are fossil bones,” and hence, require fewer assumptions than the past U-series and ESR dating on tooth enamel or antler. Based on these older dates, Zhou *et al.* (2000) correlated the layers of Locality 1 with the marine oxygen isotope stages and estimated a range of 0.78 to 0.42 Ma for Layers 14 to 1/2, with the hominin bearing layers (3-10) dating from 0.67 to 0.47 Ma.

Tanzania: The discovery by Louis Leakey in 1960 of Olduvai Hominid (OH) 9 at the Tanzanian site of Olduvai Gorge marked the first allocation of an African fossil to *H. erectus* (L. Leakey, 1961), although fossils found earlier from South Africa may also belong to *H. erectus*. In addition to OH 9, a second individual from Olduvai Gorge, OH 12, although smaller (727 versus 1067 cc; Holloway, 1973) and much less complete, is also assigned to *H. erectus*. OH 9 was found on the surface in the Side Gorge at Olduvai. The fragments of OH 12 were found on the surface at locality VEK near the junction of the Main and Side gorges (M.D. Leakey, 1971).

OH 9 is missing the majority of the superior neurocranium, as well as the right parietal. The inferior portions of both temporals and the nuchal plane of the occipital are well-preserved, as is much of the left parietal. Large fragments of the frontal bone were preserved, including almost the entire supraorbital torus and interorbital region. The basicranium is in good condition overall, though there is damage around the foramen magnum and to the left temporal bone structures. Much information can be gleaned from the preserved portions. OH 9 has a long and low cranial vault with a strongly angled

occipital bone, a robust supraorbital torus with no frontal midline keeling and the maximum cranial breadth is situated low on the vault (Rightmire, 1979). Maier and Nkini (1984) also noted a very superiorly positioned and unflexed basicranium. While the majority of workers include OH 9 in *H. erectus*, because of its similarities to the Asian hypodigm, Clarke (1990; 1994) has voiced an alternative interpretation: OH 9, along with the Turkana Basin hominins often included in *H. erectus* (e.g., ER 3733, 3883) and some South African fossils (e.g., SK 847, Stw 53), represents a separate species, *H. leakeyi* (a species name assigned to OH 9 by Heberer (1963)). *H. leakeyi* was “an *erectus*-like species with a more sapient-like temporal” (Clarke, 1990, p. 731).

The largest fragment of OH 12 consists of the rear of the braincase including parts of the occipital and parietals. Other smaller fragments derive mostly from the facial region (including part of the right supraorbital torus) and the temporal bones. Most fragments are not adjoining, though in 2001 S. Antón identified some previously unidentified fragments from the collections at the National Museums of Kenya as part of the interorbital region of OH 12. She was also able to demonstrate continuity between the supraorbital fragment and this interorbital region (Antón, 2004). OH 12 had thick cranial bones, a gracile transverse occipital torus, an angled occipital bone, possibly an angular torus but no midline parietal keeling. Nearly all researchers include OH 12 in *H. erectus* (e.g., M.D. Leakey, 1971; Rightmire, 1979; Antón, 2004), although Holloway (1973), on the basis of its smaller size, suggested it may represent a different species than OH 9. Schwartz and Tattersall (2003) noted similarities to OH 7, commonly attributed to *H. habilis* (though the great differences in cranial bone thickness would seem to argue against this, especially as they considered OH 7 to represent an adult individual).

Because OH 12 is very incomplete, it is included less often in comparative analyses than OH 9.

The 100 meter thick deposits at Olduvai are characterized by a long sequence of argon and radiocarbon dates spanning 2 to 0.01 Ma. Deposits are divided into Bed I- Bed IV with the Masek, Ndutu and Naisiusiu Beds above Bed IV. While fossils from the genera *Paranthropus* and *Homo* have been found in Bed I sediments which span the Plio-Pleistocene boundary, only *Homo* is represented above Bed I. OH 9 was recovered from the surface in several fragments at the LLK locality in the Side Gorge (M.D. Leakey, 1971). OH 9 and OH 12 were assigned to Beds II and IV, respectively, by matching matrix adhering to the fossils with these layers (M.D. Leakey, 1971). The age of OH 9 from Upper Bed II is constrained between 1.33 and 1.48 Ma while OH 12 is younger and is thought to be between 1.2 and 1.02 Ma (Hay, 1990; Tamrat *et al.*, 1995; Delson and Van Couvering, 2000).

Conclusions

The first fossils assigned to *Pithecanthropus erectus* (= *H. erectus*) were from Java. Similarities to the collection at Zhoukoudian were noted early on, and the latter are now generally considered to be conspecific with the Indonesian fossils. While OH 9 was not immediately placed within *H. erectus* (L. Leakey, 1961; Heberer, 1963), it was accepted as part of this species as early as 1964 (Le Gros Clark, 1964; M.D. Leakey, 1971). Although a few doubts have been expressed about the taxonomy of the Olduvai Gorge fossils by Clarke (1990, 1994) and Schwartz and Tattersall (2003), these

alternative viewpoints have not been widely accepted. While a second species, *H. ergaster* (Groves and Mazák, 1975), is sometimes recognized for the early African fossils, OH 9 is not generally considered as part of this hypodigm (e.g., Wood, 1991). The Olduvai fossils are therefore considered for historic and morphological reasons to be part of the ‘core’ *H. erectus* sample.

Fossils from many other sites in East Africa, Indonesia and Georgia have also been incorporated into *H. erectus*, but these species allocations are less certain. Therefore, the morphological species definition of *H. erectus* detailed below is based mainly on the ‘core’ (i.e., most widely accepted) cranial specimens from Trinil, Sangiran, Zhoukoudian and Olduvai Gorge. Taxonomic affinities of other potential *H. erectus* fossils will be evaluated against this species definition (see ‘Additional Materials’).

Morphology

Many of the features used to diagnose *H. erectus* were initially noted by Weidenreich (e.g., 1937b; 1943; 1951), though a number of workers have added to this list, including Le Gros Clark (1955; 1964), MacIntosh and Larnach (1972), Jacob (1975) and Howell (1978). Good reviews and discussion of the most frequently cited features can be found in several contributions to the 1984 *Courier Forschungs-Institut Senckenberg* issue which followed from the Koenigswald Memorial Symposium in Bad Homburg (Wood, 1984; Stringer, 1984; Rightmire, 1984; Andrews, 1984). Wolpoff *et al.* (1994) have also discussed diagnostic traits for *H. erectus* which, while similar to those used by other authors, do differ in certain details. There is interindividual variation,

and possibly variation correlated with geography, time and size, in the expression of these traits. (See ‘Variation in *H. erectus*’ below) However, most specimens display the majority of the traits. Not all characters used to describe *H. erectus* are autapomorphic for the group – some are primitive while still others are shared with Mid-Pleistocene *Homo*. Therefore, the traits discussed below are best viewed as a ‘combination’ definition, sensu Wood (1984), Turner and Chamberlain (1989) and Kimbel and Rak (1993); the appearance of all or most of these features in one individual is unique to *H. erectus* relative to earlier and later *Homo* species.

General description

In terms of overall cranial shape, *H. erectus* has a long, low sagittal profile; the vault is widest across the supramastoid crests or the angular tori and the walls converge superiorly. This is in contrast to modern humans with their more globular cranial vaults, parallel vault walls and maximum breadth positioned high on the parietals. *H. erectus* is characterized by thick cranial bones, due to expansion of both inner and outer tables, and a suite of cranial superstructures which Weidenreich (1943) described as ‘reinforcing’ the skull.

The average cranial capacity for the Sangiran, Trinil, Zhoukoudian and OH 9 fossils was 989 cc (from values compiled by Rightmire, 2004). However, endocranial volume is not particularly diagnostic for this species as there is a fair amount of variation, ranging from 813 cc (Sangiran 2) to 1225 cc (Zhoukoudian X) that overlaps with both

earlier and later taxa of *Homo*. If fossils discussed below from sites like Dmanisi, Georgia and Ngandong, Indonesia are added to the sample, then the range of cranial capacities is extended even more.

It is unclear whether the basicranium is equally or less flexed than what is seen in modern humans. Based on OH 9, Maier and Nkini (1984) determined that *H. erectus* had a flatter basicranium than later *Homo* whereas Ross and Henneberg (1995) reached the opposite conclusion. It should be noted that OH 9 is damaged in the relevant region and had to be reconstructed for these analyses. Studies on non-core *H. erectus* have not clarified the situation, as the results of Spoor (2000) were in general agreement with former, whereas the opposite conclusion was reached by other workers (Laitman, 1985; Baba *et al.*, 2003). None of these studies used large, comprehensive samples of *H. erectus*. Most studies focused on the African fossils while the Baba *et al.* study dealt with an Asian specimen (Sambungmacan 4), excluding the possibility that the discrepancy is due to regional differences; more work is clearly needed before any conclusions can be drawn.

Occipital: The occipital bone is specialized in its tight angulation when viewed laterally, and opisthocranium is coincident with inion. It has also been noted that the internal inion (endion or endinion) is separated vertically from the external inion (ectinion). There is disagreement concerning the proportions of the occipital bone – it has been said that the upper scale is shorter than the lower or that the relative lengths are variable. The occipital plane is often angled forward whereas the nuchal plane is posteriorly rotated relative to modern humans (Rightmire, 1990; Stringer, 1984).

The wide occiput is generally traversed by a transverse occipital torus which is continuous laterally with the angular torus and either the supramastoid or the mastoid crest. The torus is thickest medially and delimited inferiorly by the superior nuchal lines. In contrast to modern humans, there is no external occipital protuberance, though there is a linear tubercle where these lines meet. Superior to the torus is a supratotal sulcus. There is disagreement concerning the presence or absence of a juxtamastoid ridge, though this may be more a matter of regional variation in this feature. Weidenreich (1943) originally described a crest along the occipitomastoid suture that parallels the mastoid process in the Zhoukoudian fossils, but he did not observe this same crest in the Javanese material. Another feature found only in *H. erectus* but without a universal distribution are the postcondylar tuberosities – raised areas on the foramen magnum posterior to the occipital condyles. Jacob (1967; 1975) noted that the foramen magnum is bent along the coronal plane such that the posterior half is coplanar with the nuchal plane and the anterior half with the basisphenoid.

Frontal: The frontal bone features a prominent, continuous supraorbital torus which is sometimes quite straight across. The torus features supraglabellar hollowing and has lateral ‘wings.’ There is disagreement concerning the presence of a supratotal sulcus: Wood (1984) lists the presence of a supratotal sulcus as a *H. erectus* feature, whereas Rightmire (1990, p. 176) says that “supratotal sulci are shallow or not present.” This discrepancy may again be due to regional differences in the expression of this feature (see ‘Variation in *Homo erectus*’ below).

The sagittal profile of the frontal squama is relatively flattened. Most *H. erectus* specimens present marked postorbital constriction. The relatively low position of minimum frontal breadth means that postorbital constriction is most marked when measured relative to biorbital breadth (Rightmire, 1990). The temporal lines trace a fairly low arc, and their topography is most apparent anteriorly, where they often form a low crest. The frontal bone is keeled along the midline, which is usually continuous with a bregmatic eminence. There may also be coronal keeling that, together with the frontal keel and bregmatic eminence, forms the cruciate eminence.

Temporals: The temporal squama is flat and low, especially compared to the high arch found in *H. sapiens*. The supramastoid crests (continuous anteriorly with the posterior root of the zygomatic process) are prominent and there is often a supramastoid sulcus between that and the variably developed mastoid crest. Stringer *et al.* (1979) describe the posteroinferior part of the temporal squama as diverging laterally.

The mastoid process has been described both as small (Le Gros Clark, 1955) and as variable, but sometimes quite large (Rightmire, 1990). The tips of the mastoid processes are medially inclined. There is a fair degree of pneumatization present in the mastoid region, as well as the neighboring occipital (Howell, 1978; Balzeau and Grimaud-Hervé, 2006).

The inferior tympanic tube is thickened inferiorly and the petrotympanic crest is inferiorly extended into a petrosal spine. The petrosal spine often has a vertically oriented groove posteriorly that aligns with the styloid hollow superiorly. This crest sometimes ends medially in a process supratubarius and is separated posteriorly from the mastoid process by a mastoid fissure. Definitions of *H. erectus* usually note the lack of a

styloid process and the vaginal sheath, though the utility of the former trait has been questioned (Wolpoff, 1999), and there may be geographic variation in its expression (see ‘Variation in *Homo erectus*’ below). The petrous bone is more sagittally aligned in *H. erectus* than in other hominins while the tympanic plate is nearly perpendicular to the midline plane of the skull. The foramen lacerum is reduced or absent.

Howell (1978) cites the absence of an entoglenoid pyramid as a *H. erectus* trait though most workers recognize the presence of this structure (e.g., Rightmire, 1990). While in modern humans the sphenoid contributes to this process in the form of an inferiorly projecting sphenoid spine, there is no sphenoidal contribution to the entoglenoid in *H. erectus*. Rather, the medial wall of the mandibular fossa is “a steep slope entirely built by the (temporal) squama” (Weidenreich, 1943, p. 202). A minority of modern humans also lack a sphenoid spine. Therefore, while I will follow the majority of workers in describing this ‘slope’ as the entoglenoid process, it is important to understand that this morphology is somewhat distinct from modern humans. *H. erectus* is also distinguished by a laterally extended suprameatal tegmen. The anterior surface of the glenoid fossa is very long and inclined antero-inferiorly, so that the deep and short (antero-posteriorly) glenoid fossa is posteriorly positioned (Weidenreich, 1943; Picq, 1990). The glenoid fossa is also more laterally situated than in modern humans, so that the center of the fossa is aligned vertically with the side of the vault. The glenoid fossa narrows medially, sometimes forming a deep and narrow fissure between the entoglenoid and the tympanic tube. While *H. erectus* is frequently described as lacking an articular tubercle, a more accurate description is that the tubercle is flat (or absent) medially but is present laterally (inferior to the root of the zygomatic process) (Picq, 1990). This does

differ from the condition in modern humans, who usually (but not always) have a cylindrical or bar-like articular tubercle on the inferior surface of the temporal bone just anterior to the glenoid fossa. The postglenoid process is not well developed in most *H. erectus* specimens.

Parietals: The overall form of the parietals can be described as flattened in the sagittal direction with no parietal eminences. Although the parietals of *H. erectus* are smaller overall than those of modern humans, they are more rectangular (longer than wide). There is sometimes keeling along the sagittal suture anteriorly, and the temporal lines may form an angular torus posteriorly (a raised arc of bone on the parietal near the mastoid notch). The parietals are low and converge medially, and they are more transversely curved than in modern humans with a distinct angle around the middle of the parietal when viewed posteriorly. This angled appearance is emphasized by the parasagittal flattening on either side of the sagittal crest. The maximum parietal breadth is located inferiorly, which is different from the pattern observed in modern humans where the maximum cranial breadth corresponds to the maximum parietal breadth (across the parietal eminences).

Face: Because there are a limited number of faces available for study, few generalizations can be made. The upper and mid faces are flat and broad, and there is no midfacial inflation like that seen in Neanderthals. The zygomatic is positioned relatively high and is quite robust. Though the lower face and jaw have been reduced, there is marked maxillary alveolar protrusion. The presence of a diastema between the canine

and lateral incisor was noted in at least one Sangiran specimen, S 4. The incisive canal is located posteriorly on the palate and is angled obliquely rather than vertically. There is a 'sulcus maxillaris' (also termed a 'sulcus infraorbitalis' by Weidenreich (1943)), a furrow-like hollowing between the canine jugum and the anterior root of the zygomatic process.

The interorbital breadth is quite wide and the nasal bridge is situated relatively high on the face. The nasal bones are wide relative to the width of the nasal aperture, which is itself wide (Wolpoff *et al.*, 1994). Franciscus and Trinkaus (1988) noted that a modern, projecting nasal region first appeared in members of *H. erectus* (but possibly also some early *Homo* fossils). This modern morphology is characterized by everted lateral margins of the nasal aperture, an internasal angle, nasal bone convexity, a distinct, anteriorly positioned anterior nasal spine and an acute angle between the nasal floor and the subnasal alveolar clivus. The lateral margin of the nasal aperture ('crista nasalis' of Weidenreich (1943)) slopes forward so that it meets the floor of the nasal cavity anterior to rhinion when positioned in Frankfurt Horizontal, which is consistent with a prognathic lower face but also less nasal projection relative to modern humans (Arsuaga *et al.*, 1999). The presence of an anterior nasal spine is variable (e.g., absent in the Zhoukoudian fossils, but present in S 4).

Additional material

In the past century, a great many additional fossil cranial remains have been assigned to *H. erectus* from other sites in eastern, southern and northern Africa, the

Caucuses, China and Indonesia. While many of the Chinese fossils are widely accepted as *H. erectus*, most are not readily accessible to researchers outside of China and, because descriptions are generally published in Chinese, are often not fully incorporated into definitions of *H. erectus*. Also, some of the more complete Chinese crania are quite distorted, making it difficult to discern morphological details. The younger fossils from Java are sometimes considered to be a separate, more advanced species, *H. soloensis*, whereas many of the African and Georgian fossils are placed in a less derived species, *H. ergaster*.

Indonesia

Since the initial discoveries of *H. erectus* at Trinil, Modjokerto (Perning) and the Sangiran dome, a large amount of mainly cranial material has surfaced from the latter site (from Grogol Wetan, Bapang, Sendangbusik / Bukuran and Tanjung) throughout the 1990s (Widianto *et al.*, 1994; Widianto and Grimaud-Hervé, 2000; Larick *et al.*, 2001; Arif, 2005; Grimaud-Hervé *et al.*, 2005). Some of these fossils remain to be described fully. All finds were made by local inhabitants, which introduces some reservations regarding their geological ages. A series of calvaria and calottes were also recovered from the Eastern Javan site of Ngandong, and three semi-independent crania were also recovered from the Sambungmacan area. A single incisor attributed to *H. erectus* has been recovered from the site of Cicanca in western Java. From east to west, the potential Javan *H. erectus* sites are Modjokerto (Perning), Kedung Brubus, Ngawi, Ngandong,

Trinil, Sambungmacan, the Sangiran dome localities (most notably Grogol Wetan, Sendangbusik, Bapang, Bukuran, Tanjung and Pucung) and Cisanca (Figure 1.1c).

Grogol Wetan: The Grogol Wetan (Grogolwetan) hominin, discovered in 1993 from the Bapang layers, is a nearly complete calvaria. This fossil shares many features with other Sangiran dome *H. erectus*, including a flat frontal bone with midline keeling, a low cranial vault with maximum width low down and a sharply angled occipital bone with a transverse occipital torus (Widianto and Grimaud-Hervé, 2000). An $^{40}\text{Ar}/^{39}\text{Ar}$ date of 0.78 Ma from the site of Grogol Wetan has been reported (Saleki, 1997) though Larick *et al.* (2001) position this fossil just below a level dated by hornblende $^{40}\text{Ar}/^{39}\text{Ar}$ to 1.24 Ma.

Sendangbusik / Bukuran: Two discoveries have been reported from Sendangbusik / Bukuran region of the Sangiran dome. The first consists of several cranial fragments named Hanoman 1 that were found in 1989 by local inhabitants in a valley between the villages of Sendangbusik and Bukuran. The approximately 16 fragments include portions of the occipital, parietals and frontal bones. A preliminary reconstruction shows marked postorbital constriction, weak sagittal keeling, maximum cranial breadth across the temporals and thick cranial bones. Specific details of morphology align this specimen with both the Sangiran / Trinil series (degree of postorbital constriction, sphenoidal shape in *normal verticalis*) and the Ngandong / Sambungmacan series (frontal inclination) (Widianto *et al.*, 1994). This preliminary reconstruction, however, may be inaccurate because the occipital bone is quite curved rather than angled as in nearly all

other *H. erectus* fossil crania. Geological trenching by Widiyanto *et al.* (1994) found both Bapang and Sangiran deposits, and the small landslide which uncovered the fossil fragments was located near the boundary between these two formations. The fossil fragments are thought to derive from the uppermost Sangiran deposits, making Hanoman 1 around 0.9 Ma (Grimaud-Hervé *et al.*, 2005) or older if the dates of Larick *et al.* (2001) are applied.

The second hominin from Bukuran discovered in 1996 has yet to be fully described. This individual is more complete than Hanoman 1 and consists of two large fragments: one with the parietals and occipital and a second consisting of the frontal bone. Both frontal and sagittal keeling as well as a bregmatic eminence are visible. There is a continuous supraorbital torus and an angular torus and the skull is widest across the supramastoid crests. Like Grogol Wetan, it is thought to be from the Bapang layers of the Sangiran dome, specifically from the lower part of this Formation (Grimaud-Hervé *et al.*, 2005).

Tanjung: The fossil calvaria uncovered in 1993 by local inhabitants near the town of Tanjung in the Sangiran dome has been referred to as Skull IX (Sartono and Tyler, 1993) and Tjg-1993.05 (Larick *et al.* 2001). Like Grogol Wetan, the Tanjung cranium derives from the Bapang Formation, placing it in either the Middle or Early Pleistocene (Arif, 2005). The specimen is fairly complete, with much of the vault, some of the left temporal and large piece of the maxilla preserved. Although Tyler and Sartono (2001) argue that it is more similar chronologically (from the Pucangan Formation) and morphologically to ER 3733, Arif (2005) notes similarities to the other Sangiran and

Trinil fossils. If the latter perspective is correct, then together the Grogol Wetan, Tanjung and possibly Hanoman 1 specimens confirm a fairly homogenous form of *H. erectus* from the Upper Sangiran and Bapang layers of the Sangiran dome and Trinil regions.

Ngandong: The Ngandong cranial series was uncovered from river terraces (High Terraces, Bartstra *et al.*, 1988) ~20 m above the Bengawan (Great) Solo River in Eastern Java in the early 1930s through excavations headed by C. ter Haar of the Geological Survey. Within the original collection of 25,000 mammal fossils were 12 individual hominin calottes or calvariae and two tibiae (von Koenigswald, 1951). The majority of the non-hominin fossils have since been lost. Later excavations next to the original site uncovered an additional 1,200 fossils, including two partial hominin crania and hominin pelvic fragments (Moelyadi, 1982 cited by Swisher *et al.*, 1996). The most complete calvaria are Ng 7 and 12, which preserve the majority of the basicranium, in addition to complete neurocrania and frontal bones. Ng 6 and 10 preserve most of the neurocranium and the inferior surface of at least one temporal, plus the nuchal plane. Ng 3 is missing the anterior half of the frontal bone and most of the right lateral and posterior cranial vault; a small portion of the left inferior temporal is preserved. Ng 5 preserves only the parietals and frontal bone, while Ng 9 consists of two parietals attached along the sagittal suture with plaster. Both Ng 1 and 6 are missing the (left and right, respectively) lateral corner of the supraorbital torus. Though Weidenreich (1951) proposed that Ng 5 and 9 were juvenile based on the premise that suture closure occurred earlier in development in these hominins than in modern man, Antón (1999) has suggested, on the basis of suture development, cranial superstructures, bone thickness and vault shape, that these likely

represent adults. This same study found that two other less complete individuals, Ng 2 and 8, are a juvenile and an older juvenile / young adult, respectively.

In the original description, Oppenoorth (1932) noted similarities between some Ngandong crania to Neanderthals, though he erected the genus *Javanthropus* for this group. The comparison to Neanderthals prompted von Koenigswald (1934) to apply the nomen *H. neanderthalensis soloensis* to the Ngandong specimens but Weidenreich (1936, 1937c, 1951) noted similarities to Chinese and particularly to other Indonesian *Pithecanthropus*. It has since been argued that the Ngandong individuals should be included within *H. erectus* by Jacob (1967; 1976), Santa Luca (1980), Rightmire (1990) and Antón (1999). The Ngandong fossils share the same basic cranial form with the Sangiran hominins including a receding frontal bone, a strong horizontal supraorbital torus, strong occipital tori, angled occipital bones, low temporal squamae and maximum widths located low on the vault. The major difference lies in their larger endocranial capacity (average 1151.4; Holloway, 1981a) and cranial dimensions (Weidenreich, 1951). There are also detailed morphological differences, some of which will be discussed in the section ‘Variation in *Homo erectus*.’

The Ngandong fossils were found in the Solo High Terrace deposits that overlie the Notopuro deposits, which are composed of “agglomerates, volcanic conglomerates and occasional lahars” (Bartstra and Basoeki, 1989, p. 241). While several lines of evidence, including faunal correlation, paleomagnetism and fission-track dating of the underlying Notopuro beds points to an age around 250-300 ka (Jacob, 1978; Suzuki and Wikarno, 1982; Sémah, 1984), workers initially posited an early Pleistocene age for the

Ngandong hominins based on geological, faunal and taphonomic evidence (Oppenoorth, 1932; von Koenigswald, 1934; 1939; De Terra, 1943).

U-series dates obtained on fauna from the site of Ngandong provided a range of ages from 100 – 30 ka (Bartsra *et al.*, 1988), and more recent dating work by Swisher *et al.* (1996) also suggested a recent age for the Ngandong hominins on the order of 53-27 ka, based mainly on ESR dating of bovid teeth. U-series dating on fossil bovid teeth gave older ages, but this was attributed to a loss of uranium from the teeth late in their burial history (Swisher *et al.*, 1996). These young dates have been criticized on a several grounds by Grün and Thorne (1997). For one, they find the leaching of uranium from teeth to be an unlikely explanation for the discrepancy between the ESR and U-series dates. Grün and Thorne (1997) also contend that the Ngandong fossils are not contemporaneous with the surrounding fauna (a view also held by Santa Luca, 1980) and assert that the terrace where they were found is “a mélange of materials reworked from different levels, sites, and ages” (Grün and Thorne, 1997, p. 1575). They stress that the Ngandong hominins differs in color and texture from the nearby fossil fauna, suggesting they are not the same age. However, Von Koenigswald (1951, p. 218), based on the original fauna (which has since disappeared) found with the Ngandong hominins, stated that the hominins were contemporaneous with the other fauna on the basis of “their preservation which is exactly the same as in the numerous animal bones found in the same deposit.” This contention is supported by Bartstra *et al.* (1988) and Swisher *et al.* (1996), who argue further that the probability of so many hominin fossils being reworked without other contemporaneous faunal elements is highly unlikely. However, Dennell and Roebroeks (2005) find it equally unlikely that cranial elements would comprise such

a high frequency of the total hominin remains unless they were preferentially relocated by fluvial transport, making them older than their surrounding deposits. An alternative explanation was that the bones accumulated as the result of activities (like head hunting) practiced by the Ngandong hominins (von Koenigswald, 1951). While Rightmire (1990) describes a lot of surface abrasion, possibly the result of water transport, Swisher *et al.* (1996) note that the preservation of delicate structures like the pterygoid plates argue against extensive water transport.

If, as appears likely, the Ngandong calvaria were found in situ, then they are of Late Pleistocene age (though how late continues to be a source of contention). If, however, they were redeposited in the upper terraces from older deposits, then their age would remain unknown.

Sambungmacan: Three crania have now been uncovered from Central Java in the region of Sambungmacan. However, whether these are all from the same site or time period is not known definitively, and they should probably be treated individually (Schwartz and Tattersall, 2003; Dennell and Roebroeks, 2005). The first, Sm 1, was uncovered in 1973 and described by Jacob *et al.* (1978). A few postcranial fragments, including a fragment of a tibia (Sm 2), were also recovered from excavations at the Sm 1 findspot (Matsu'ura *et al.*, 1990; Baba *et al.*, 1990). Sm 3 (first named Poloyo-1 (Pl-1); Mowbray *et al.*, 2000) was originally found in 1977 and briefly described by Boedhihartono (1998) before being illegally exported from Indonesia. It was recovered in a natural history curios store in New York City in 1999 (Delson *et al.*, 2001). The most recent find was Sm 4, which was discovered by local workers in 2001 (Baba *et al.*, 2003). The cranial capacities for

these three calvariae are 1035, 917 and 1006 cc, respectively. None of the three preserve the face below the supraorbital torus. Of the three, Sm 4 is in the best condition with a very well-preserved basicranium compared to Sm 1 and 3, both of which are missing the middle part of the base. Sm 1 is also missing the left anterior corner of the frontal bone.

All three specimens have low sagittal profiles with receding frontal bones; the squama in Sm 3 is especially flat in its sagittal contour. The occipital torus is also most marked in Sm 4 and the arc from bregma to lambda appears less rounded in this fossil. The posterior profile of Sm 1 and 3 appear especially similar. All three have a marked supraorbital torus, but it is probably largest in Sm 1. Expression of keeling is variable, with very little in Sm 1, midline frontal and parietal in Sm 3 and both midline and coronal in Sm 4. Both Sm 1 and 4 have an angular torus, which is absent in Sm 3. The occipital bone appears more angled in Sm 1 and 4 than in Sm 3. Sm 1 and Sm 4 may “represent a transition linking the Trinil/Sangiran and Ngandong hominids morphologically and possibly temporally” (Baba *et al.*, 2003, p.1387), a viewpoint also echoed by Jacob (1976; 1981) and Wolpoff (1992). Morphological and morphometric analysis suggested that Sm 3 was most similar to Sm 1 (Sm 4 had not been discovered yet) and the Ngandong fossils, though it differed from all *H. erectus* in its steeper frontal squamal profile, less projecting glabella and more rounded occipital in *norma lateralis* (Delson *et al.*, 2001). Sm 3 also has the smallest endocranial volume of the three.

Very little is known about the age of the Sambungmacan remains. None of the calvaria were recovered in controlled excavations. Sm 1 was recovered in a sandy layer about 8 m below the surface during canal digging (Jacob *et al.*, 1978). Sm 3 and 4 were recovered during dredging and while collecting sand for construction, respectively. Sm 4

was found approximately 4 km from Sm 1 and about 100 m from the possible Sm 3 findspot, on the south bank of the Solo River within the Sambungmacan district. The fauna at the Sm 4 findspot may represent a mixed fauna, though Sm 4 is most likely from Kabuh deposits of Middle Pleistocene age (matrix found on the fossil reinforces this conclusion), which can be found within 6 km upstream (Baba *et al.*, 2003). Jacob *et al.* (1978) also assigned Sm 1 to the Kabuh Formation though Sartono (1979) identified the same deposits as Late Pleistocene in age. The Sm 2 tibial fragment also appears to derive from the Kabuh Formation, based on “multielement analyses of bone using inductively coupled plasma (ICP) spectrometry, accompanied by fluorine assay” (Matsu’ura *et al.*, 2000, p. 297). ESR dating of a single bovid tooth from the Sm 1 findspot supported a more recent date between 53 and 32 ka (Swisher *et al.*, 1996), though Matsu’ura *et al.* (2000) question the provenience of the tooth.

Ngawi: The Ngawi calvaria was uncovered a bit south of Ngandong in Eastern Java in 1987 by local farmers (Sartono, 1990). The calvaria is well-preserved with the complete vault, supraorbital region and cranial base intact. The specimen exhibits a number of classic *H. erectus* features including a straight, robust and continuous supraorbital torus, an angular torus, midline and coronal keeling with a bregmatic eminence and a well-developed transverse occipital torus. Despite its smaller cranial capacity (870 cc; Zeitoun and Widiyanto, 2001), initial analysis suggests its affinities with the later *H. erectus* populations of Ngandong and Sambungmacan, and it is clearly within the range of variation for *H. erectus* (Widiyanto and Zeitoun, 2003). There is no secure date for this fossil, though Sartono (1990) hypothesizes that it may be derived from the Pitu terraces

to the west because these terraces are the same age as the Ngandong terraces. He also acknowledges that it could have derived from the earlier Bapang Formation.

While the Sambungmacan and Ngandong (and possibly Ngawi) fossils represent the upper end of the time range for *H. erectus*, there is still uncertainty regarding just how recently this group existed in Indonesia.

Cisanca: There is a single proposed *H. erectus* site in Western Java. This site, Cisanca, has yielded a single lateral lower incisor (RH1) which has been compared to orangutans, macaques, modern humans and *H. erectus*. It is clearly differentiated from the non-hominin primates, and while it is similar in size to modern humans, it is more similar in shape to *H. erectus*. On the basis of similarities to Sangiran incisors and its age (0.5-0.6 Ma based on electron paramagnetic resonance spectroscopy (EPR) of enamel from a bovid of similar age), the describers provisionally assign this specimen to *H. erectus* (Kramer *et al.*, 2005). This extends the range of *H. erectus* from Eastern and Central to Western Java.

China

Because of the large sample size, the thoroughness of Weidenreich's descriptions, and the availability of the casts of the Zhoukoudian fossils, these remain better studied and understood than fossils from other Chinese sites. There are, however, a number of other Chinese *H. erectus* sites (Figure 1.1b). Within China, Zhoukoudian and Yiyuan are the two most northern sites; Zhoukoudian is located near Beijing, and Yiyuan is about

340 km southeast of Zhoukoudian. Hexian and Nanjing are about 860 km south of Zhoukoudian but also more to the east. Approximately 960 km west of Nanjing, *H. erectus* remains have been recovered from Gongwangling and Chenjiawo (sometimes referred to as Lantian, the county in which they are located) and Yunxian, with the latter being further south. Only Yuanmou is located in the south of the country, near the border with Myanmar to the west. Contra Antón (2002), Hexian is located at approximately the same latitude as Nanjing, and not more southerly. There is another town by the name of Hexian (also called Babu) which is located in south China, but this is not the fossil *H. erectus* site. In fact, Hexian and Nanjing are quite close to one another, with Zhoukoudian positioned more to the north, as is clearly illustrated by the map in Wu *et al.* (2006, p. 254) and here in Figure 1.1b.

It has been claimed that a mandibular fragment with two cheek teeth and an isolated maxillary lateral incisor from Longgupo Cave (associated with lithic tools) also represent *H. erectus s.l.* from 1.9 Ma, which would be the oldest hominin evidence in the Far East (Huang *et al.*, 1995; Larick and Ciochon, 1996). However, it now seems clear that the mandibular remains cannot be distinguished from a more generalized hominoid and the incisor may belong to a modern human (Schwartz and Tattersall, 1996; Wang, 1996; Wu, 2000; Etler *et al.*, 2001; Brown, 2001).

Yiyuan: The site closest to Zhoukoudian is Yiyuan, although not much information is available about the cranial fragments (Sh.y. 001) from this site. It was originally described by Lu *et al.* (1989), whose paper was summarized by Wu and Poirier (1995). There are fragmentary cranial, dental and postcranial remains. The cranial fragments are

reportedly more similar to the Zhoukoudian than the Hexian (see below) morphology because of the overall robusticity and details of dental and supraorbital morphology (Lu *et al.*, 1989; Etler, 1996), though its fragmentary state does not exclude it from being more similar to Dali and hence an example of later *Homo* (Wu and Poirer, 1995). A date of 440 ka has been reported for Yiyuan on the basis of faunal correlation (Lu *et al.*, 1989).

Nanjing (Tangshan): Two specimens (Nanjing 1 and 2) were discovered in 1993 in Huludong Cave on the Tangshan hills just east of Nanjing by a joint IVPP and Nanjing Institute of Geology and Palaeontology team. Nanjing 1 is the more complete specimen and is composed of large fragments comprising most of a calotte and the left side of the face. In common with other *H. erectus*, Nanjing 1 has a long, low cranial outline, an angled occipital, a transverse occipital torus that is continuous with an angular torus and a flat frontal with a straight supraorbital torus. It has been compared favorably with Zhoukoudian (Mu *et al.*, 1993; Etler, 1996; Wu *et al.*, 2002a, b). Multivariate morphometric analysis suggested similarities between Nanjing 1 and Zhoukoudian as well (Liu *et al.*, 2005). Nanjing 2 consists of most of a calotte, but it is missing the supraorbital torus, and there appears to be some distortion present. Nanjing 2, which is thought to be younger, shares features both with Asian *H. erectus* and also with later Asian *Homo*. Shang and Wu (2002) conclude that Nanjing 2 represents either a more advanced form of *H. erectus* than Nanjing 1 or a different species altogether. It appears from the faunal, phytolith and oxygen isotope records that Nanjing cave deposits accumulated during cold climatic conditions (Wu *et al.*, 2002a). While initial age estimates were around 350 ka (Chen *et al.*, 1996), more recent thermal ionization mass

spectrometric (TIMS) dates on speleothems and amino acid racemization of fossil mammal teeth have concluded that the fossils are older than 500 or 580 ka and may be in the range of 638-624 ka (Wang *et al.*, 2002; Liu *et al.*, 2002; Zhao *et al.*, 2001).

Hexian: Another IVPP team, in association with local archaeologists, found a nearly complete calvaria (PA 830), in addition to fragmentary mandibular, dental and postcranial remains, in the Longtandong Cave in Hexian County in the early 1980s. The fossils from Hexian are younger than those of Nanjing, with a thermoluminescence age of around 195 ka (Li and Mei, 1983) or ESR / U-series ages for bovid teeth of around 400 ka (Grün *et al.*, 1998). With the exception of Wu and Poirier (1995), all descriptions have been published in Chinese, making Hexian one of the less well known Chinese *H. erectus* fossils, despite its completeness (Brown, 2001). PA 830 resembles other *H. erectus* fossils in having the maximum breadth across the supramastoid crests, a flat frontal with a prominent supraorbital torus, an angular torus and transverse occipital. Like Zhoukoudian and Nanjing, it has a frontal tuberosity but the supratatorial sulcus is shallower than in Zhoukoudian (Wu and Poirer, 1995). Hexian also differs from Zhoukoudian in its decreased postorbital constriction, the higher curvature of the temporal squama and the increase in cranial breadth (Etler, 1996). While all workers have placed Hexian with *H. erectus*, there is not agreement concerning whether it is more similar to the Javan or the Zhoukoudian fossils (Wu and Dong, 1982; Dong, 1989).

Yunxian (Quyuan River Mouth): Two crania were recovered by farmers in Yunxian in 1989 and 1990 (EV 9001 and 9002) (Li and Etler, 1992). The Middle Pleistocene fauna

appears consistent with the ESR date of 581 ka from tooth enamel (Li *et al.*, 1991; Chen *et al.*, 1997). Both crania, despite suffering extensive crushing and deformation due to diagenetic forces, are clearly quite massive. A number of traits of the cranial vault and base align them with *H. erectus*, though some facial features were linked to more recent Chinese *Homo* (Li and Etler, 1992). Brown (2001) also sees similarities between the Yunxian faces and the face of Sangiran 17. The assignment of these fossils to *H. erectus* has been questioned because a number of diagnostic *H. erectus* traits could not be accurately assessed due to the postmortem damage (Zhang, 1998) while other traits were more modern (Wu and Poirier, 1995). Both studies conclude that EV 9001 and 9002 are more similar to later *Homo* like Dali or Jinniushan. Principal components analysis of a recent 3-D reconstruction of EV 9002 (Viale *et al.*, 2005) indicates that either (1) these efforts were not sufficient or (2) EV 9002 is outside of the range of variation of *H. erectus* (though not in the direction of more modern *Homo*), of which the former seems more likely. If the reconstruction is accurate to the original biology, then the sagittal profile of this specimen is exceptionally low and flat. The cranial capacity of EV 9002 was estimated between 1000 and 1300 by Li and Etler (1992) though Viale *et al.* (2005) suggest that the reconstruction decreased this volume somewhat.

Lantian: The cranial fossils from the nearby site of Gongwangling in Lantian county also suffered postmortem damage. A maxillary molar and several large cranial fragments (frontal, much of the parietals, right temporal, nasals, right maxilla and some of the left maxilla) were recovered by IVPP in 1964. The individual represented by the fragments, PA 1051-6, had a flat frontal bone with a robust supraorbital torus. The lack of a

supratoral sulcus is different from the condition found at Zhoukoudian. The cranial vault bones are also very thick, and the face would have been prognathic (Wu and Poirier, 1995). There are a wide range of dates assigned to this fossil site, from ~750 ka to 1.15 Ma (An and Ho, 1989; Wu *et al.*, 1989; An *et al.*, 1990), making this possibly the oldest Chinese *H. erectus* site. Much of the disagreement over dating is due to correlation with the paleomagnetic time scale. The fauna from this site is more tropical and subtropical than cold-adapted, in contrast to *H. erectus* sites like Zhoukoudian and Nanjing. Chenjiawo was a fairly complete mandible found a year before Gongwangling. The mandible is more recent, being dated by paleomagnetism to ~650 or 500 ka (Wu *et al.*, 1989; An *et al.*, 1990).

Yuanmou: The other potentially early *H. erectus* site is also the most southern site in China, Yuanmou. The two incisors were found in 1965, and excavations by the IVPP in the 1970s and 2000-2001 (Qi and Dong, Eds., 2005) failed to uncover any additional hominin fossils, just non-hominin fauna and artifacts. The two incisors are large and shovel shaped, which is common in *H. erectus* (Zhou and Hu, 1979), but does not rule out other hominins, making this a less definitive *H. erectus* site. In addition to this uncertainty, there are also issues with the stratigraphy and exact provenience of the incisors (Brown, 2001), and dates range from <730 ka to 1.7 Ma (Liu and Ding, 1983; Qing, 1985; Qian *et al.*, 1991).

While the fossils from Nanjing, Hexian and Lantian and are almost universally considered *H. erectus*, more derived features have been noted in Yunxian and Nanjing 2 and like the less complete remains from Yiyuan and Yuanmou these may not represent *H.*

erectus.

Archaeological sites: Some of the oldest sites with definite hominin presence (if not actual hominin fossils) are located in northern China, about 200 km west of Zhoukoudian. The site of Majuangou located in the Nihewan basin of northern China contains many choppers, scrapers and cores made from chert, quartz, andesite and sandstone. Paleomagnetic dating efforts constrained the four artifact-bearing layers to between 1.66 and 1.32 Ma (Zhu *et al.*, 2004). Also in the Nihewan basin are the archaeological sites of Xiaochangliang (1.36 Ma; Zhu *et al.*, 2001) and Donggutuo (1.1 Ma; Li and Wang, 1982). Many large, Acheulean-like tools but no hominin fossils were found at numerous sites from the Bose Basin in southern China. Sites in the Bose Basin have been securely dated to 800 ka (Hou *et al.*, 2000), again by paleomagnetic methods. Unfortunately no isotopic dates are available for these sites. It is also not clear what hominins made these stone tools.

Middle East

The Early and early-Middle Pleistocene archaeological sites of Erq-el-Ahmar (Erk-el-Ahmar), 'Ubeidiya and Gesher Benot Ya'aqov in Israel document the presence of hominins in the Middle East at ~1.8, ~1.4 and 0.78 Myr, respectively (Tobias, 1966; Tchernov, 1987; Bar-Yosef and Goren-Inbar, 1993; Goren-Inbar *et al.*, 2000; Ron and Levi, 2001; Belmaker *et al.*, 2002). Erq-el-Ahmar is an Oldowan site while the other two are both Acheulean. The dearth of fossil hominin remains (three isolated teeth of *Homo*

incertae sedis; Tobias, 1966; Belmaker *et al.*, 2002) makes it impossible at this time to determine which hominins occupied those sites.

Africa

Kenya: In addition to Olduvai Gorge, specimens attributed to *H. erectus* have also been recovered from the Koobi Fora and Ileret regions on the east shore of Lake Turkana. The most complete East African fossil cranium, ER 3733, was discovered in 1975 from area 104 at Koobi Fora (R. Leakey, 1976). This cranium preserves most of the vault, face and basicranium. ER 3883 is a second well-preserved cranium from Ileret (further north along Lake Turkana), though less of the face is preserved, and there is greater warping in the cranial vault (R. Leakey and Walker, 1985). Both of the Turkana hominins preserve a low cranial vault with well-defined supraorbital tori and sulci, angled occipital bone and strong post-orbital constriction. A more fragmentary specimen, ER 730, has also been assigned to African *H. erectus* (Howell, 1978) or *H. ergaster* (Wood, 1991). This specimen consists of mandibular, maxillary, parietal, frontal and occipital fragments, but only two of these pieces articulate (the occipital and left parietal). Their *H. erectus* status is based on the presence of thickened cranial bones, a transverse occipital torus and a distinct supraorbital torus with a supratrochlear sulcus. Fragments of this specimen were found by M.D. Leakey in 1970 and 1980 at area 103 of Koobi Fora (M.D. Leakey, 1971; R. Leakey and Walker, 1985). Several mandibles and other small cranial fragments have also been assigned to *H. erectus* (the fragments mostly on the basis of their overall thickness). The most notable of these fragments (because of its estimated age of ~1.9

Ma) is ER 2598, an occipital fragment with thick walls, a prominent occipital torus and angled occipital and nuchal planes.

Koobi Fora and Ileret are found on the east side of Lake Turkana and are part of the East African Rift Valley system. As at Olduvai Gorge, both *Paranthropus* and *Homo* fossils have been recovered from sites in this region. Both the Koobi Fora and Ileret regions are located in the Plio-Pleistocene fluvial and lacustrine deposits of the Koobi Fora Formation (Brown, 2000). The Koobi Fora Formation, part of the Omo Group of sediments, has been correlated with the Shungura, Nachukui, Nkalabong, Usno and Mursi Formations elsewhere in the [Omo-]Turkana basin (McDougall and Brown, 2006). These deposits alternate with tuff layers and lava flows, providing a secure geochronology in the Turkana Basin.

Most of the hominins recovered from Koobi Fora and Ileret are from the Upper Burgi, KBS and Okote Members, dated to between 1.9 and 1.3 Ma. More specifically, ER 3733 and ER 3883 were assigned ages of 1.78 (KBS Member) and 1.57 Ma (Okote Member), respectively (Feibel *et al.*, 1989). However, more recent work suggests that all *H. erectus* from Koobi Fora are between 1.45 and 1.65 Ma, with ER 3733 estimated to fall closer to 1.65 Ma. This revision was based on the proximity of the White Tuff, dated to 1.63 Ma (Brown *et al.*, 2006) to area 104 (where ER 3733 was found) (Gathogo and Brown, 2006). This new stratigraphy was questioned by Feibel *et al.* (2007) mainly on the basis of the documented paleomagnetic chronology in the region.

ER 730 was assigned an age of 1.7 Ma based on its attribution to the upper KBS Member, though it could also be from the lower Okote Member (Feibel *et al.*, 1989). Gathogo and Brown (2006) now assign it an age of ~1.6 (nearly the same age as ER

3733). The occipital fragment ER 2598 is dated to between 1.88 and 1.9 Ma (Feibel *et al.*, 1989; Gathogo and Brown, 2006); it may represent the oldest *H. erectus* cranial fossil anywhere.

By far the most complete individual *H. erectus* skeleton was initially identified in 1984 from a piece of cranial vault by Kamoya Kimeu at the Nariokotome III (NK3) site, on the west side of Lake Turkana (Brown *et al.*, 1985). Subsequent excavations uncovered the majority of the postcranial skeleton as well as the skull (R. Leakey and Walker, 1993). Despite the subadult status of WT 15000, “Nariokotome Boy” compares favorably in its cranial and mandibular anatomy with other African *H. erectus*, including both East Turkana fossils and OH 9 (Walker and R. Leakey, 1993). The dentition is also quite similar to the Zhoukoudian dentition. Overall, the cranium is long and low with a low, receding forehead and maximum cranial breadth across low on the temporals.

WT 15000 was found in the lowest part of the Natoo Member of the Nachukui Formation, between the KBS and Chari Tuffs, dated to 1.88 and ~1.39 Ma, respectively. Correlation with the Morutot Tuff in the Koobi Fora Formation further constrains the age to younger than 1.64 Ma. Based on interpolation between these tuffs, the age is approximately 1.51 Ma, though extrapolation yields a slightly earlier age of 1.56 Ma (Brown and McDougall, 1993).

New Kenyan fossils: Two additional fossil calvaria have been attributed to *H. erectus* from the sites of Olorgesailie and Ileret, both in Kenya. These cranial fossils are smaller than most representatives of this species, which would increase the known size range of African *H. erectus* (M.E. Leakey *et al.*, 2003; Potts *et al.*, 2004). The Olorgesailie cranial

fragments (OL 45500, a frontal, left temporal and many smaller fragments) were found in 2003, though the frontal was in a block initially excavated in 1999 (Potts *et al.*, 2004).

While the evidence is fragmentary, comparisons with the Dmanisi crania suggest that this specimen would have had a small cranial capacity of less than 800 cc. Both the frontal and temporal bone exhibit typical *H. erectus* features: keeling on the midline of the frontal, “shelf-like morphology of the posttoral sulcus” and a low flat temporal squama (Potts *et al.*, 2004, p. 77). It shares the more arched appearance of its supraorbital tori with ER 3733 and Daka. It varies from the Asian condition in having a small mandibular fossa and no supramastoid crest. Overall, it does resemble other *H. erectus* metrically. Schwartz (2004) suggests that Olororgesailie, like many other more traditional members of *H. erectus*, does not resemble the type specimen (Trinil 2) or the Sangiran fossils which approach the type most closely. He does not, however, offer an alternative taxonomic allocation.

The Olororgesailie basin is found within the Gregory Rift Valley, part of the East African Rift in southern Kenya, to the east of Lake Turkana. The Olororgesailie Formation is composed of ~80 m of deposits from ancient lakes, rivers and volcanic activity that cover a time span of 1.2 to 0.2 Ma (Deino and Potts, 1990; Potts *et al.*, 1999). $^{40}\text{Ar}/^{39}\text{Ar}$ dates constrain the fossil-bearing layer to between 747 and 974 ka, with the Matuyama – Brunhes boundary at 790 ka between the two. Based on a lack of evidence for a lag between the older date and fossil position, the fossil is estimated to be between 970 and 900 ka (Potts *et al.*, 2004).

The second Kenyan specimen, ER 42700 was found at Ileret site 103, near the northeastern end of Lake Turkana (the same region where ER 3883 was recovered). The

specimen is a subadult or young adult with a partially fused synchondrosis. Like the Olororgesailie and Dmanisi fossils, this is a relatively small calvaria, with cranial dimensions in the range of early *Homo*. Unlike OL 45500, the supraorbital toral / sulcal region is not well developed and there are no angular or occipital tori. However, there is keeling on both the frontal and parietal midline, which aligns it with other *H. erectus* (M.E. Leakey *et al.*, 2003). The overall shape of the vault, including flattening above lambda and details of the temporal bone, also places it within the range of *H. erectus* variation, though the more vertical occipital plane and bossed parietals differentiate it from other east Turkana specimens. ER 42700 was found in situ about 1.5 – 2 meters below a tuff that is correlated to a tuff in the Koobi Fora Tuff Complex in Area 103. This sets the age at 1.5 – 1.6 Ma.

North Africa: The first fossils found outside of Asia assigned to *H. erectus* were several jaws and an isolated parietal fragment from Tighenif (previously Ternifine or Palikao) in the Oran region of northern Algeria. These were initially assigned to *Atlanthropus mauritanicus* (Arambourg, 1954) but have since been frequently included in *H. erectus*. Recent analyses also found some derived features that linked the Tighenif mandibles and dentition with later *Homo* (Dean and Delson, 1995; Schwartz and Tattersall, 2000; Hublin, 2001; Delson and Baab, 2006; Schwartz, 2004) and their status remains unclear. These fossils are dated to the Middle Pleistocene.

Also from the Middle Pleistocene of North Africa is most of a posterior braincase from Salé, Morocco, found during quarrying in 1971. The many *erectus*-like features (long, low sagittal profile with thick cranial walls) and cranial capacity of 880 cc, well

within the *H. erectus* range have resulted in its placement within *H. erectus* (Jaeger, 1975; Holloway, 1981b; Rightmire, 1990; 2004). However, the Moroccan fossil from Salé has a very different temporomandibular fossa morphology from other *H. erectus* (Picq, 1990) and has more derived features that argue against its placement in *H. erectus*, including the expanded parietals and more rounded occipital with a minimal occipital torus. Hublin (1985) argued that some of these more advanced traits may be due to pathology in the nuchal region, leaving the taxonomic status of this specimen in doubt (see also Rightmire, 1990). The most recent evaluation of the taxonomic affinities of this specimen have aligned it with other Middle Pleistocene African fossils such as Bodo, Ndutu, Saldanha and Kabwe (Hublin, 2001).

A few other fragmentary remains from Sidi Abderrahman and the Thomas Quarries, also in Morocco, may also belong to *H. erectus* (Howell, 1978; Rightmire, 1990), though none of the cranial material is complete enough to include in this analysis. One early 3D study suggested that the Thomas 3 cranial remains may, like Salé, belong to a later form of *Homo* (Kalvin *et al.*, 1995).

A final locality worth mentioning is the archaeological site of Ain Hanech in Algeria. This site contains Oldowan tools and is dated by paleomagnetic and biochronological dating methods to 1.78 Ma (Sahouni *et al.*, 2002; Sahnouni, 2006). This early Pleistocene date would make Ain Hanech the oldest hominin site in northern Africa.

South Africa: Researchers have also noted resemblances to *H. erectus* in fossils from Swartkrans, South Africa. A new genus and species, *Telanthropus capensis*, was

originally erected to accommodate fragmentary remains (including a mandible, SK 15 and maxilla, SK 80) from Swartkrans that appeared more advanced than *Paranthropus robustus* which was well-known from the site (Broom and Robinson, 1949; Robinson, 1953). These were later moved into *Pithecanthropus capensis* (Simonetta, 1957) and finally *H. erectus* (Robinson, 1961). SK 80 was later found to articulate with SK 846b and SK 847 (now known as just SK 847), creating a partial cranium with a palate, the left face, infratemporal fossa and temporal bone. The initial description of the new composite cranium indicated its *Homo* status and its resemblance to *H. erectus* (Clarke *et al.*, 1970). Its affinity with other African *H. erectus* has been confirmed by several workers (Groves and Mazák, 1975; Tobias, 1978; Walker, 1981; Clarke, 1985). The supraorbital torus is marked and there are similarities between the nasal region of SK 847 and Sangiran 4 (as first noted by Robinson, 1953). This fossil has been dated to ~1.7 Ma (Brain, 1993).

However, some workers have emphasized resemblances between the SK 847 cranium and fossils attributed to both *Australopithecus* (Mann, 1970; Wolpoff, 1971) and early *Homo* (Clarke and Howell, 1972; Howell, 1978). It has even been suggested on the basis of morphometric analysis that this fossil, along with Stw 53 from Sterkfontein, represents a uniquely South African species of early *Homo* (Grine *et al.*, 1996). Clarke (1990; 1994) also places the two South African fossils together, but he includes ER 3733, 3883 and OH 9 (and some mandibular fossils from Swartkrans and East Turkana) with them in *H. leakeyi*, which is generally *erectus*-like but with a temporal bone that is more similar to later *Homo*. While Rightmire (1990; 2001) expresses uncertainty about the taxonomic position of SK 847, he is more confident in the *H. erectus* affinities of the

dentognathic fossil SK 15. In addition to these craniodental remains, some postcranial fossils have also been identified as *Homo cf. erectus* at Swartkrans from Members 1, 3 and possibly 2 (Susman *et al.*, 2001).

Ethiopia and Eritrea: Similarities to *H. erectus* have also been noted in more recent discoveries from two sites in the Afar Depression. These are the Ethiopian site of Daka and the Eritrean site of Buia, though the latter has not yet been formally placed within *H. erectus* (Abbate *et al.*, 1998; Asfaw *et al.*, 2002). These specimens may extend the African distribution of *H. erectus* to the northeast and provide information about the taxon in the period around 1 Ma. In the mid-1990s fossils were discovered at Buia in the Danakil (Afar) Depression in Eritrea (Abbate *et al.*, 1998). The fossils were included a very complete cranium, two incisors and a fragmentary pelvis from the Danakil Formation (see also papers in Abbate *et al.*, Eds, 2004).

The Buia cranium features a number of *H. erectus* traits including a long and low neurocranium with the greatest width at the supramastoid crests, a prominent supraorbital torus and coincidence of opisthocranion and inion. The large browridges are arched and the frontal bone is elevated with a midline keel. However, the parietals do not converge superiorly as in other *H. erectus* but rather are more parallel as in *H. sapiens*. The cranial capacity of 750-800 cc is within the range of *H. erectus* but is small relative to Middle Pleistocene *Homo*. The cranium is unusual in being very narrow for its length and breadth (Abbate *et al.*, 1998). The cranium has only recently been cleaned and remains to be described more fully – as a result its current taxonomic status is *Homo* sp. indet. Biostratigraphy and paleomagnetism converge on a date of ~1 Ma for this fossil.

The Daka cranium, missing only the facial skeleton below the frontal torus, was found in the Bouri Formation in the Middle Awash Valley of Ethiopia in 1997 about 250 miles south of Buia and also dated to around 1 Ma by a combination of $^{40}\text{Ar}/^{39}\text{Ar}$ and paleomagnetic methods (Asfaw *et al.*, 2002). The original description of Daka indicated similarities in morphology to both Asian and East African *H. erectus* and the cranial capacity of 995 cm^3 is within the *H. erectus* range. Midline sagittal keeling on the frontal is more similar to the Asian than the African condition and the frontal bossing resembles the Zhoukoudian frontals. As in the Turkana hominins, the sagittal profile is relatively shorter antero-posteriorly, there is no occipital torus / sulcus complex and the supraorbital tori are strong. Several features related to the supraorbital torus, the degree of postorbital constriction and the presence of a juxtamastoid eminence link this specimen to OH 9. However, nearly all discrete traits on the frontal bone shared between Daka and OH 9 are also found in Ceprano which is often assigned to a more advanced species of *Homo* (with the exception of the juxtamastoid ridge which is present in OH 9 and Daka but is absent in Ceprano).

While Asfaw *et al.* (2002) view Daka as evidence of a single species (*H. erectus*) spread across Africa and Asia, Manzi *et al.* (2003), using phenetic methods, found greater similarities between Daka and the early African *H. erectus*, which they called *H. ergaster*. These results are suspect, however, as their neighbor-joining and UPGMA trees also grouped Dmanisi and Ngandong together and place OH 9 by itself, but closest to the Asian group, seriously undermining their argument for a significant African – Asian *erectus* split.

While the Daka and Buia crania are similar to *H. erectus* both metrically and in many details of the cranial anatomy, they also share at least one trait which is more derived: less medially converging parietals (Abbate *et al.*, 1998; Asfaw *et al.*, 2003). On the basis of vault form, in particular the more vertical walls and “greater breadth on the parietals,” Antón (2003, p. 141) excludes Buia from *H. erectus*. She does, however, accept Daka as a *H. erectus* fossil, arguing that “the two differ metrically and in some important morphological ways” (p. 139). Yet it is not clear from published photographs, measurements or descriptions that these two specimens are very different in these characters: both are described as having vertical parietal walls but with the greatest breadth located inferiorly (across the mastoid or supramastoid crests), and both the biparietal and maximum cranial breadths are actually greater in Daka (133 ± 2 and 141 ± 2 mm; Asfaw *et al.*, 2002) than Buia (125 and 130 mm; Abbate *et al.*, 1998). What is apparent is that the neurocranium of Buia is quite narrow, and there is less lateral development of the mastoid / supramastoid region of the temporal in this specimen. The Daka cranium, as noted by Schwartz (2004), at least superficially resembles the Ceprano cranium, particularly in the supraorbital region. More complete descriptions and comparative work are needed to clarify the taxonomic affinities of these 1 Ma fossil hominins from the Afar triangle.

Caucasus

The first *H. erectus* fossils were recovered from the Caucasus fairly recently. The original hominin fossil from Dmanisi (a mandible, D 211) was found in 1991, and since that time a multitude of fossil hominin calvaria, mandibles and postcranial bones have

been excavated, all in situ (Gabunia, 1992; Gabunia and Vekua, 1995; Gabunia *et al.*, 1999, 2000b; Lordkipanidze *et al.*, 2005). Four well-preserved skulls or crania have been described. D 2280, a cranium with an incomplete base is the least well-preserved of the four. The other three skulls, D 2282, 2700 and 3444 each preserve the vault, face, base and mandible (D 211, 2735 and 3900, respectively). D 2282 is very warped while D 2700 and 3444 are a subadult and older (edentulous) individual, respectively. Numerous postcranial elements and a fourth, very large, mandible (D 2600) have also been recovered. Like the new Kenyan fossils, the Georgian crania are smaller than the majority of the hypodigm. While acknowledging shared likenesses between early *Homo* and the Dmanisi fossils, most workers assigned these fossils to very small-brained African-like *H. erectus* or *H. ergaster* (Gabunia and Vekua, 1995; Gabunia *et al.*, 2000b, 2001; Vekua *et al.*, 2002; Rightmire *et al.*, 2006). These studies emphasized the many ways in which the anatomy of the Dmanisi fossils mirrors the *H. erectus* hypodigm, especially the Turkana hominins. In particular, the Dmanisi crania have flat frontal bones with strong postorbital constriction, keeling on the parietals, angular tori, low and flat temporal squamae, greatest width at the supramastoid crests, flexed occipitals and sagittally oriented petrous pyramids (Rightmire *et al.*, 2006). According to this taxonomic scheme, those traits shared in common with *H. habilis*, including smaller endocranial volumes in all individuals, a similar facial profile to ER 1813 and a rounded occiput of (both seen in D 2700; Vekua *et al.*, 2002), are interpreted as plesiomorphies. An alternative proposed by Gabunia *et al.* (2002) and de Lumley *et al.* (2006) interprets these plesiomorphies as evidence that the Dmanisi hominins are a more primitive species than *H. erectus*: *H. georgicus*.

The site of Dmanisi is located in southern Georgia directly underneath the medieval town of Dmanisi on a promontory at the confluence of the Masavera and Pinesauri (Pinezaouri) Rivers. $^{40}\text{Ar}/^{39}\text{Ar}$ dating has assigned a date of 1.85 Ma to the Masavera Basalt (which lies directly under the fossil site) and a date of 1.81 Ma to the volcanic ashes lying directly above the basalt (Gabunia *et al.*, 2000b; de Lumley *et al.*, 2002). Some of the Dmanisi hominin fossils are found in this ash layer and are thus ~1.81 Ma. According to Gabunia *et al.* (2000b), the normal polarity of the basalt indicates it is from the Olduvai Subchron. The overlying layer A sediments are also of normal polarity, but the upper-most layer B sediments are of reversed polarity. This suggests that the A-B contact approximates the Olduvai-Matuyama boundary of 1.77 Ma. The majority of hominin fossils have been found in numerous infills within A layers which, unlike the surrounding A sediments, have reversed polarity. Lithographic and stratigraphic correlation supports the identification of the infill sediment as basal B sediments. This, in addition to evidence from associated fauna, supports a latest Pliocene to earliest Pleistocene date for the Dmanisi hominins (Gabunia *et al.*, 2000b).

Europe

In addition to Java, China, east and south Africa and Georgia, a number of finds from Europe have, at times, been placed within *H. erectus*. However, all fossils from this region have also been assigned to other taxa (generally later *Homo* species), and it is not known whether *H. erectus* settled Europe at all.

In the past some well preserved fossil calvaria like those from Petralona, Greece, Arago, France and Bilzingsleben, Germany have been assigned to *H. erectus*. However, these are generally now assigned to *H. heidelbergensis* ('archaic' *H. sapiens*), as discussed below. The single exception may be the Italian fossil from Ceprano.

The calvaria found at Ceprano in central Italy was initially described as the sole European outpost of *H. erectus* at 0.7 - 0.8 Ma (Ascenzi *et al.*, 1996). In 1997 it was subjected to a major reconstruction by R.J. Clarke. He concluded that the specimen shared many characters with the *H. erectus* hypodigm, but did expand the known variation in this species (Clarke, 2000b). Additional adjustments to the reconstruction by M.A. de Lumley and F. Mallegni resulted in essentially the same conclusion (Ascenzi *et al.*, 2000).

The Ceprano cranium shares with *H. erectus* features like thick cranial bones, widest breadth across the supramastoid crests, a thick and continuous supraorbital torus, an angular torus, an angled occipital bone and a strong occipital torus. It does differ from the larger hypodigm in some details of its morphology. For example, while the sagittal profile is low, it is also short rather than elongated (a feature also seen in Sambungmacan 3). The occipital torus is not continuous with the mastoid crests or angular torus laterally, there is not marked postorbital constriction (though this is also seen in younger Javanese fossils) and the superior border of the temporal squama is not low. The presence of more derived features in the Ceprano calvaria have suggested to some researchers that Ceprano occupies a more derived phylogenetic position, possibly representing an adult *H. antecessor* (Manzi *et al.*, 2001) or *H. mauritanicus* (Hublin *et al.*, 2001; Delson, 2002, Delson and Baab, 2006).

Indian subcontinent

Between the Middle East and southeast Asia there is only one fossil hominin site, located near Hathnora in the Narmada Valley of central India. This site is of uncertain (middle to early-late) Pleistocene age. The initial species allocation for the Narmada calvaria was *H. erectus narmadensis*, an ‘advanced’ type of *H. erectus* (Sonakia, 1984; 1985; de Lumley and Sonakia, 1985; Sonakia and de Lumley, 2006) but it has since been aligned morphologically with later *Homo* (Kennedy *et al.*, 1991; Kennedy, 1999; Cameron *et al.*, 2004). In addition, two archaeological sites in Pakistan, Riwat and Pabbi Hills, have been assigned early dates of ~2.0 Ma (Rendell, *et al.*, 1987; Dennell *et al.*, 1988). These sites yield of simple tools more similar to the Oldowan industries of Africa than to the Acheulean.

Other remains

‘Advanced’ *Homo erectus* in Africa and Europe: In addition to the Arago, Petralona, Bilzingsleben and Narmada calvaria, numerous middle Pleistocene *Homo* from Africa, like Bodo, Kabwe, Elandsfontein, and Ndutu, were also assigned to an ‘advanced’ form of *H. erectus* (Hemmer, 1972; Howells, 1974; Clarke, 1976; Vlček, 1978; Stringer *et al.*, 1979; Asfaw *et al.*, 2002), although they are more often assigned today to later species of *Homo* like *H. heidelbergensis* (Howell; 1978; Stringer *et al.*, 1979; Stringer, 1981; Rightmire, 1983; 1996, 2001, 2004; Bräuer, 1984; Kennedy *et al.*, 1991; Kennedy, 1999; Clarke, 1990) or *H. rhodesiensis* (Hublin, 2001; Delson and Baab, 2006). While these

calvaria do display some primitive features like prominent supraorbital tori, flattened frontal squamae and some midline keeling, they also exhibit more modern morphology in their facial anatomy, longer occipital planes and more parallel vault walls (Rightmire, 2001). It has been shown that the increase in brain size with the advent of this group was statistically significant and consistent with a speciation event (Rightmire, 2004). Most of these are classified as *H. heidelbergensis* or 'archaic' *H. sapiens*, a group which may well contain the common ancestor of both Neanderthals and modern humans. These fossils are Middle Pleistocene in age, ranging from ~600 (Bodo, Elandsfontein) to perhaps 280 Ka (Bilzingsleben) (Clark *et al.*, 1994; Schwarcz *et al.*, 1988; Klein *et al.*, 2006).

Another specimen that was initially compared favorably to *H. erectus* but has since been transferred to later *Homo*, usually to 'archaic' *Homo* (Day and Stringer, 1991) but sometimes to early modern *H. sapiens*, is Omo 2 (McDougall *et al.*, 2005). Fragments of three individuals (Omo Kibish 1-3) were found in 1967 in the Omo River Valley. Omo 2 is the most complete of the three, consisting of a well-preserved cranium missing the face and some of the anterior and medial base. While the less complete Omo 1 is modern in its rounded occipital profile and greatest width across the parietals, Omo 2 has a distinctly archaic sagittal profile, greatest width across the supramastoid crests, a prominent occipital torus, inion and opisthocranium which are coincident and a thickened inferior tympanic tube which are all *H. erectus* traits. Omo 2 clearly retains a more primitive anatomy than Omo 1, and they have been considered different taxa by some workers (Day and Stringer, 1982, 1991). Others argue that they represent a single variable subspecies or population of *H. sapiens* (Howell, 1978; McDougall *et al.*, 2005). Both Omo 1 and 2 are assigned to Member 1 of the Kibish Formation (Butzer, 1969). A

Th/U date of >130 Ka from *Etheria* shells (Butzer *et al.*, 1969) has recently been revised to ca. 195 Ka based on interpolation between two $^{40}\text{Ar} / ^{39}\text{Ar}$ dates on feldspar crystals from pumice clasts (McDougall *et al.*, 2005). However, while Omo 1 clearly derives from Member 1, Omo 2 was a surface find and some uncertainty must surround its stratigraphic position. If Omo 2 does indeed date from 195 Ka, then archaic cranial morphology but a larger cranial capacity of 1435 cc (Day, 1969) were present fairly recently.

Mandibular and fragmentary cranial remains of Homo erectus

Mandibular and postcranial fossils attributed to *H. erectus* have been uncovered from many of the same sites that have produced cranial remains of this species, including Olduvai Gorge, Koobi Fora, Swartkrans, Dmanisi, Zhoukoudian, Sangiran and Omo. In *H. erectus*, the size of the mandibular corpus, the verticality of the symphysis, the occlusal area of the cheek teeth and the number of roots are all intermediate between early *Homo* and *H. sapiens* (Antón, 2003). The ER 992 mandible from Koobi Fora is worth mentioning in particular because it is the type specimen of *H. ergaster* (Groves and Mazák, 1975). While Walker (1993) and Wood (1991) observed similarities between this fossil and the mandible of WT 15000, Schwartz and Tattersall (1999, p. 246) find the two “clearly distinguishable.” Further similarities between the ‘Nariokotome Boy’ and ER 3733 and 3883 (and differences from the Asian group) have prompted Wood (1991) to apply the nomen *H. ergaster* to this entire group.

The mandibular fossils at Dmanisi are interesting because one (D 2600) is much larger than the others and suggests either inflated sexual dimorphism or multiple species at this site (Gabounia *et al.*, 2002; Skinner *et al.* 2006). A mandible from Konso (KGA 10-1) dated to 1.5-1.45 Ma may also belong to *H. erectus* (Asfaw *et al.*, 1992; Wolpoff, 1999; Antón, 2004). The possible assignment of cranial fragments found at the Ethiopian sites of Omo and Gomboré II (Melka Kunturé) to *H. erectus* (e.g., Howell, 1978; Wolpoff, 1999) was based mainly on the overall thickness of the bones.

Many isolated mandibles and teeth recovered from Javanese sites in the Sangiran dome and at Kedung Brubus (east of Ngandong) are also generally included within this species. A few damaged and distorted cranial remains, S 27 and S 31, and one better preserved calvaria, S 4, were also found in the Sangiran (Pucangan) Formation. Most of the earlier remains (from the Sangiran Formation) have previously been assigned to other species like *Meganthropus palaeojavanicus* and *Pithecanthropus dubius*, which were variably linked to the australopiths (Weidenreich, 1945; Robinson 1953; von Koenigswald, 1973; Tobias and von Koenigswald, 1965; Howell, 1978; Howells, 1980; Tyler *et al.*, 1995). Other analyses have emphasized similarities between the earlier and later Javanese fossils, assigning them all to the same taxon (Le Gros Clark, 1964; Lovejoy, 1970; Kramer, 1994; Kramer and Konigsberg, 1994; Rightmire, 1990; Wolpoff, 1999; Antón, 2002; 2004). The most recent and comprehensive review of all dentognathic remains from Sangiran concluded that the earlier sample was more primitive than, or as primitive as, early African *H. erectus* but derived relative to early African *Homo* (i.e., *H. habilis* / *H. rudolfensis*) in terms of discrete mandibular features and both mandibular and dental metrics (Kaifu *et al.*, 2005). Hence, they concluded that

“if we take the conservative standpoint that all earlier *Homo* populations that are sufficiently derived from African early *Homo* belong to *H. erectus*, the Grenzbank/Sangiran group is allocated to a primitive group of this species” (Kaifu *et al.*, 2005, p. 17).

Postcranial remains

Postcranial remains are scarce at Asian sites, though some have been recovered from Trinil, Sangiran, Kedung Brubus, Ngandong, Sambungmacan and Zhoukoudian. It is difficult to assign isolated postcranial bones to the species level at East Turkana because several species are known to have existed simultaneously at these sites. In addition to the very complete WT 15000 skeleton, a less complete skeleton, ER 1808, including both cranial and postcranial elements, was also found at East Turkana. The limb bones of both individuals are fairly long. If the ER 3228 innominate is considered *H. erectus*, it is slightly older than the ER 2598 occipital (1.95 Ma) (Wolpoff, 1999). The WT 15000 skeleton also suggests that the scapula was in a more protracted position relative to modern humans and the clavicle was shorter (Larson *et al.*, 2006). While the postcranial skeleton is generally similar to later humans, it does differ in some ways from other hominins. Some of the differences include larger articular surfaces and narrower pelvis than in early *Homo*. Also, *H. erectus* limb elements have thick cortical bone, and the midshafts of the femora are often flattened antero-posteriorly (platymeria) (Kennedy, 1983, 1985).

While Wolpoff (1999) emphasizes the larger body size of early *H. erectus* from East Turkana, it is now clear that the Dmanisi hominins were considerably smaller than the individuals represented by WT 15000 and ER 1808. Height estimates based on a vertebral column and a metatarsal from Dmanisi are similar, 4'7" and 4'9" (Gabounia et al., 2000a; Meyer, 2005) and much smaller than the estimated 6' for Turkana Boy.

Temporo-geographic range

At its most extensive, the geographic range of *H. erectus s.l.* extends from South, East and North Africa through the Levant and the Caucasus east to China and Indonesia, though there are significant gaps in the record through mainland southern Asia. A more conservative approach would limit the taxon to East Africa, the Caucasus and East Asia. The African and Georgian material as a whole is older than the Asian material, with a maximum time range of 1.9 to 0.03 Ma, nearly two million years. There is ambiguity concerning both the earliest and latest appearances of this species. The date of 1.9 Ma is from ER 2598 – a small occipital fragment. The earliest relatively complete and well-dated African *H. erectus* fossil is ER 3733, previously dated to 1.78 Ma, but more recently estimated to ~1.65 Ma. The Georgian fossils are dated to between 1.81 and 1.77 Ma and are therefore older than most of the African fossils. While SK 847 may be of comparable early Pleistocene age, neither its membership in *H. erectus* nor its age are unambiguous.

While there have been proposals of earlier dates in Asia, most of these have been seriously criticized. The early date for Longgupo appears to be a moot point as the

fossils are likely not *H. erectus* or even hominin at all, while the sample which provided an age of 1.8 Ma for the Mojokerto specimen was likely not from the findspot. However, radiometric analyses in Asia do seem consistent with dates closer to 1.5 Ma, such as Javanese hominins close to the boundary between the Sangiran (Pugancan) and Bapang (Kabuh) Formations. Within China, most paleontological sites have been assigned wide date ranges between 400 and 600 ka. The Yuanmou incisors may be as old as 1.7 Ma but the taxonomic affinities of the teeth are unclear. Archaeological sites in both northern and southern China are more securely dated and help establish a long chronology in this part of the world. Together these archaeological sites confirm the presence of hominins (though not definitely *H. erectus*) in southern China at 0.8 Ma and in northern China by 1.66 Ma. Ngandong and Sambungmacan are most likely the latest surviving examples of *H. erectus*, and while most evidence points to a late Pleistocene date, an older age cannot be entirely ruled out.

Variation in *Homo erectus*

Geographic variation

Both morphometric and character based analyses have highlighted variation within and among the temporo-geographic subsamples of *H. erectus* (Bräuer, 1994; Bilsborough, 2000; Kidder and Durband, 2000, 2004; Antón, 2002). However, because the composition of samples as well as the linear measures and discrete characters vary among studies, the results are not always comparable. Moreover, a strong reliance on the

descriptions found in Weidenreich's work may have resulted in the Zhoukoudian morphology being used as a proxy for Asian morphology as a whole, meaning that oft-cited East African – Asian differences actually reflect the effects of climatically induced isolation (genetic drift) in the Zhoukoudian sample (Antón, 2002). Also the African and Georgian fossils are, on average, of greater antiquity and smaller size than the Asian hominins, so that the effects of geography, time and size are confounded to a large extent. Newer fossils and re-dating of some sites has helped to fill in gaps, but it may not be entirely possible to examine any one of these three variables independently of the other two. Despite these caveats, some generalizations can be made, and certain patterns are apparent.

Numerous discrete traits have been identified in the Asian hypodigm that are not found in the fossils from Koobi Fora and Olduvai Gorge (Andrews, 1984; Stringer, 1984), though Wood (1984, 1994) differentiates between the Koobi Fora and Asia / OH 9 samples. See Table 1.1 for more details. These traits said to distinguish the Asian from the African hominins include thicker cranial bones, a more angled occipital bone in the sagittal plane, a shorter upper scale of the occipital, and an occipital torus that is continuous with the angular torus and mastoid crest laterally. Additional characteristics of the Asian populations include a straighter frontal torus in anterior and superior views, a higher frequency of midline keeling on the frontal bone and along the sagittal suture and an angular torus at the mastoid angle of the parietal. Temporal bone traits not found in the African fossils include a thicker tympanic plate and fissures between both the tympanic plate and the entoglenoid pyramid and between the petrosal crest and the mastoid process. In addition, the supramastoid crest is more marked in the Asian

populations than the African ones (Villmoare, 2005). In the Asian sample the styloid process appears not to have fused to the cranial base at all or as early as in modern humans (where fusion normally occurs within the first year) (Arsuaga *et al.*, 1999). In contrast, the styloid process of ER 3733 and OH 9 is fused to the base (R. Leakey and Walker, 1985; Rightmire, 1990; Arsuaga *et al.*, 1999). A wide interorbital breadth and short wide face are also considered Asian characteristics. The lack of a continuous supratrochlear sulcus appears to be a uniquely Indonesian character state whereas this sulcus is expressed (though variably) in both the African and Zhoukoudian hominins. While the vertical separation between inion and endinion and between inion and opisthocranium have been put forward as Asian features (Andrews, 1984; Wood, 1984), these traits could not be evaluated in the African fossils (Stringer, 1984; Andrews, 1984), which leaves open the possibility that these traits are more widely distributed geographically.

The general lack of cranial superstructures in the African fossils is mirrored in the Georgian fossils (Antón, 2003), though some individuals exhibit midline keeling and angular tori, as well as transverse occipital tori. However, many of these proposed Asian autapomorphies may have a broader distribution in African and Georgian *H. erectus* and even outside of *H. erectus* (Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992; Brown, 1994; Villmoare, 2005). For example, a sagittal keel on the frontal bone is present in ER 42700, 3733 and some of the Dmanisi crania. It has also been suggested that many of these features are related to hypertrophy of the skull, and may be developmentally related and not, therefore, independent characters (Hublin, 1986).

Table 1.1: *Homo erectus* autapomorphies. Key: X – listed character as a *H. erectus* autapomorphy; A – character found only in Asian part of *H. erectus* hypodigm.

<i>H. erectus</i> autapomorphies		Wood (1984)	Andrews (1984)	Stringer (1984)	Rightmire (1990)	Wolpof f <i>et al.</i> (1994)
Overall Features	Increase in endocranial capacity				X	
	Thick cranial vault bones		X, A	X, A**	X	(both cotices and diploe) X
Occipital	Sharply angled occipital bone	X, A		X, A**	X	X
	Relatively large occipital arc	X				
	Occipital plane is shorter than nuchal plane	X, A				X
	Inion and endinion separated in Frankfurt Horizontal	X, A	X, A	X, A**		
	Inion and opisthocranium are coincident	X, A				X
	Occipital torus in conjunction with angular torus and continuous with mastoid crests	X, A			X	
	Wide occipital squama				X	
Frontal	Midline keeling		X, A	X, A**	X, A***	
	Browridge is thick and continuous with a flat shelf posterior				X	
	Post-toral sulcus	X, A*				
	Prominent supraorbital torus, straight anterior and superior profiles			X, A**		
	Browridges that are anteriorly projecting					X

Temporals	Process supratubarius at medial extent of petrotympanic crest				X
	Robust tympanic plate		(elongated antero-posteriorly)	X, A	A
	Strong petrotympanic crest on tympanic bone				X
	Mastoid fissure between mastoid process and petrotympanic crest	X, A	X, A		
	Fissure between entoglenoid pyramid and tympanic plate	X, A			X
	Strong supramastoid crest that turns superiorly				A
Parietals	Sagittal keeling on parietal bones	X, A	X, A**		
	Angular torus on mastoid angle of parietal bones	(in assoc. with occipital torus) X, A	X , A	X, A	X
Face	Large interorbital breadth			X, A	
	Short and wide face			X, A**	

* - Wood (1984) states that assessment of ER 3733 and 3883 indicate that they do not present any of the autapomorphies except a long occipital arc relative to the parietal arc (p. 107), but earlier he states that 3733 has "a definite post-toral sulcus." (p. 105)

** - Andrews (1984, p. 137) states that "only the Asian hominids show this assemblage with any consistency and could therefore be referred to as *H. erectus* sensu stricto...it seems clear that the Asian and African forms are similar in plesiomorphies rather than apomorphies." However, his Table 1.1 clearly shows that several traits could not be evaluated in the African forms, and these should not therefore be regarded as absent.

Traditional morphometric analyses have highlighted differences among different subsamples of *H. erectus* (Bräuer, 1994; Bilsborough, 2000; Antón, 2002). For example, the Zhoukoudian population has a narrower biasterionic breadth and a wider biauricular breadth. Ngandong and Sambungmacan have a wider minimum frontal breadth and the

East African sample has the greatest degree of postorbital constriction and a shorter parietal sagittal chord and arc. Bräuer (1990) also identified differences in the mandibular fossa, occipital sagittal curvature, parietal curvature and posterior parietal length among regional groups. Despite these variations, there was overlap between different groups for most measures and different geographic groups exhibited a high degree of variation for certain measures.

Significant intra-Asian variation has also been described (e.g., Weidenreich, 1943; Bräuer, 1994; Antón, 2002; Antón *et al.*, 2002b; Kidder and Durband, 2004; Balzeau and Grimaud-Hervé, 2006). Weidenreich (1943), while highlighting overall resemblances between the Zhoukoudian and Javanese (Sangiran and Ngandong) samples, also noted a few important differences between the two Asian samples. The Zhoukoudian fossils have a more marked frontal tuberosity (frontal bossing) and continuous posttoral sulcus while the frontal squama was flatter and ran smoothly onto the frontal torus in the Indonesian hominins. However, the Indonesian fossils displayed greater height in the area of obelion relative to the flattening present in its Zhoukoudian counterparts. When viewed superiorly, the Zhoukoudian occipitals were narrower and more elongated compared to the broader and more rounded occipitals of the Sangiran hominins (Weidenreich, 1943), an observation confirmed by later morphometric studies (Bilsborough 2000). The Zhoukoudian calvariae have a higher average cranial capacity (1029 cc) than the Sangiran hominins (928 cc) but smaller than the Ngandong hominins (1151 cc).

Some discrete cranial features are also differentially distributed between the two Asian groups. The Chinese specimens (Zhoukoudian, Nanjing 1 and Hexian) share the

following traits to the exclusion of the Indonesian calvaria (Trinil 2, Sangiran, Sambungmacan and Ngandong): marked postorbital constriction and a supratotal sulcus across the width of the frontal bone. In contrast, the Indonesian hominins have a supraorbital torus which is most anteriorly projecting medially, a supramastoid sulcus, a squamotympanic fissure located in the most superior part of the mandibular fossa and an occipital crest (Antón, 2002). The majority of these traits are variable within the Indonesian or within both regional groups. The temporal bones of the Zhoukoudian calvaria exhibited more extensive pneumatization than the Ngandong and Sambungmacan individuals (Balzeau and Grimaud-Hervé, 2006), and the glenoid fossa was less narrow antero-posteriorly and positioned higher, above the Frankfurt Horizontal, in the Zhoukoudian sample compared to the Indonesian hominins (Picq, 1990). While the results of Antón (2002) suggest that Ngandong fits the general Indonesian pattern both metrically and morphologically, Wolpoff (1999) has interpreted their morphology as intermediate between the Sangiran / Trinil fossils and modern humans from southeast Asia / Australia.

Within China, Zhoukoudian and Nanjing in particular have been singled out as having a unique cranial shape relative to Hexian. This cranial shape featured a narrow occipital and frontal compared to the wider midvault (Kidder and Durband, 2000, 2004; Antón, 2002). Several explanations have been proffered: either the pattern evident in the Zhoukoudian and Nanjing populations was a result of environmental adaptation, genetic isolation (genetic drift) or the measurements for Hexian are incorrect (Wolpoff, 1999; Antón, 2002; Kidder and Durband, 2004). Though Nanjing and Hexian are geographically close together (~100 km), they may differ in their paleoecology. Both

sites include northern faunal elements like those at Zhoukoudian, but Hexian also incorporates more southern subtropical taxa (*Ailuropoda*, *Stegadon*, *Megatapirus*) (Huang *et al.*, 1982; Xu and You, 1984; Etler, 1996). Etler (1996) and Kidder and Durband (2004) see this as a fundamental difference between these two sites, one which may explain the greater similarities between Zhoukoudian and Nanjing 1. However, Nanjing also incorporates at least one southern Chinese faunal element, *Stegadon* (Xu, 2002), throwing this conclusion into doubt.

Differences among the samples on Java have more often been attributed to temporal change, as all of these sites are geographically clustered within a limited area. However, population replacement has also been suggested to explain differences between some groups. This is discussed in more detail below (“Temporal Variation”).

Within Africa, individual fossils dated between 1.7 and 1.5 Ma include those from East Turkana (ER 730, 3733, 3883 and 42700) and Olduvai Gorge (OH 9). Numerous authors have noted the larger size and more robust morphology of OH 9 relative to the Turkana hominins, including thicker cranial bones, a very thick supraorbital torus and thickening at the mastoid angle of the parietal bone (‘incipient angular torus’). The mastoid process was also larger in OH 9 (and OH 12) (Antón, 2004) and OH 9 may also have a flatter basicranium than ER 3733 (Maier and Nkini, 1984; Laitman, 1985; but see Ross and Henneberg, 1995). Fossils dated between 1 and 0.7 Ma are OH 12, OL 45500, Daka and Buia (which has not yet been formally assigned to *H. erectus*). Three of the four remain to be fully described, making comparisons difficult. Of the three, the Kenyan fossil is much smaller. Asfaw *et al.* (2002) emphasized overall phenetic

similarities between Daka and Buia implying geographic homogeneity in this region (but see Antón, 2003).

Temporal variation

Given the long time span of *H. erectus*, there is potential for anagenic change in many aspects of morphology. The characters used to distinguish early African fossils as *H. ergaster* can be categorized as either more primitive or less specialized than those seen in *H. erectus* (Wood and Richmond, 2000). Because the Koobi Fora material is some of the oldest, it is possible that temporal changes could explain some of these differences. However, few analyses have focused on temporal trends.

Most studies have identified the well-documented increase in cranial capacity (Wolpoff, 1984; Leigh, 1992; Antón and Swisher, 2001; Rightmire, 2004). There is also limited evidence of diachronic change in the degree of postorbital constriction, the width of the glenoid fossa and the antero-posterior length of the parietal bone (the sample included only Zhoukoudian, Sangiran and East Africa) (Bräuer, 1994).

There is not strong evidence of any temporal trends within Africa, though this may change with the addition of recently described fossils (Antón, 2003). The exception is the apparent anagenic change found in several features associated with the temporomandibular joint. In particular, Picq (1990) appears to recognize a sequence from early *Homo* through a ‘pre-*erectus*’ group (ER 3733, 3883 and 1805) through OH 9 (*H. erectus*) and on through Indonesia, up through Ngandong. The postglenoid became reduced in size, the glenoid fossa became antero-posteriorly constricted and the anterior

wall of this fossa became long and anteroinferiorly sloping. As noted earlier, the pattern differed between Indonesia and Zhoukoudian.

Within Indonesia, diachronic change has also been documented. In terms of overall endocranial volume, the cranial capacities of the Sangiran hominins are smaller than the later Ngandong fossils, with non-overlapping ranges of variation (Rightmire, 2004). With the exception of Sm 1, the Sambungmacan individuals also had smaller endocranial volumes than the Ngandong series and may be intermediate in age, though this is not certain. Related to the increase in brain size were the decrease in postorbital constriction and an increase in neurocranial height (Antón, 2003). On the basis of dentognathic evidence, Kaifu *et al.* (2003; 2005) found that within the Sangiran sample alone there is variation attributable to either *in situ* anagenic change or to population replacement. Dental and mandibular size decreased from the earlier (Sangiran Formation) to the later (Bapang Formation) sample. From the Sangiran to the Ngandong / Sambungmacan calavaria there was an increase in the average size of the mastoid processes, a depression at glabella was more common and the presence of a supramastoid sulcus became a fixed trait (Antón, 2003). Wolpoff (1999) described Sm 1 as intermediate between the Sangiran hominins from the Kabuh layers and the Ngandong / Ngawi sample. In the later populations he observed the development of a lateral frontal trigone (a triangular flattening of the frontal squama posterior to the lateral corner of the supraorbital torus), expansion of both the frontal (resulting in a less receding frontal squama and narrower medial supraorbital torus) and occipital regions. The size of the upper plane of the occipital increased in proportion to the lower plane and the transverse occipital torus increased in size. There were also changes between the early and middle

Pleistocene Javanese populations that were not continued into the late Pleistocene, like an increase in basal pneumatization (Wolpoff, 1999).

Size-related and sexual variation

A final source of intraspecific variation that must be considered is that of sexual variation. Sex determination in fossil specimens is notoriously difficult (Armelagos and van Gerven, 1980) and can induce circularity into arguments concerning sexual variation in cranial morphology. For example, it is difficult to discuss sexual variation in the development of features like the supraorbital tori, mastoid process, sagittal keeling and occipital torus if these have provided, in part, the basis for initial sexual discrimination. However, if some sites are accepted as sampling a single biological population (e.g., Dmanisi) then certain patterns of variation may be interpretable as the result of sexual selection. Thus, though variations within the East Turkana, Sangiran, Ngandong and Zhoukoudian sites have been attributed to sexual differences (e.g., Weidenreich, 1943; Santa Luca, 1980; Wolpoff, 1999), these conclusions must be viewed cautiously.

It is less advisable to interpret variation in terms of male-female difference if the fossils span long time ranges, even at single sites. However, it is possible to examine size-related variation both at single sites and across multiple sites. This variation is likely attributable to at least two factors: sexual variation and allometric variation. Some workers have noted similarities in smaller specimens versus larger specimens regardless of age or geography, both within *H. erectus* as a whole (Rightmire, 1990) and within the Indonesian sample in particular (Sartono, 1975; Antón, 2002). It is also likely that

overall cranial robusticity, as reflected in discrete traits such as midline keeling and the transverse occipital torus, is related to sex as is the case in modern humans (Lahr and Wright, 1996; Baab *et al.*, 2006). These findings are in agreement with recent work that highlighted the effect size can have on certain aspects of cranial shape often used to define *H. erectus* like occipital angulation, cranial bone thickness and degree of postorbital constriction (Spoor *et al.*, 2005). The work by Spoor *et al.* (2005) is the first systematic attempt to quantify character variation as an effect of size, but further work is needed especially since there is a great deal of size variation encompassed not just in *H. erectus s.l.* but in both the Dmanisi and Javan *H. erectus* samples. Compared to geographic and temporal variation, the less attention has been paid to size-related variation.

The presence of variation within the broad *H. erectus* sample has been interpreted, as above, in terms of either intraspecific variation or anagenic change. Alternatively, it has been suggested that this variation either exceeds the amount or diverges from the pattern expected in a single species and has thus been interpreted as evidence for multiple species.

Evolutionary history and taxonomy

Certain aspects of *H. erectus* phylogeny are generally accepted: (1) *H. erectus* first evolved in Africa sometime before 1.78 Ma (and perhaps by 1.9 Ma); (2) the initial population resembled the fossils from East Turkana; and (3) sometime after their initial emergence, perhaps around 1 Ma, a more advanced form of *H. erectus* spread throughout

Asia (and maybe Europe) from Africa. In addition, it is implicit that *H. erectus* was the first and only hominin to disperse from Africa around the Plio-Pleistocene boundary. Alternative scenarios have been proposed concerning all elements of this formulation as a result of new fossil discoveries, revised site chronologies and more sophisticated analyses. Different lines of evidence have provided tantalizing hints that the evolution and population movements of *H. erectus* were more complex and dynamic than previous models acknowledged.

Origin of Homo erectus

The emergence of *H. erectus* must have occurred before 1.9 Ma *if* the occipital fragment from Koobi Fora is accepted as *H. erectus*. The likely ancestors are represented by early *Homo* fossils from the sites in east and south Africa (*H. habilis* and *H. rudolfensis*), though it is also possible that a yet unrecognized species may be ancestral to *H. erectus* (Wolpoff, 1999; Delson, 2002). The most complete early *Homo* fossils are from Olduvai Gorge, Koobi Fora and Hadar, Ethiopia (Wood, 1991; Tobias, 1991; Kimbel *et al.*, 1996, 1997) though it is likely represented from the South African sites of Sterkfontein and Swartkrans as well (Grine *et al.*, 1996). Less complete specimens of early *Homo* were also described from Chiwondo, Malawi and Chemeron, Kenya (Bromage *et al.*, 1995; Hill *et al.*, 1992; Sherwood *et al.*, 2002). The alpha taxonomy of this fossil sample has been the subject of controversy since L. Leakey *et al.* (1964) first applied the nomen *H. habilis* to OH 7.

While some workers argue that all fossils can reasonably be retained within a single, sexually dimorphic species (Kramer *et al.*, 1995; Miller, 2000), more convincing arguments have been forwarded that at least two species are present at Koobi Fora and Olduvai Gorge, though several different subdivisions have been proposed (Stringer, 1986; Groves, 1989; Wood, 1991; Rightmire, 1993). According to the taxonomy of Wood (1991), *H. habilis* is represented by smaller-brained fossils from Olduvai Gorge and Koobi Fora which display a smaller dento-facial complex than *H. rudolfensis* from Koobi Fora which exhibits an larger endocranial volume but also greater prognathism and postcanine megadontia. The differences between the two taxa are perhaps most apparent in a comparison of ER 1813 (*H. habilis*) and ER 1470 (*H. rudolfensis*).

Traditionally workers have supported either *H. habilis* as the ancestor of *H. erectus*, which implies the parallel evolution of enlarged cranial capacity in the *H. rudolfensis* and *H. erectus* lineages or *H. rudolfensis* as the ancestor which requires convergent acquisition of numerous features, especially in the facial skeleton, in *H. habilis* and *H. erectus* (Bilsborough and Wood, 1986; Chamberlain and Wood, 1987; Lieberman *et al.*, 1996; Grine *et al.*, 1996; Strait *et al.*, 1997; Wood, 1992; 1993; Foley, 2002). However, it has long been recognized that it is difficult to ascertain the phylogenetic sequence that resulted in the origin of *H. erectus*, in part due to the complexities surrounding the taxonomy of early *Homo* (Chamberlain and Wood, 1987; Asfaw *et al.*, 2002). Antón (2003, p. 141) even hints at site specific ancestry for *H. erectus* from East Africa:

Likewise, the extent to which the anatomy of OH 12 is foreshadowed by that of earlier Olduvai *H. habilis* (and that of ER 3733 is foreshadowed by Koobi Fora

Homo) ... suggests that our understanding of the origin and variation of early African *H. erectus* is far from clear.

The discovery of early, small-brained fossils which are plausibly assigned to *H. erectus* (e.g., Dmanisi) suggests that there was more variation in cranial capacity in early *H. erectus* than previously recognized. This in turn removes one of the largest challenges to acceptance of a *H. habilis* ancestry for *H. erectus*, that the larger cranial capacities of ER 1470, 3733, 3883 and WT 15000 were a shared derived feature. Perhaps the smaller endocranial volumes found in the Dmanisi fossils was a primitive retention and the enlarged cranial capacity evolved later (according to Gathogo and Brown (2006), ER 3733, the earliest large brained *H. erectus*, was about 120-150 ka younger than the Dmanisi fossils). Alternatively, it may support the presence of multiple lineages (for example a small brained lineage including Dmanisi and ER 42700 and two larger brained lineages, one including ER 3733, 3883 and WT 15000 and a second including OH 9 and the Asian fossils) though clearly more comparative morphological work would be necessary before this scenario is proposed.

Though not often considered, *H. erectus* may instead have evolved outside of Africa. The limited size and observable morphology of the occipital fragment from Koobi Fora is tenuous evidence for the presence of *H. erectus* in Africa around 1.9 Ma. The attribution of the pelvis ER 3228 from 1.95 Ma is even more questionable because other hominins are also present from this time period at East Turkana (Antón, 2003). Revising the age of ER 3733, formerly the oldest definitive *H. erectus* fossil, from 1.79 to 1.65 Ma (Gathogo and Brown, 2006) implies that the first appearance of this taxon may be at Dmanisi, outside of Africa. The date of 1.81-1.77 Ma for the site of Dmanisi means

that this population may have been the result of a migration very soon after *H. erectus* diverged from the ancestral *Homo* stock in East Africa. Alternatively, a population of early *Homo* (pre-*H. erectus*) may have dispersed out of Africa, giving rise to *H. erectus*, which later returned to Africa (Clarke, 1990; 2000a; Wang and Tobias, 2001). Indeed, many resemblances to early *Homo* have been noted in the Dmanisi hominins that are not apparent in early African *H. erectus*, such as a facial profile similar to ER 1813 (in D 2700 – though this is a juvenile individual; Vekua *et al.*, 2002), a flatter frontal and a narrower occipital (de Lumley *et al.*, 2006). The presence of more primitive characters is expected in a population transitional between early *Homo* and *H. erectus* but is also compatible with an interpretation of the Dmanisi hominins as early members of *H. erectus*. While not as common as the scenario where *H. erectus* evolves in Africa and from there migrates across the Old World, the idea that either *H. erectus s.l.* or *H. erectus s.s.* (excluding Turkana Basin *H. erectus*) evolved outside Africa is not a new one (Swisher *et al.*, 1994; White, 1995; Clarke, 2000a; Wang and Tobias, 2001; Asfaw *et al.*, 2002; Dennell and Roebroeks, 2005).

Dispersal

Timing of early dispersals: The initial dispersal out of Africa, whether of early populations of *H. erectus* or an even more primitive species, clearly occurred before 1 Ma. Dmanisi provides solid evidence for extra-African hominins at the Plio-Pleistocene boundary but a ‘long chronology’ (i.e., hominins in Asia before 1.5 Ma) is also supported by isotopic chronologies in the Sangiran dome, regardless of whether or not the very old

dates of 1.66 and 1.8 Ma are accepted for S 27 / S 31 and Modjokerto, respectively (Swisher, 1997; Larick *et al.*, 2001; Antón and Swisher, 2004).

Nature of early dispersers: As described above, the nature of the first dispersers from Africa was considerably more primitive than previously envisioned, and may have even have occurred pre-*erectus*. Dmanisi may provide corroborating evidence for the view that early Sangiran dome fossils represent a more primitive form of hominin than later Javanese *H. erectus* (e.g., Robinson, 1953; Tobias and von Koenigswald, 1965; Howell, 1978). Recently, Kaifu *et al.* (2005) found significant difference between earlier and later dentognathic samples from within the Sangiran dome. The earlier sample was considerably more primitive whereas the later population resembled later *H. erectus*. Based on these observations, they argued that the first hominin migrants into Java were not descended from early African *H. erectus* (i.e., from East Turkana) but rather from an even less derived form of *H. erectus* (like that seen at Dmanisi).

Multiple dispersals: The differences between earlier and later forms of Sangiran dome hominins were best explained by either rapid *in situ* evolution or by population replacement later in the Pleistocene (Kaifu *et al.*, 2005). The latter option suggests multiple dispersals within the evolutionary history of *H. erectus*. Variations between the Dmanisi and Javanese populations may support different ancestral populations (Antón and Indriati, 2002). Archaeological evidence from Israel may also support multiple waves of dispersing populations. Two sites from the Pleistocene of Israel (‘Ubeidiya and Gesher Benot Ya’aqov) exhibit different Acheulean lithic traditions which can be traced

to separate African origins, suggesting separate dispersal events (Goren-Inbar and Saragusti, 1996).

Direction of dispersal(s): Throughout prehistory migrations were not restricted to a west-east direction, and Asia to Africa dispersals have been recorded for other mammals like horses and bovids (Lindsay *et al.*, 1980; Vrba, 1995). As mentioned above, *H. erectus* may have evolved outside of Africa and it is possible that southerly (from Eurasia) or westerly (from east Asia) migrations were responsible for the presence of either / both early *H. erectus* or *H. erectus* s.s. in East Africa. The number and direction of hominin dispersals requires a dense sampling of fossil sites and a well-established chronology for those sites. It seems that a more complex history of migrations is as likely, given the fossil evidence from Georgia, the Middle East and Sangiran, as the traditional out-of-Africa model for *H. erectus* dispersal.

Mechanisms of dispersal: The catalyst for these diasporas (in either direction) is unclear. Because *H. erectus* is often (but not always) associated with a shift from Oldowan to Acheulean stone tool kits, it was thought that this new technology either provided the technological edge needed to expand into new niches or implied a change in behavior and cognition that allowed them to disperse out of Africa (Klein, 1999). However, it now seems clear that the earliest migrants did not utilize tools much advanced from the Mode 1 technology seen in Africa since 2.5 Ma (Gabunia *et al.*, 2000b; Dennell and Roebroeks, 2005). Larger body size may have influenced foraging and ranging behaviors in early *H. erectus*: an increase in body size led to increased energy requirements, which may have

been met through an increase in the consumption of meat and other animal products, as well as underground storage organs (Aiello and Wells, 2002). This shift in foraging behaviors, coupled with longer legs (which allowed for larger daily ranges than earlier, shorter legged hominins), may in turn have led to bigger foraging areas in early *H. erectus* (Shipman and Walker, 1989; Aiello and Wells, 2002). *H. erectus* females in particular were subjected to greater energetic demands tied to reproduction (especially lactation). The increased energy demands may have been offset by a shorter interbirth interval (which reduced the energetically expensive lactation period) but also by changes in foraging and other social behaviors (Aiello and Key, 2002). A complex model explaining the initial population movements out of Africa was advanced by Antón and colleagues based on some of the same principles: an increase in body size led to larger home ranges while an increase in both body and brain size coupled with a decrease in sexual dimorphism (the result of larger females) led to greater energy requirements, most likely met through increased levels of carnivory. Together these factors resulted in rapid dispersal from Africa after perhaps 4 million years of intra-African evolution (Antón *et al.*, 2002a; Antón, 2003; Antón and Swisher, 2004). In general the average body size of *H. erectus* is estimated to be larger than the average in *H. habilis*, but it remains to be established whether this was the case for early *H. erectus* from Dmanisi whose crania were not very different in size from their putative ancestors (*H. habilis* / *H. rudolfensis*). Similar questions pertain to whether brain size increased sufficiently early in *H. erectus* evolution to explain the initial dispersal. There is also considerable sexual dimorphism associated with the Dmanisi mandibles (Skinner *et al.*, 2005), which raises questions about when a decrease in size dimorphism occurred. Whether increased population sizes

or, as suggested above, complex shifts in biological and physiological variables led to changes in foraging ecology, it is clear that early populations of *H. erectus* or even pre-*erectus* populations were active dispersers around the Plio-Pleistocene boundary.

Movement into diverse habitats: Migrations brought tropical-adapted hominins into contact with new, more temperate climates and different geography outside Africa. While much of Pliocene Asia was savannah habitat like Africa, there were still variations within Asia. For example, island southeast Asia was more forested than the mainland, and some Chinese sites were colder and others more tropical or subtropical (Brown, 2001; Dennell and Roebroeks, 2005). It is likely that adaptation to new ecological niches impacted the behavior and biology (and hence morphology) of these hominin populations.

From this review, it is clear that old assumptions must make way for new hypotheses regarding the origin and dispersal of *H. erectus*. While not all propositions are equally likely or equally testable, more and better data regarding *H. erectus* morphology will bring some clarity to this situation. The discoveries at Dmanisi and revised stratigraphies, especially on Java and at Ileret, have only recently turned the spotlight on the early part of *H. erectus* evolution. Previously, more attention was paid to the later period of their evolutionary history, which has proven very controversial. The nature of both the relationships within the populations loosely labeled *H. erectus* and between *H. erectus* and later *Homo* taxa have been the focus of debate since the middle of the 20th century – a debate which continues today.

Alternative taxonomies of and within Homo erectus s.l.

Three major taxonomic / phylogenetic scenarios have been proposed in regard to *H. erectus*. Each of these three theories will be reviewed and critiqued in detail below after a brief introduction. First, the single polytypic species model proposes that fossils from Africa, Asia and the Caucasus can be accommodated within a single polymorphic and polytypic species. Locally, some populations of this species went extinct while others may have been ancestral to later species of *Homo*. This model emphasizes the strong similarities among individuals assigned to *H. erectus* despite the temporally and geographically widespread nature of this taxon. The second model proposes a moderately or substantially bushier tree for Plio-Pleistocene *Homo*, including *H. erectus*. Those workers adhering to a multiple species model have proposed the presence of a uniquely African or African / Georgian species, *H. ergaster*, among others, based mainly on the distribution of discrete traits. These workers see the Asian *H. erectus* s.s. as strictly a dead end lineage. The final model views *H. erectus* as the earliest grade in the evolution of *H. sapiens*, which gradually evolved into modern humans in several main regions throughout the Old World. Of the three, this is the only model in which the Asian representatives of *H. erectus* contribute meaningfully to the gene pool of later (regional) populations of modern humans.

Single polytypic species model: As early as 1940, workers recognized that similarities between the Javanese (*Pithecanthropus*) and Chinese (*Sinanthropus*) fossils might

suggest congeneric if not conspecific status as *Pithecanthropus erectus* (Le Gros Clark, 1937, 1955; von Koenigswald and Weidenreich, 1939; Weidenreich, 1943). Mayr (1944, 1950) considered these two genera, plus *Telanthropus* and *Meganthropus*, as synonymous and part of our own genus, thus creating *H. erectus*. This ‘lumping’ trend was continued by Le Gros Clark (1964) who also transferred *Atlanthropus* and *H. leakeyi* (OH 9) into *H. erectus*. Thus, the consensus from the 1940s until the mid 1980s was that *H. erectus* incorporated fossils from east, north and south Africa, as well as China and Java. The Ngandong remains were generally considered to be of an evolutionary stage equivalent to the Neanderthals of Europe or as archaic *H. sapiens* and were generally not included within *H. erectus* (e.g., Le Gros Clark, 1955; Von Koenigswald, 1958; Howell, 1967; Howells, 1980; Bräuer, 1984). Variations among *H. erectus* populations were generally interpreted within an intraspecific framework (and sometimes recognized at the level of the subspecies, Campbell, 1965, 1972).

H. erectus was variably placed as an ancestor of *H. sapiens* or an evolutionary dead end. Before any of the African *H. erectus* fossils had been discovered, Howells (1942) argued that the expanded cranial vault of modern humans (as seen in Swanscombe) was present at the same time if not earlier than “the backward Javan-Pekin family” and thus removed them from ancestry of modern humans. The idea that Asia represented an evolutionary deadend was echoed by Movius (1949) on archaeological grounds and by Howell (1960) on morphological grounds. Le Gros Clark (1955, p. 74) proposed that a small-brained type of hominin “represented by the *Pithecanthropus* stage of ... evolution” gave rise to an archaic form of *H. sapiens* which then gave rise to two species, modern humans and Neanderthals. Howell (1967, 1978) describes *H. habilis*, *H.*

erectus and *H. sapiens* as evolutionary species and suggested that *H. sapiens* (which included *H. sapiens neanderthalsensis*) diverged from *H. erectus* perhaps in the Middle Pleistocene.

The single species viewpoint is still prevalent today, and proponents use a ‘grade based’ species definition to define a distinct but polymorphic *H. erectus* species (Le Gros Clark, 1964; Howell, 1978; Rightmire, 1984; 1990; 1998a; Turner and Chamberlain, 1989; Delson, 1990; Bräuer, 1990; Harrison, 1993). These ‘grade based’ species definitions included pleisiomorphic, synapomorphic and autapomorphic characters. These traits taken together served to differentiate Plio-Pleistocene fossils from Java, China and a few sites in Africa from earlier and later *Homo* species in Africa, Asia and Europe.

Though there is clear polytypism, morphometric comparisons of the fossil hypodigm with extant primate species, usually humans and African apes, have supported the conclusion that variation is within the range of a single species (Bilsborough and Wood, 1986; Kramer, 1993; Bilsborough, 2000; Kidder and Durband, 2004; Villmoare, 2005). It is unclear, however, what effect the inclusion of new specimens from Africa and Georgia would have on *H. erectus* inter-specific variation, as they were not included in these studies. Conflicting results were obtained when variation was examined in the Dmanisi mandibles and crania. Skinner *et al.* (2006) found size and shape dimorphism among the Dmanisi mandibles to be excessive for a single species. In contrast, variation in cranial dimensions and endocranial capacity within the Dmanisi sample was within the range of a single species (Macaluso *et al.*, 2004; Lee, 2005). The D 2600 mandible is considerably larger than the other three mandibles. If the cranium that corresponds to the

D 2600 mandible is comparably large, then the Dmanisi population may retain the primitive condition of high sexual size dimorphism. Under this model the four crania thus far described from Dmanisi would all be female individuals.

The acceptance of a single polytypic species presumes a great deal of genetic continuity throughout the evolutionary lifetime and across the geographic range of *H. erectus*. This could be accomplished by having a populated 'core' which gave rise to multiple dispersals over time, each of which eventually went locally extinct without speciation. These 'cores' may have been related to climatic fluctuations, acting as refugia during more adverse climatic cycles. Alternatively, the population density and movements were sufficient across the range to maintain genetic and morphological continuity.

If we accept the widespread and polytypic nature of *H. erectus*, then it is reasonable to conclude that some temporal or geographic populations (e.g., from Java) went extinct while others (e.g., from Africa) left evolutionary descendants (Rightmire, 2001). Rightmire (1998b; 2000; 2001; 2004) proposed that around 0.8 Ma, *H. erectus* speciated in Africa or western Eurasia, giving rise to the more derived species *H. heidelbergensis* which was, in turn, ancestral to both Neanderthals and modern humans later in the Pleistocene. According to this scenario, *H. heidelbergensis* would include fossils from Africa (Bodo, Kabwe, Elandsfontein), Europe (Petalona, Arago, Sima de los Huesos, Gran Dolina) and maybe Asia (Dali, Jinniushan) which preserve certain primitive features from *H. erectus* (e.g., flat frontals with massive browridges and thick cranial bones) but also exhibit more derived traits like larger endocranial volumes, wider midvaults and parietal bossing, more vertically oriented noses and higher and more

arched temporal squamae. The increase in brain size and encephalization seen between *H. erectus* and *H. heidelbergensis* argues against a gradual shift from *erectus*-grade to *heidelbergensis*-grade humans (Rightmire, 2004). If the species which includes Bodo, Arago and Kabwe gave rise to modern humans (and maybe Neanderthals), as suggested by Rightmire (2001) then *H. erectus* would be on the direct lineage to *H. sapiens*. A modification of this proposal allows for a second speciation event; the more modern hominins from China like Dali constitute their own species (Asfaw *et al.*, 2002).

Bermúdez de Castro *et al.* (2004) argued that recently described fossils from the TD6 levels of the Gran Dolina site at Atapuerca, Spain may, along with Ceprano, constitute a species of *Homo* (*H. antecessor*) that is ancestral to both the modern human and Neanderthal lineage (which passed through an earlier *H. heidelbergensis* stage). It is possible that *H. erectus* in Africa or Western Eurasia (considered by these workers to be *H. ergaster*) was ancestral to *H. antecessor*. Alternatively, if the Tighenif material is also included in a species with Ceprano and the TD6 fossils, then this species would be called *H. mauritanicus*. *H. mauritanicus* would then be ancestral to both Neanderthals and to modern humans, possibly via *H. heidelbergensis* and *H. rhodesiensis*, respectively (Hublin, 2001; Delson and Baab, 2006).

Critique: Criticisms of the one species model focused on the ambiguity of grade-based definitions, arguing that it is the presence of autapomorphies which ultimately define species (Andrews, 1984; Stringer, 1984 but see Harrison, 1993; Kimbel and Rak, 1993). It has also been argued that paleoanthropologists as a whole focus too much on intraspecific rather than interspecific variation (Tattersall, 1986). Some consider this

widely expanded *H. erectus* hypodigm to be without definition and would prefer to limit the species to the type specimen from Trinil and those Sangiran fossils to which it is most similar arguing that including such a vast array of fossils in this species will inevitably result in similarities among them, but not necessarily meaningful ones (Schwartz, 2004). Another criticism of the single species model is that according to cladistic principles, if the African population gave rise to both the Asian populations and a separate species in Africa, then these must be regarded as three separate species, even if one branch continued essentially unchanged.

Multiple species model: Cladistic methodologies first expounded by Hennig (1966) were introduced to paleoanthropology nearly a decade later (Delson, 1975; Delson and Andrews, 1975; Eldredge and Tattersall, 1975; Delson *et al.*, 1977). Concerns about the ambiguous nature of grade-based definitions led to the application of cladistic principles to a *H. erectus* species definition (i.e., the phylogenetic species concept [PSC]) in the 1980s (Andrews, 1984; Stringer, 1984; Wood, 1984). Most previous definitions of *H. erectus* focused on differentiation from modern humans only, allowing for the inclusion of plesiomorphies. The initial investigations of the distribution of *H. erectus* autapomorphies supported the recognition of an additional species, *H. ergaster*. According to this two species model, *H. erectus* s.s. was more derived than *H. ergaster* which was restricted to Africa.

In a series of publications Tattersall and Schwartz (Tattersall, 1986; 1997; Schwartz, 2000, 2004; Schwartz and Tattersall, 1999, 2003, 2005) have argued that species diversity in *Homo* is higher than commonly recognized. The premise of their

argument is that morphological divergence is not necessarily commensurate with speciation so that any discernable differences among fossils likely represent separate species. They have argued that interspecific rather than intraspecific variation should be emphasized. Schwartz and Tattersall (1999, 2003) and Schwartz (2004) recognized multiple ‘morphs’ within traditional *H. erectus* material, even from single sites like Koobi Fora or Dmanisi. While these ‘morphs’ do not necessarily equate to full species, Tattersall (1992) has suggested that they are best interpreted in this manner. Schwartz (2004) would apparently limit *H. erectus* to the Trinil and Sangrian material, a fairly extreme position.

Though less commonly accepted, separate species have been proposed for the Dmanisi sample as well as for the Ceprano cranium (Manzi *et al.*, 2001; Gabounia *et al.*, 2002; Mallegni *et al.*, 2003; de Lumley *et al.*, 2006). Some workers also recognized multiple species and even genera within the Asian fossil sample (e.g., Jacob, 1973, 1975; Tyler *et al.*, 1995; Howell, 1999; Cameron *et al.*, 2004).

A cladistic species definition requires the presence of autapomorphies, and several authors have addressed this issue, with differing conclusions (Andrews, 1984; Stringer, 1984; Wolpoff *et al.*, 1994) (Table 1.1). In one of the first attempts to identify *H. erectus* autapomorphies, Eldredge and Tattersall (1975) identified three: a long, low and flat cranial vault with prominent supraorbital tori and thick cranial bones, though the Koobi Fora material had yet to be added to the hypodigm. The most-cited autapomorphies in the literature are thick cranial bones (including both the cortices and diploë), an angular torus, and a highly angled occipital bone. Less frequently cited traits

are an inion and endinion separated vertically in Frankfurt Horizontal and midline keeling on the frontal bone.

The observation by some workers that most if not all *H. erectus* autapomorphies were distributed only within the Asian or within the Asian / OH 9 subset of the hypodigm led to the assertion that the (early) African material, particularly the craniomandibular fossils from Koobi Fora which resembled *H. erectus*, were less derived than the Asian hominins and therefore might represent a separate species (Wood, 1984, 1991, 1994; Stringer, 1984; Andrews, 1984). Because the mandible ER 992 was included by Wood (1991) in this species, the nomen *H. ergaster* was available.

A more strict African / Asian division was proposed by Clarke (1990, 1994) who suggested that temporal bone anatomy was less derived in all African *erectus*-like specimens, including the Olduvai Gorge fossils. He also cited the lack of Acheulean tools in the Asian archaeological record as evidence of geographic and genetic isolation of the Asian population (Clarke, 1990; but see Hou *et al*, 2000). As a result, the nomen *H. leakeyi* was applied to the African group, which also included fossils more commonly attributed to earlier *Homo* like SK 847, 15 and Stw 53 (Clarke, 1990), though this name is not available because it was proposed by Heberer (1963) only provisionally (Simons *et al.*, 1969; Szalay and Delson, 1979; Harrison, 1993). Comparisons are often made between the African (excluding the South African fossils) and Asian *H. erectus* (eg., Rosas and Bermudez de Castro, 1998; Villmoare, 2005) but this does not correspond to either of the two species models proposed by Wood (1991, 1994) or Clarke (1990, 1994, 2000a). Similarities between the Georgian crania and the Koobi Fora fossils (Vekua *et al.*, 2002) may argue in favor of their classification as *H. ergaster* in a two species model.

The two species model advocated by Wood (1991) implies that *H. erectus* s.s. was distributed across both Africa and Asia, whereas *H. ergaster* was limited to East Africa, and possibly Georgia.

In addition to strictly cladistic approaches, Villmoare (2005) concluded that while variation in linear measurements is compatible with a single species hypothesis, non-metric trait variability supported a two species model. Villmoare (2005) included both *H. ergaster* and *H. erectus* s.s. (i.e., OH 9 and 12) in the ‘African group’ but did not include any South African fossils, complicating the interpretation of his results in either two species model discussed above. Very few traits were found to consistently differentiate between the African and Asian groups (only the supramastoid crest consistently separated the two, though the angular torus and midline frontal keeling are more often expressed in the Asian fossils). An examination of his non-metric trait scores shows no support for an *H. ergaster* / *H. erectus* division. At best this is viewed as weak support for the two species model proposed by Clarke (1994, 2000a).

According to both models, *H. erectus* s.s. was more derived but not in the direction of modern humans, so the less derived *H. ergaster* or *H. leakeyi* was a more likely candidate for modern human ancestry (Groves, 1989; Clarke, 1990, 1994; Wood, 1991, 1994; Tattersall, 1995). *H. ergaster* and *H. erectus* would be closely related sister species, or *H. ergaster* may be ancestral to *H. erectus*. Clarke (1990) proposed that *H. erectus* s.s. and ‘*H. leakeyi*’ diverged at least 1.5 Ma and that populations of *H. habilis* gave rise to *H. erectus* s.s. and ‘*H. leakeyi*’ separately in Africa and Asia. The same evolutionary transitions noted earlier for African *H. erectus* also roughly apply to *H. ergaster* and ‘*H. leakeyi*’: they may have been ancestral to species of ‘archaic’ *H. sapiens*

like *H. heidelbergensis* or *H. antecessor*. A more recent proposal by Clarke (2000a) reasserted the claim that *H. erectus* s.s. evolved outside of Africa but in a departure from his earlier scenario, he recognized *H. ergaster* in Africa and characterized OH 9 and Ceprano as evidence of *H. erectus* s.s. migration into Africa and Europe. He also took the unusual stance that *H. erectus* s.s. was on the lineage leading to Neanderthals while *H. ergaster* was ancestral to modern humans. According to this scenario, the last common ancestor of humans and Neanderthals was around 2 Ma, a perspective which is inconsistent with a human – Neanderthal DNA sequence divergence date of ~700-465 Ka (Krings *et al.*, 1997, 1999; Green *et al.*, 2006; Noonan *et al.*, 2006).

In addition to recognizing *H. ergaster*, a minority of workers also prefer to place the fossils from Dmanisi into their own species, *H. georgicus*, which would be closely related to early *Homo*. According to Gabounia *et al.* (2002) and de Lumley *et al.* (2006), the affinities of *H. georgicus* lie closer to *H. habilis* / *rudolfensis* than to *H. erectus*. This decision was initially based on mandibular evidence from D 211 and particularly D 2600 (Gabounia *et al.*, 2002). More recent craniofacial analysis found further differences between the Georgian fossils on one hand and *H. habilis* / *rudolfensis* and *H. erectus* / *ergaster* on the other. The lower sagittal profile of the neurocranium, narrow occipital, less robust facial architecture, and details of the mastoid and petrotympanic regions of the temporal bone all serve to distinguish the Dmanisi population from *H. erectus* (de Lumley *et al.*, 2006). There has yet to be a systematic examination of the relationships among *H. georgicus* and other species of *Homo*.

The fossil calvaria from Ceprano, Italy was initially assigned to *H. erectus* and later hypothesized to be an adult *H. antecessor*. Later analysis concluded that the

Ceprano fossil is intermediate between early African *H. erectus* (*H. ergaster*) and Middle Pleistocene *Homo* (Manzi *et al.*, 2001). Particular features linked Ceprano to African specimens like Bodo, Kabwe and Saldanha, rather than European fossils like Arago or Peralona. Manzi *et al.* hypothesized that Ceprano represented a late Early Pleistocene migration of an African population which was then replaced by later migrations (pre-Neanderthals). The population which was ancestral to Ceprano also gave rise to specimens like Bodo and Kabwe. Derived features linking Ceprano to African and European Middle Pleistocene *Homo* include reduced postorbital constriction, a lack of midline or coronal keeling, and a higher and more arched temporal squama while traits related to the supraorbital torus, like mid-orbital “torsion” and “the discontinuous thickness of the torus” link it more specifically with African Middle Pleistocene specimens like Kabwe, Saldanha and Bodo (Manzi *et al.*, 2001, p. 10015). They argued that Ceprano may represent the adult morphology of *H. antecessor* though a less parsimonious option is the existence of two European *Homo* species in this time period.

Because it is difficult to evaluate the former given the incomplete and juvenile status of the *H. antecessor* hypodigm, Mallegni *et al.* (2003) proposed the latter option. Emphasizing both the more derived aspects of the Ceprano cranial anatomy and the unique features of the frontal bone not shared with Middle Pleistocene *Homo* from Africa or Europe (*H. heidelbergensis*), they argued for a separate species diagnosis for Ceprano, *H. cepranensis*. Ceprano was differentiated from Middle Pleistocene *Homo* by the “complex morphology of the frontal, especially in the toral area in which Ceprano shows a slight groove separating the supraciliar relief from the supratotal sulcus” (Mallegni *et al.*, 2003, p. 156).

Multiple species and even genera are sometimes also recognized within the Javan sample. Jacob (1973, 1978) maintained the use of *Pithecanthropus*, which included three species, *P. modjokertensis*, *P. erectus* and *P. soloensis*. Though Sartono (1975) followed a similar taxonomic scheme, recognizing (in geochronological order) *P. dubius*, *P. modjokertensis*, *P. erectus* and *P. ngandongensis*, he states these names are just used “to separate various fossil men scattered over an extensive region and of different geologic ages, while keeping in mind that they all belong to *Homo erectus*” (p. 346). Numerous workers have also separated the Javanese and Chinese material at the species level, including Howell (1999) and Cameron *et al.* (2004). Within China, a distinction is sometimes made between the Zhoukoudian and Lantian samples at the species level (Sartono, 1975). In addition to *Pithecanthropus*, both workers recognized a second genus and species, *Meganthropus palaeojavanicus*, for fragmentary mandibular remains.

Meganthropus specimens are larger and more robust than other fossils and come from early in the Sangiran dome sequence, from the Sangiran (Pucangan) Formation. Tyler *et al.* (1995) also attribute some cranial remains to *Meganthropus* (Sangiran 31 and an occipital fragment). Robinson (1953) first noted resemblances between these mandibular fragments and robust australopithecines, and a small number of workers have maintained that *Meganthropus* was more closely related to *Australopithecus* or early *Homo* than *H. erectus* (Tobias and von Koenigswald, 1965; Krantz, 1975; Franzen, 1985; Tyler *et al.*, 1995). As discussed above, this position has been opposed by many workers who agreed that these fossils belonged within *H. erectus*, and *Meganthropus* is not used here (Lovejoy, 1970; Kramer and Konigsberg, 1994; Kramer, 1994).

Several Indonesian researchers have focused on the evolutionary process within Javanese *H. erectus*. In addition to the Ngandong calvaria, Jacob (1975, 1978) also includes the Sm 1 and S 17 fossils in *P. soloensis* and suggests that these are the direct descendants of *P. modjokertensis* (which also includes some mandibulo-dental remains). This speciation event may have occurred at the beginning of the Middle Pleistocene.

Though the use of multiple nomina was introduced to clarify which fossils were being discussed, the taxonomy used in Sartono (1975), with multiple genera, species, subspecies and types is actually quite unclear. It is my interpretation that Sartono (1975) recognized two subdivisions within *H. erectus*: a smaller-brained (Sangiran 1, 2, 3, 4, 12, Modjokerto, Lantian?) and a larger-brained (Sangiran 17, Zhoukdoudian, Ngandong) group. He suggested that the smaller-brained subspecies chronologically preceded the larger one (though they likely overlapped in the late Middle Pleistocene), and both may have had wide Asian, and even African (if *H. habilis* is included in the smaller-brained subspecies) distributions. He suggests either an ancestor-descendant relationship among the small-brained and large-brained groups (separately in Java and China) or the genesis of the large-brained group outside of Java and the eventual absorption / replacement of the smaller-brained populations (Sartono, 1975). He clearly favored the former. Further, the large-brained populations may have been ancestral to at least some Australian groups (e.g., Kow Swamp).

Critique: Most researchers do not recognize multiple species or genera within Asia, nor do they accept '*H. leakeyi*', *H. georgicus* or *H. cepranensis*. Contra Clarke (1990, 1994), most workers would not accept Stw 53 and OH 9 as representing the same species, but

would place the Sterkfontein fossil in an earlier species of *Homo*. Indeed, in a more recent scenario, Clarke (2000a) abandoned *H. leakeyi* in favor of *H. ergaster*, positing OH 9 as evidence of migration into Africa from Asia. Also, at least one of the five temporal traits listed in support of '*H. leakeyi*' must be questioned. The presence of a roughened inferior surface of the petrous pyramid has been described for Ngandong 7 and 12, and is therefore not restricted to the African sample (Rightmire, 1990). The many unique *H. erectus* traits like an angular torus, midline keeling and an angled occipital found in the Dmanisi fossils argue strongly for their inclusion as basal members of this species. The very minor distinctions between *H. cepranensis* and other European Middle Pleistocene *Homo* seems tenuous evidence upon which to base the creation of a new species. In general quantitative analyses, while recognizing regional variation within Asia, do not support species or genus level differences (e.g., Kramer, 1994; Antón, 2002; Kaifu *et al.*, 2005).

While *H. ergaster* is more widely recognized, there are also arguments against the recognition of this species which are perhaps best summarized by Walker (1993). The primary criticism is that variability within a species can result in autapomorphies which can then be mistaken for interspecific variation. A serious criticism of a cladistic / PSC approach to species identification is that species should be identified *prior* to phylogenetic analysis and not as the result of this analysis (Harrison, 1993; Manzi *et al.*, 2003). It is also unclear what the new African fossils will mean for the two species model. There is evidence that some of the 'Asian' autapomorphies are also found in recently-described African specimens, and Asfaw *et al.* (2002) argued that Daka blurs the distinction between Asian and African forms.

Grade within *Homo sapiens*: Around the same time that le Gros Clark and Mayr began the ‘lumping’ trend by moving *Pithecanthropus*, *Sinanthropus*, *Telanthropus* and *Atlanthropus* into *H. erectus*, Weidenreich espoused a different point of view: groups of modern humans evolved from archaic populations of *Homo* in their respective regions. He found the strongest evidence of these transitions in Australasia and Africa and to a lesser extent in China (Weidenreich, 1943). In Australasia, he saw continuity from *Pithecanthropus* to *Homo soloensis* to current day Australian aborigines. Some of the features he listed in support of this lineage were a strongly developed supraorbital region with a flat, receding frontal squama, a “torus-like demarcation line between occipital and nuchal plane” and a flexed occipital bone (Weidenreich, 1943, p. 249). Phyletic evolution also explained the transition from populations represented by Kabwe to Florisbad to Boskop and finally to modern South Africans. He does not find many similarities between the Zhoukoudian Upper Cave modern humans and the *H. erectus* (*Sinanthropus*) fossils from the Lower Cave but does mention shoveling of (especially lateral) maxillary incisors, sagittal keeling, Inca bones and several facial features that link Chinese *H. erectus* with later Mongolian, Eskimo and Amerindian groups.

Weidenreich’s polycentric view of human evolution lies at the core of more recent arguments made by Wolpoff and colleagues (Thorne and Wolpoff, 1981; Jelínek, 1982; Frayer *et al.*, 1993; Wolpoff *et al.*, 1984; 1994). They have argued for regional continuity between *H. erectus* and local populations of modern humans, particularly in China and Australasia while other forms of archaic *Homo* (e.g. Neanderthals) are ancestral to local modern human populations in Africa and Europe. According to this viewpoint, *H. sapiens* emerged when forms like ER 3733 first appear in the fossil record,

migrated across the Old World and became regionally differentiated but maintained a single gene pool by virtue of genetic exchange up to the present day. Inter-regional variations, coupled with intra-regional homogeneity, result from evolutionary processes described as the “center and edge” hypothesis (Thorne and Wolpoff, 1981). After the initial expansion of hominins from Africa around 2 million years ago, the peripheral populations became less variable as a result of local selection and genetic drift. Gene flow between regions (i.e., a trellis model) maintained stability within the gene pool and prevented allopatric speciation. Because the traits defining this lineage relative to earlier *Homo* are found in individuals from both *H. erectus* and *H. sapiens*, no cladogenetic event characterized the origin of modern humans. Therefore, *H. erectus* and *H. sapiens* are not separate species, but rather a “single evolutionary species” – *H. sapiens* (Wolpoff *et al.*, 1994, p. 341).

Within Australasia, continuity can be seen in the following sequence: Sangiran / Trinil to Sambungmacan to Ngandong to earlier (Willandra Lakes and Lake Mungo) and finally to later (Kow Swamp, Keilor, and Wadjak) Australian / Indonesian modern humans. There are strong similarities within the Indonesian fossil sample with the Ngandong, Sambungmacan and Ngawi fossils differing from earlier Javanese specimens primarily in their larger size (Frayer *et al.*, 1993), but also in their increased cranial height and more parallel sides of the vault, less rectangular, more square-shaped parietal bones and the expansion of the frontal and occipital regions of the brain (Wolpoff, 1999). A unique combination of 12 traits which were shared among the *H. erectus* and modern human groups supports a regional evolutionary sequence in Australasia (Frayer *et al.*, 1993) as summarized in Table 1.2. Nearly half of these traits (5/12) are related to the

face despite the fact that Sangiran 4 and 17 are the only Indonesian hominins to preserve a facial skeleton, and Sangiran 4 is only a lower face.

Table 1.2: Morphological features cited by Frayer *et al.* (1993) that indicate genetic continuity in Australasia and China.

Australasia	China
thickened vault bones	smaller facial skeleton
long flat frontal squama	smaller teeth
prominent, straight supraorbital tori with no posttoral sulci	horizontal and flaring cheeks located anteriorly
minimum frontal breadth positioned posteriorly	rounder forehead region separate from brow ridges
prebregmatic eminence	frontal process of maxilla is anteriorly oriented
large faces that project anteriorly	distinct paranasal inflation
large, anterolaterally oriented cheek bones	often have incisura malaris
large postcanine teeth	often have shovelled incisors
inferior edge of orbits rounded	

In terms of neurocranial, supraorbital and basicranial anatomy, the Ngandong hominins approach late Pleistocene *H. sapiens* in their reduced post-orbital constriction, a smaller supraorbital torus with a glabellar depression, a better-defined articular eminence, an expanded occipital and reduced nuchal plane (Hawks *et al.*, 2000; Wolpoff *et al.*, 2001). Also, Willandra Lakes Hominid 50 (WLH-50) was found to resemble the Ngandong hominins more closely than early African or Middle Eastern modern humans in non-metric features. The three traits specifically cited that connect these two groups

exclusively are “a transversely extensive nuchal torus, a projecting inion and a lateral frontal trigone” (Hawks *et al.*, 2000, p. 19). This study also found that WLH-50 grouped with Ngandong in a discriminant function analysis of five metric features, one of which was thickness of the parietal eminence.

There may also have been morphological continuity from Chinese *H. erectus* fossils to Middle Pleistocene specimens like Dali and Jinniushan and finally to modern Chinese people (Wolpoff *et al.*, 1984; Wu, 1988, 1990; Pope, 1991, 1992; Frayer *et al.*, 1993). The features that united this evolutionary sequence were mainly facial (listed in Table 1.2), despite the relative dearth of facial bones in the Zhoukoudian collection. Overall the faces were smaller and less robust with more anteriorly located, flat and flaring cheeks with malar notches and the frontal processes of the maxilla are flat. The teeth were smaller and there was a high frequency of upper incisors that were shoveled in both the living and fossil groups. The frontals were bossed and there were supratatorial sulci separating the tori from the frontal squama. According to Frayer *et al.* (1993), this set of features separates the present day modern humans from Australia and China, in the same way that it separated the corresponding hominin populations in the past.

The case made by Frayer *et al.* (1993) for regional continuity from *H. erectus* through modern Africans is considerably weaker, although the fossil record is equally strong in this part of the world (Stringer and Bräuer, 1994). Frayer *et al.* (1993) did not list any features which characterize this transition, though they argued that Africa represents the center of the “center and edge” hypothesis, and, as such, might be expected to show increased variation relative to other, more peripheral populations. A recent argument was made for continuity in India between Narmada and local populations of

modern humans though this was not supported by any real analysis (Sonakia and de Lumley, 2006).

Critique: This model has been criticized on several grounds. Genetic evidence, while not entirely unambiguous, provides more support for a single, recent (and probably African) origin for modern human populations (as reviewed by Howell, 1999). Secondly, a number of workers found the features proffered to define the various regional transitions to be either more widely distributed or to be primitive features (Stringer, 1992; Lahr, 1994, 1996). When Hawks *et al.* (2000) and Wolpoff *et al.* (2001) evaluated the affinities of WLH-50 using non-metric features, they did not examine other modern human populations, and the pairwise distance analysis was criticized on several grounds by Bräuer *et al.* (2004). In the metric analysis of WLH-50 the thickened diploë is responsible for the thicker cranial bones whereas both the diploë but especially the tabular bone is thick in *H. erectus* (Weidenreich, 1943; Kennedy, 1991; Brown, 1992). In addition, it is possible that the increased cranial bone thickness of WLH-50 is pathological (Brown, 1989; Webb, 1990). The metrical association of WLH-50 with Ngandong may, therefore, be based in part on a non-homologous thickening of the cranial bone at the parietal eminence but may also reflect the large size of both the Ngandong and WLH-50 specimens, which is of questionable phylogenetic value. Artificial deformation of some aboriginal Australian crania may also explain similarities in the frontal region to *H. erectus* (Brothwell, 1975; Brown, 1981).

Finally, the chronology of modern human fossils seems to support an African origin for modern humans, as the oldest modern humans are from African sites like

Herto, and maybe Omo Kibish, Ethiopia between 195 and 150 ka (White *et al.*, 2003; McDougall, *et al.*, 2005) and the next oldest are in the Middle East (Skhul and Qafzeh, Israel) around 135-100 ka (Grün *et al.*, 2005).

Dissertation overview

It is clear from the above review that there are several major gaps in our current knowledge about *H. erectus*. This primary questions addressed by this study are: 1) how many species are represented by the fossil sample commonly attributed to *H. erectus*?; 2) what aspects, if any, of cranial shape are unique to *H. erectus* versus those facets of shape shared with earlier or later *Homo* taxa?; 3) what type of shape change occurred at proposed evolutionary transitions along the *Homo* lineage, particularly at those nodes involving *H. erectus*?; and 4) how is the intraspecific variation in *H. erectus* patterned in regard to geography, geological age and size? Chapters 2-4-were designed to be semi-autonomous but still inter-related. Each of these three chapters addresses particular questions using carefully designed subsets of specimens and landmarks / curves. Therefore, details pertaining to the entire sample and to the full landmark / curve protocol employed are provided below.

Data collection

In order to address these questions, data were collected from a wide range of fossil hominins assigned to *H. erectus* from Africa, Europe and Asia (Table 1.3), as well

as the most complete representatives of early *Homo* (*H. habilis*, *H. rudolfensis*), middle Pleistocene *Homo* (*H. mauritanicus*, *H. rhodesiensis*, *H. heidelbergensis*) and Neanderthals (Table 1.4). In addition, comparative data were also collected from a large modern human sample (Table 1.5). Data were collected from 20 to 51 adult individuals from each modern human group, with approximately equal numbers of males and females represented.

Table 1.3: *Homo erectus* sample, organized geographically. The completeness of each specimen in terms of the preservation of 3D landmarks is noted, as are relevant notes about the fossils, and the institution where the original fossils are housed

Region	Specimen	% of unique 3D landmarks	Notes	Institution*
Africa				
Tanzania				
	Olduvai Gorge			
	OH 9	51%		NMT
	OH 12	20%	multiple pieces	NMK
Kenya				
	Koobi Fora			
	ER 3733	83%		NMK
	ER 730	9%	multiple pieces	NMK
	ER 2598	N/A	small fragment	NMK
	Ileret			
	ER 3883	69%		NMK
	ER 42700	59%	subadult	NMK
	Olorgesailie			
	OL 45500	36%	multiple pieces	NMK
	West Turkana			
	WT 15000	82%	subadult	NMK
Ethiopia				
	Daka			
	BOU-VP 2/66	59%		NME
South Africa				
	Swartkrans			
	SK 847	56%		TM
Europe / Caucasus				

Georgia				
Dmanisi				
	D 2280	49%	cast	GSM
	D 2282	67%	cast	GSM
	D 2700	92%	cast	GSM
	D 3444	72%	cast	GSM
Asia				
Indonesia				
Trinil				
	Trinil 2	17%		NM
Sangiran dome				
	S 3	5%		SM
	S 2	45%		SM
	S 12	18%	cast	ITB
	S 10	18%		GMU
	S 17	81%	cast	ITB
	S 4	60%	multiple pieces	SM
	S 27	20%	multiple pieces	GMU
Mojokerto / Perning				
	Mojokerto 1 (Perning 1)	42%	child	GMU
Sambungmacan				
	Sm 1	45%		GMU
	Sm 3	50%		GMU
Ngandong				
	Ng 1	41%		GMU
	Ng 2	N/A	subadult	GMU
	Ng 3	14%		GMU
	Ng 4	N/A	fragmentary	GMU
	Ng 5	22%		GMU
	Ng 6	53%		GMU
	Ng 7	58%		GMU
	Ng 8	N/A	subadult, fragmentary	GMU
	Ng 9	9%		GMU
	Ng 10	46%		GMU
	Ng 11	55%		GMU
	Ng 12	56%		GMU
Ngawi				
	Ngawi	49%	cast	MMT
China				

Zhoukoudian				
Zkd 3	51%	cast	AMNH	
Zkd 2	26%	cast	AMNH	
Zkd 5	44%	cast	AMNH	
Zkd 10	35%	cast	AMNH	
Zkd 11	50%	cast	AMNH	
Zkd 12	49%	cast	AMNH	
Reconstruction	76%	Tattersall and Sawyer, 1996		AMNH

* Institution abbreviations are as follows: AMNH - American Museum of Natural History, NHM - Natural History Museum, NMK - Kenya National Museum of Kenya, NME - National Museums of Ethiopia, NMT - National Museums of Tanzania, TM - Transvaal Museum, GSM - Georgian State Museum, NM - Naturalis Museum, SM - Senckenberg Museum, ITB - Institute of Technology Bandung, GMU - Gadjara Mada University, MMT - Museum Mpu Tantular.

Table 1.4: Sample of non-*erectus* *Homo* fossils, organized geographically. The consensus taxon, as well as the percentage of landmarks collected is indicated for each fossil. The completeness of each specimen in terms of the preservation of 3D landmarks is noted, as are relevant notes about the fossils, and the institution where the original fossils are housed.

Region	Specimen	% of unique 3D landmarks	Taxon	Notes	Institution*
Africa					
Tanzania					
Olduvai Gorge					
	OH 5 ¹	91%	<i>P. boisei</i>		NME
	OH 13 ¹	28%	<i>H. habilis</i>	multiple pieces	NMK
	OH 16 ¹	26%	<i>H. habilis</i>	multiple pieces	NMK
	OH 24	79%	<i>H. habilis</i>		NMK
Laetoli					
	LH 18 ¹	71%	<i>H. heidelbergensis</i>	multiple pieces	NMT
Ndutu					
	Ndutu	58%	<i>H. heidelbergensis</i>		NMT
Kenya					
Koobi Fora					
	ER 406	85%	<i>P. boisei</i>		NMK

	ER 407	41%	<i>P. boisei</i>		NMK
	ER 732	56%	<i>P. boisei</i>		NMK
	ER 13750	45%	<i>P. boisei</i>		NMK
	ER 17400	46%	<i>P. boisei</i>		NMK
	ER 23000	49%	<i>P. boisei</i>	multiple pieces	NMK
	ER 1470	55%	<i>H. rudolfensis</i>		NMK
	ER 1805	59%	<i>H. habilis?</i>	multiple pieces	NMK
	ER 1813	86%	<i>H. habilis</i>		NMK
West Turkana					
	WT 17000	83%	<i>P. aethiopicus</i>		NMK
Chesowanja					
	CH 303/304	N/A (too fragmentary)	<i>P. boisei</i>		NMK
Eliye Springs					
	ES 11693	53%	<i>H. heidelbergensis</i>		NMK
Ethiopia					
Omo Kibish					
	Omo 323 a-i ¹	47%	<i>P. boisei</i>		NME
	Omo 1	17%	<i>H. sapiens</i>		NME
	Omo 2	49%	<i>H. heidelbergensis</i>		NME
Bodo					
	Bodo	59%	<i>H. heidelbergensis</i>		NME
	Bodo VP	N/A (parietal)	<i>H. heidelbergensis</i>		NME
Morocco					
Salé					
	Salé	60%	<i>H. heidelbergensis</i>	Pathology in nuchal region	MPI
South Africa					
Sterkfontein					
	Stw 53	49%	Early <i>Homo</i>	multiple pieces	UW
Saldanha					
	Saldanha	23%	<i>H. heidelbergensis</i>		SAM
Klasies River Mouth					

	AP 6269 (temporal)	7%	<i>H. sapiens</i>		SAM
	AP 6098, 6103, 6222	N/A (fragments)	<i>H. sapiens</i>		SAM
	Fish Hoek				
	AP 4692	88%	<i>H. sapiens</i>		SAM
Zambia					
Kabwe					
	Kabwe	92%	<i>H. heidelbergensis</i>		NHM
Europe					
Greece					
Petalona					
	Petalona	88%	<i>H. heidelbergensis</i>		UT
France					
Arago					
	Arago 21	54%	<i>H. heidelbergensis</i>		MT
	Arago 47 (parietal)	5%	<i>H. heidelbergensis</i>		
La Ferrassie					
	La Ferrassie	82%	Neanderthal	cast	MH
La Chapelle					
	La Chapelle	76%	Neanderthal	cast	MH
Cro Magnon					
	Cro Magnon 1	86%	<i>H. sapiens</i>	cast	MH
	Cro Magnon 2	30%	<i>H. sapiens</i>	cast	MH
Abri Pataud					
	Abri Pataud	94%	<i>H. sapiens</i>	cast	MH
Spain					
Atapuerca -TD6					
	ATD6-69	36%	<i>H. antecessor / mauritanicus</i>		MNCN
	Other ATD6 fragments	4-9%, each	<i>H. antecessor / mauritanicus</i>		MNCN
Gibraltar (UK)					
	Gibraltar	68%	Neanderthal		NHM
Italy					
Ceprano					
	Ceprano	38%	<i>H. antecessor / mauritanicus</i>		UR
Saccopastore					

	Saccopastore 1	81%	Neanderthal		UR
	Saccopastore 2	72%	Neanderthal		UR
England	Swanscombe				
	Swanscombe	19%	Neanderthal		NHM
Middle East					
Israel	Jebel Irhoud				
	Jebel Irhoud 1	65%	<i>H. sapiens</i>	cast	MA
	Jebel Irhoud 2	41%	<i>H. sapiens</i>	cast	MA
	Jebel Qafzeh				
	Qafzeh 6	69%	<i>H. sapiens</i>	cast	IPH
	Qafzeh 9	58%	<i>H. sapiens</i>	cast	RM
	Skhul				
	Skhul 5	86%	<i>H. sapiens</i>		PM
	Skhul 6	17%	<i>H. sapiens</i>		PM
Australasia					
Indonesia	Wadjak, Java				
	Wadjak 1	78%	<i>H. sapiens</i>		NM
	Wadjak 2	N/A (too fragme ntary)	<i>H. sapiens</i>		NM
	Liang Bua, Flores				
	LB 1	88%	<i>H. floresiensis</i>	stereolith print out	PPA
China					
Dali	Dali	65%	Late <i>Homo</i>	cast	IVPP
Liujiang	Liujiang	85%	<i>H. sapiens</i>	cast	IVPP
Australia	Willandra Lakes				
	WLH-50	27%	<i>H. sapiens</i>	cast	-
	Kow Swamp				
	Kow Swamp 17	24%	<i>H. sapiens</i>	cast	-

* Institution abbreviations are as follows: AMNH - American Museum of Natural History, PM – Peabody Museum, NHM - Natural History Museum, NMK - Kenya National Museum of Kenya, NME - National Museums of Ethiopia, NMT - National Museums of Tanzania, TM - Transvaal Museum, UW - University of the Witwatersrand, SAM - Iziko: South African Museum, GSM - Georgian State Museum, MT - Musée de Tautavel Centre Européen de Préhistoire, MH - Musée de L’Homme, MPI - Max Planck Institute for Evolutionary Anthropology, UR - Università’ di Roma, NM - Naturalis Museum, SM - Senckenberg Museum, UT - University of Thessaloniki, MA – Musée Archéologique, RM – Rockefeller Museum, IPH – Institut de Paléontologie Humaine, ITB - Institute of Technology Bandung, GMU - Gadjadara University, MMT - Museum Mpu Tantular, PPA - Pusat Penelitian Arkeologi.

Table 1.5: Recent (Holocene) *Homo sapiens* sample. The North African sites of Afalou and Taforalt are about 10 ka and thus are terminal Pleistocene / early Holocene in age.

Population	Sample size	Institution*
Afalou / Taforalt (Morocco and Algeria)	33	IPH
Andaman Islands	32	NHM
Aboriginal Australians	46	NHM, AMNH, DC
Greifenberg, Austria	51	AMNH
Khoe-San, South Africa	37	UCT, AMNH
Mixed Asian	33	AMNH
Grand Gulch, Utah	48	AMNH
Ipiutak, Alaska	49	AMNH
Lachish, Palestine	34	NHM
Mongolia	20	AMNH
Teita, Kenya	34	DC
Total	417	

* Institution abbreviations are as follows: AMNH – American Museum of Natural History, NMH – Natural History Museum, DC – Duckworth Collection, University of Cambridge, UCT – University of Cape Town.

Table 1.6: Complete list of cranio-facial landmarks and curves collected. Both abbreviations and definitions are provided.

Landmark	Abbr.	Definition	Ref.
<i>Dorsal Landmarks</i>			
Inion	IN	point at which the superior nuchal lines merge in the external occipital protuberance (or linear tubercle)	2
Opisthocranium	OPC	the most posterior midline ectocranial point	
Lambda	LA	the apex of the occipital bone at its junction with the parietals, in the midline; there is often an intercalary or apical bone at the site, in which case lambda is to be found by extending the general curving course of each half of the lambdoid suture to their intersections with the midline (or halfway b/t these intersections)	1
Apex	AP	ectocranial midline point placed where a coronal plane through the right and left poria meet the midsagittal plane superiorly	2
Bregma	BR	posterior border of the frontal bone in the midline; the sutures may meet with rounded external edges, resulting in a cleft or depression at their junction. Bregma is then to be established “in the air,” i.e., at its correct position but at the level of the general surface of the bone	1
Midline post-toral sulcus	PTS	minima of concavity on midline post-toral frontal squama	6
Glabella	GL	most anterior midline point on the frontal bone, usually above the frontonasal suture	2
Nasion	NA	the intersection of the fronto-nasal suture and the median plane; if there is irregularity near the midline, rectify the general curve of the fronto-nasal suture so as to find the correct level for nasion	1
Rhinion	RH	midline point at the inferior free end of the internasal suture	2
Anterior nasal spine	ANS	thin projection of bone on the midline at the inferior margin of the nasal aperture	2
Alveolare	AL	midline point at the inferior tip of the bony septum between the upper central incisors	2
Infraorbital foramen	IF	Most superior point on the infraorbital foramen (located inferior to the orbit on the maxilla)	2

Alare	ALR	the most lateral point on the margin of the nasal aperture	2
Zygomaxillare	ZM	most inferior point on the zygomaticomaxillary suture	2
Zygoorbitale	ZO	point where the orbital rim intersects the zygomaticomaxillary suture	2
Dacryon	DA	point where the lacrimomaxillary suture meets the frontal bone	2
Supraorbital notch	SON	point of greatest projection of notch into the orbital space, taken on the medial side of the notch; if there is a foramen, take on the orbit on the lateral side of the foramen	6
Orbitale	OR	the lowest point on the orbital margin	2
Frontomalare temporale	FMT	point where the frontozygomatic suture crosses the temporal line (or outer orbital rim)	2
Frontomalare orbitale	FMO	point where the frontozygomatic suture crosses the inner orbital rim	2
Mid-torus inferior	MTI	point on inferior margin of supraorbital torus roughly at the middle of the orbit (on superior margin of orbit)	3
Mid-torus superior	MTS	point on superior aspect of supraorbital torus, directly above mid-torus inferior on anterior aspect of torus, before it slopes back to the frontal squama	3
Frontosphenomolare	FSM	point on external cranial vault where frontal, sphenoid and malar bones join	6
Anterior pterion	AP	where coronal suture intersects sphenofrontal or sphenoparietal suture	
Superior zygomatico-temporal suture	SZT	anterosuperior point of zygomaticomaxillary suture (taken at orbit rim)	3
Jugale	JG	the point in the depth of the notch between the temporal and frontal processes of the zygomatic	2
Porion	PO	uppermost point on the margin of the external auditory meatus	2
Auriculare	AU	a point vertically above the center of the external auditory meatus at the root of the zygomatic process, a few millimeters above porion	2
Infero-lateral ectotympanic tube superior	ETS	point on superior border of inferior margin of ectotympanic tube, directly inferior to porion	
Infero-lateral ectotympanic tube inferior	ETI	point on inferior border of inferior margin of ectotympanic tube, directly inferior to porion	

Malar root origin	MR	point where malar root arises from the maxilla (often a point of convexity between molar juga and malar root)	6
Root of the zygomatic process	ZP	Malar root origin projected onto inferior buccal alveolar surface	4
Coronale	CO	point on the coronal suture where the breadth of the frontal bone is greatest	2
Stephanion	ST	the intersection of the coronal suture and the limit of the temporal muscle (the inferior temporal line)	1
Frontotemporale	FT	the point where the temporal line reaches its most anteromedial position on the frontal	2
Parietal notch	PN	forms on the posterosuperior border of the temporal where the squamosal and pareitomastoid sutures meet	2
Asterion	AS	the common meeting point of the temporal, parietal, and occipital bones, on either side; if the meeting point is occupied by a wormian bone, extend the lambdoid suture onto its surface, and then extend the other two sutures (temporo-parietal, temporo-occipital) to the first line, finding asterion as the point midway between the intersections if these do not coincide; if the lambdoid (or other) suture is complex or composed of wormian bones, trace a line along the center of the area covered by the complexity, as well as can be done, to find the main axis of the suture	1
Posterior temporal line	PT	point of intersection of superior temporal line and suture (extrapolated if necessary); landmark usually falls on an area of raised bone between the parietal notch and asterion	

Ventral Landmarks

Opisthion	OP	midline point at the posterior margin of the foramen magnum	2
Basion	BA	midline point at the anterior margin of the foramen magnum	2
Hormion	HO	most posterior midline point on the vomer; taken on the basisphenoid directly below the posterior midline point of the vomer	2
Staphylion	SP	point on the interpalatal suture where a line drawn between the deepest parts of the notches (free edges) at the rear of the palate crosses the midline	2

Midline anterior palatine	MAP	Junction of palato-maxillary and inter-palatine sutures; if palato-maxillary sutures do not meet on the midline then take halfway between them	6
Incisvion	IV	midline point at posterior margin of the incisive foramen (oral)	6
Inferior zygomaticotemporal suture	IZT	anteroinferior point of zygomaticomaxillary suture, in antero-lateral view	3
Posterior occipital condyle	POC	most posterior point on long axis of occipital condyle, taken on condyle	
Anterior occipital condyle	AOC	most anterior point on long axis of occipital condyle, taken on condyle	
Mastoidiale	MA	most inferior point on the mastoid process	2
Occipitomastoid crest	OMC	most inferior point between mastoid notch and groove for the occipital artery (this may correspond to the juxtamastoid eminence or occipitomastoid crest)	
Tympanomastoid fissure	TM	point on lateral border of the tympanomastoid fissure	
Medial petrotympanic crest	MPT	most medial point of petrotympanic crest at level of carotid canal	5
Lateral petrotympanic crest	LPT	lateral origin of petrotympanic crest; if the petrotympanic crest splits, point is on posterior branch	5
Stylomastoid foramen	SF	posterior border of sylomastoid foramen	4
Anterior jugular fossa	AJF	most antero-medial point of the jugular fossa (anterior point on long axis of fossa)	4
Posterior jugular fossa	PJF	most postero-lateral point of the jugular fossa (posterior point on long axis of fossa)	4
Postglenoid	PG	Infero-lateral most point posterior to glenoid fossa and anterior to ectotympanic tube (corresponds to postglenoid tuberosity or postglenoid crest)	3
Inferior entoglenoid	IEG	most inferior point on the entoglenoid pyramid	4
Lateral articular fossa	LAF	deepest point on the lateral margin of the articular eminence (root of the articular eminence); *located on point of maximum concavity	4

Center of mandibular fossa	CMF	point of intersection of the long axis and the axis perpendicular to the long axis of the mandibular fossa	
Medial squamotympanic fissure	MST	intersection of squamotympanic fissure / petrotympanic fissure with medial edge of mandibular fossa	
Lateral squamotympanic fissure	LST	Intersection of squamotympanic fissure with lateral edge of mandibular fossa	
Foramen spinosum	FS	point on posterior margin of foramen spinosum	
Lateral hornion	LH	postero point on sphenoid in basal view, just anterior to the tip of the petrous pyramid of the tympanic	
Spheno-palatine suture	SP	suture between palatine and sphenoid bones (taken just posterior to alveolar tooth row)	4
Temporo-sphenoid suture	TS	point where temporo-sphenoid suture passes from squama to cranial base (often on infratemporal crest)	
Lateral prosthion	LP	equivalent to prosthion, but between central and lateral incisors	3
Lingual canine margin	LC	most lingual aspect of canine alveolar process	6
Canine-P3 contact	CP3	point of contact projected onto buccal alveolar surface	6
P3-P4 contact	P3P4	point of contact projected onto buccal alveolar surface	6
P4-M1 contact	P4M1	point of contact projected onto buccal alveolar surface	6
M1-M2 contact	M1-2	point of contact projected onto buccal alveolar surface	3
M2-M3 contact	M2-3	point of contact projected onto buccal alveolar surface	6
Distal M3	DM3	distal midpoint projected onto buccal alveolar surface	3
Maxillary tuberosity	MT	most posterior point on 'occlusal' surface of alveolus	6
Metopion	ME	point midway between glabella and bregma on the midline, extracted from midline curve <i>a postieri</i>	2
Mid-parietal	MP	point midway along the parietals on the midline, extracted from midline curve <i>a postieri</i>	

Mid-temporal squama	MTP	point midway along the temporal squama suture, extracted from the temporal squama curve <i>a postieri</i>
<i>Curves</i>		
Midsagittal Profile 1	MSP1	from glabella to bregma in a straight line; if bregma is not on the midline then extend the line to the midline as far back as bregma
Midcoronal Profile	MCP	from auriculare to apex in a straight line
Anterior Coronal Profile	ACP	from anterior pterion to bregma along coronal suture (approximate a straight line)
Temporal Line	TL	from frontotemporale to posterior temporal line along superior temporal line
Temporal Squama Profile	TSP	from temporo-sphenoid suture to parietal notch along temporal suture
Midsagittal Profile 2	MSP2	from bregma to opisthocranion, along midline
Lamboid Suture	LS	from asterion to lambda along lambdoid suture (approximate a straight line)
Oblique Parietal 1	OP1	from bregma to asterion through midparietal point
Oblique Parietal 2	OP2	from anterior pterion to lambda through midparietal point
Midsagittal Profile 3	MSP3	from opisthocranion to opisthion along midline
Supraorbital Torus	SOT	from frontomalarotemporale to midpoint above glabella, along superior edge of maximally protruding (in an anterior direction) part of supraorbital torus; if there is no anterior projection laterally, then create a smooth arc from frontomalarotemporale to the superior most point
Foramen Magnum	FM	from opisthion to basion, along rim, not on surface of condyle

¹ Howells, 1973 ² White and Folkens, 2000 ³ Frost, 2001 ⁴ Harvati, 2001 ⁵ Harvati, 2003 ⁶ McNulty, 2003

Data were collected from fossils and casts curated at institutions across the world (Tables 1.3 to 1.5). Similar data collected from large ape and cercopithecine samples by fellow colleagues in the NYCEP Morphometric Group (NMG, primarily Kieran McNulty and Stephen Frost) further provide an extensive comparative framework. These samples are described briefly in chapter 2. For more details on these samples, please refer to McNulty (2003) and Frost (2001).

A Microscribe 3-D digitizer was used to acquire a maximum of 131 three-dimensional landmarks (of which 114 were bilateral). The landmark protocol was based on the work of other NMG (NYCEP Morphometrics Group) members but additional landmarks were also designed. In particular, additional landmarks were incorporated from the base as there are several well-preserved basicrania in the *H. erectus* hypodigm. A set of curves were also collected. These curves were a series of semilandmarks taken at a high density along meaningful cranial contours like the midsagittal outline. By resampling these semilandmarks to the same number across all specimens, they could be treated as landmark data. An additional four landmarks, metopion, the mid-parietal and the mid-temporal squama (left and right), were calculated *a posteriori* as midpoints along ‘curves’ taken between glabella and bregma, bregma and lambda and along the temporal squama suture, respectively. Table 1.6 provides definitions and abbreviations of all landmarks and curves collected in this study, which are illustrated in Figure 1.2.

Organization of dissertation

I addressed *H. erectus* taxonomy primarily in chapters 2 and 4. In chapter 2, I evaluated claims for multiple species within the traditional *H. erectus* hypodigm from Asia, Africa and the Caucasus. The magnitude of intraspecific variation was assessed within a representative sample of *H. erectus* by use of pairwise Procrustes distances. Like the coefficient of variation (CV), a measure often used with traditional morphometric data, this approach focuses on the magnitude of intraspecific variation. By comparison of these interindividual distances within *H. erectus* to a wide range of other primate taxa, it was possible to test for differences in degree of intraspecific variation. This analysis was an important first step in quantifying overall variation within *H. erectus* and interpreting this variation within a larger primate context. It differed from past studies because it included a greater range of comparative taxa, it used a new metric (Procrustes distance) and it included a wider range of *H. erectus* fossils.

In addition to the magnitude of variation, the pattern of variation is also relevant to assessing claims of multiple species. Even if variation within the *H. erectus* sample is within the range of a single species, the presence of a strong African – Asian dichotomy in cranial shape (or, alternatively, an African – Asian / OH 9 dichotomy) would support claims for *H. ergaster*. Chapter 4 examines the geographic distribution of cranial shape variation and its implications for the *H. erectus* species question.

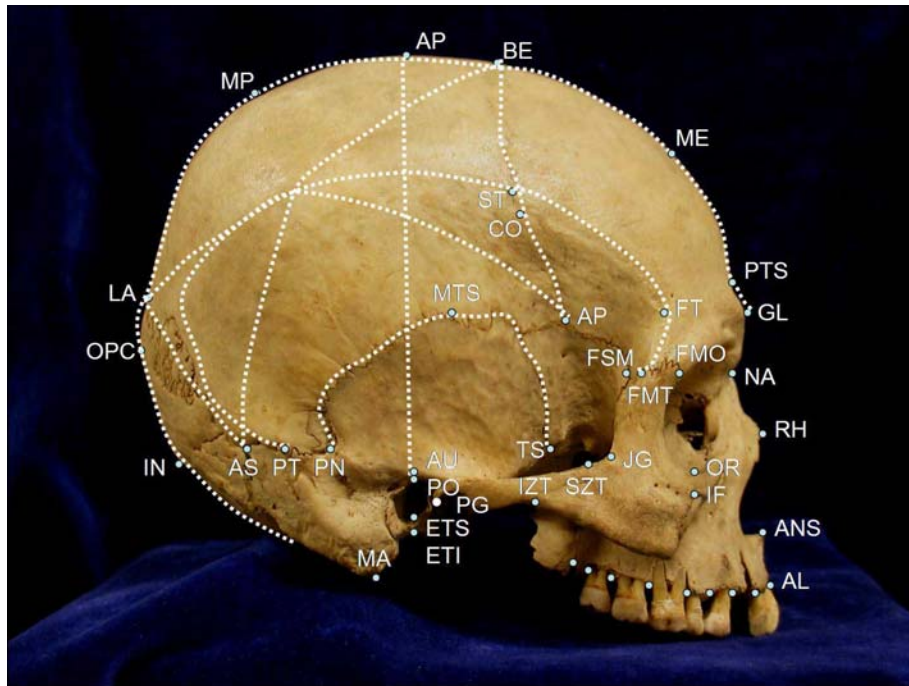
This dissertation also focuses on *H. erectus* taxonomy by contributing information about cranial shape to previous *H. erectus* species definitions. This aspect of *H. erectus* taxonomy is addressed specifically in chapter 3 by comparison of cranial shape in a

broad range of *Homo* taxa, including *H. habilis*, *H. rudolfensis* and numerous species of post-*erectus Homo*. While traditional species definitions (e.g., Weidenreich 1943, 1951; Le Gros Clark, 1955, 1964; Howell, 1978) have emphasized the more primitive aspects of *H. erectus* relative to modern humans, this thesis identified cranial shape characteristics that differed from more closely related *Homo* species including the likely ancestors of *H. erectus*. This approach allows for discrimination between ancestral and derived features of cranial shape as well as the identification of novel aspects of cranial shape. By comparing *H. erectus* to other species which are similar in their cranial architecture, such as *H. rhodesiensis*, it was possible to evaluate more controversial claims for *H. erectus* fossils in North Africa (e.g., Salé) and Europe (i.e., Ceprano), further delineating the species boundary of *H. erectus*.

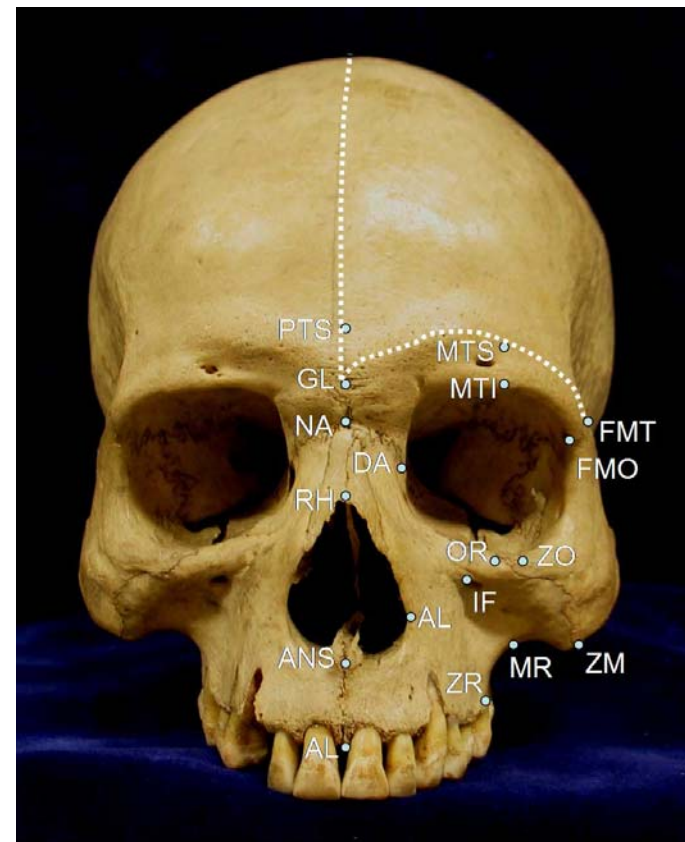
Despite taxonomic ambiguities, *H. erectus s.l.* occupies a key position in hominin phylogeny, and at least some populations were likely on the lineage leading to later *Homo* species including *H. sapiens*. While there is general agreement that *H. habilis* represents a likely ancestor for *H. erectus*, there is less agreement concerning the phylogenetic relationships among populations of *H. erectus* and later species of *Homo*. The major point of disagreement is whether Asian *H. erectus* was an evolutionary dead end, or whether these populations contributed significantly to the gene pool of modern humans in Southeast Asia / Australia. There is also considerable debate surrounding whether *H. erectus* was ancestral to the hominins found on Flores in 2003 and 2004 (Brown *et al.*, 2004; Morwood *et al.*, 2005). In chapter 3, I examined the proposed phylogenetic relationships of *H. erectus* and the implications of these phylogenies for the evolution of cranial shape in the genus *Homo*.

Figure 1.2: All landmarks and curves recorded illustrated on a modern human cranium. Abbreviations refer to Table 1.4 where descriptions of all landmarks and curves can be found. The cranium is shown in right lateral (a), anterior (b) and inferior (c) views. A detailed view of the temporomandibular joint is also provided in (c).

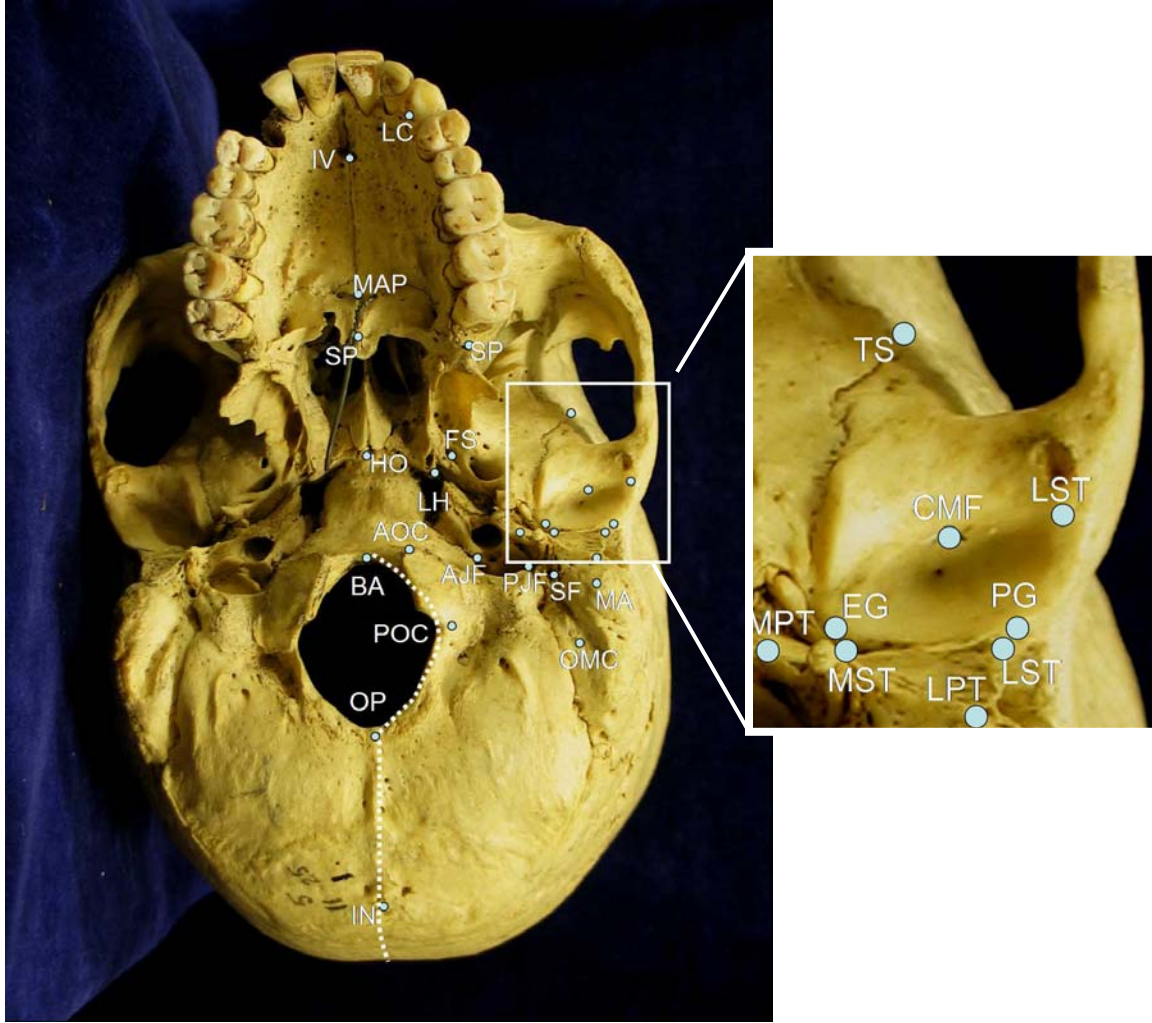
a)



b)



c)



Once the distinct cranial shape and composition of *H. erectus* were determined in chapters 2 and 3, it was possible to address intraspecific variation in the cranial shape of *H. erectus*. In chapter 4, I explored the relationship of cranial shape to temporal, geographic and size-related variation within this sample. As mentioned previously, these analyses had implications for the alpha taxonomy of *H. erectus* in terms of whether there were distinct African and Asian cranial morphs. These analyses also had implications for the population history of *H. erectus*. For example, it was possible to evaluate the proposed Indonesian - Chinese (particularly Zhoukoudian and Nanjing) dichotomy in terms of cranial shape (Antón, 2002). A second issue addressed was whether the Sambungmacan hominins represented an evolutionary intermediate between the Sangiran and Ngandong populations or whether they shared a closer relationship with the Ngandong hominins.

Broader implications of this research

This dissertation addressed a wide range of issues related to the taxonomy and evolution of *H. erectus* by focusing on variation in cranial shape within this taxon. This thesis is unique in several regards: it was the first application of 3D geometric morphometrics to a large sample of (mostly) original *H. erectus* fossils; the fossil *H. erectus* sample is comprehensive, incorporating specimens from Africa, Asia and Europe including newly described fossils from Kenya (ER 42700, OL 45500) and Ethiopia (Daka); and it evaluates *H. erectus* cranial shape by comparison to its closest evolutionary relatives rather than just *H. sapiens*. Determining the number of species

present within the large *H. erectus* sample is a necessary first step toward understanding both patterns of species diversity in, and reconstructing the evolutionary history of, Plio-Pleistocene *Homo*.

Fossils commonly attributed to *H. erectus* are geographically widespread, span a long time interval from 1.8 Ma to possibly 50 ka and exhibit a wide size range, making it an ideal hominin taxon in which to study geographic, temporal and size-related variation. The pattern of intraspecific variation has implications for other hominin taxa, as well. In particular, some of the disagreement concerning the status of many middle Pleistocene hominins in Africa, Europe and Asia (i.e., ‘archaic’ *Homo*) stems from an incomplete understanding of intra- versus inter-specific variation. Identifying those aspects of cranial shape which vary intraspecifically in a similarly widespread taxon may clarify the significance of variation in mid-Pleistocene *Homo*.

In nearly all proposed hominin phylogenies (e.g., Rightmire, 1990; Frayer *et al.*, 1993; Clarke, 2000a; Hublin, 2001; Lieberman, 2001), at least some populations of *H. erectus* are on the direct lineage leading to modern humans. However, there are also several unresolved issues related to the evolutionary history of *H. erectus*. While morphometrics was not designed to construct cladograms, shape data were useful in evaluating hypotheses concerning the population history of *H. erectus* (e.g., whether OH 9 represents a migration of *H. erectus* s.s. from Asia) and in clarifying the chronology of changes in cranial morphology during the evolution of *Homo*.

Chapter 2: Inter-individual Variation in *Homo erectus*: Taxonomic Implications

Introduction

The success of *H. erectus* is clearly demonstrated by both its wide geographic and long temporal range. At its most extensive, the geographic range of *H. erectus* extends from south, east and possibly north Africa through the Levant and the Caucasus east to China and Indonesia, though there are significant gaps in the record through mainland southern Asia. An alternative approach would limit the taxon to east Asia (or east Asia and Olduvai Gorge) while recognizing at least one other species, such as *H. ergaster* for the fossils from East Africa and the Caucasus. The earliest representatives of *H. erectus* are from East Africa and Georgia around the Plio-Pleistocene boundary, whereas Indonesian populations may have survived into the late Pleistocene, thus spanning nearly 1.9 Myr. *H. erectus* is also almost surely the first human species to disperse out of Africa into more temperate habitats, and it is likely that at least some populations within this larger taxon are on the lineage leading to modern humans.

Since 1991 the sample of *Homo erectus sensu lato* (including fossil specimens from Indonesia, China, the Caucasus and Africa) has been enlarged considerably, resulting in a greater geographic and morphological range. A considerable amount of material has been introduced recently from the Georgian site of Dmanisi, including at least four crania, all of which are smaller than the majority of traditional *H. erectus* fossils (Gabunia *et al.*, 2000b; Lordkipanidze *et al.*, 2005; Rightmire *et al.*, 2006; Lordkipanidze *et al.*, 2006). Like the Georgian fossils, new crania from the Kenyan sites

of Ileret (Leakey *et al.*, 2003; Spoor *et al.*, 2005) and Olorgesaille (Potts *et al.*, 2004), are considerably smaller than previously recognized *H. erectus* fossils, increasing the known size range of this taxon. Similarities to *H. erectus* have been noted in recent discoveries from the Ethiopian site of Bouri (Asfaw *et al.*, 2002) and the Eritrean site of Buia (Abbate *et al.*, 1998), though only the former has been placed within *H. erectus*. These specimens may extend the African distribution of *H. erectus* to the northeast and provide information about the taxon in the period around 1 Ma. The fossil calvaria from Ceprano, Italy may mark the first discovery of European *H. erectus* at ~700-800 Ka (Ascenzi *et al.*, 1996), though more recent analyses have suggested affinities with *H. antecessor* (Manzi *et al.*, 2001) or assigned it a new nomen, *H. cepranensis* (Mallegni *et al.*, 2003).

While some workers assign these new fossils to an expanded *H. erectus* hypodigm, others have raised concerns that the variation in the sample exceeds what is expected for a single, albeit polytypic and long lived species. It is possible that the entire *H. erectus* hypodigm samples a single, polytypic species, with some populations (namely those in Africa) giving rise to the modern human lineage (Delson, 1990; Bräuer, 1990; 1994; Rightmire, 1990; 1998b; Harrison, 1993; Asfaw *et al.*, 2002). Other researchers argue that the early material from Africa (and perhaps Georgia) should be given full species status separate from the primarily Asian *H. erectus* (Groves and Mazak, 1975; Wood, 1984, 1991, 1994, Andrews, 1984; Groves, 1989; Schwartz and Tattersall, 2003). This taxonomy is most compatible with the view that a cladogenetic event led to the divergence of *H. erectus*, which was an evolutionary dead end compared to *H. ergaster*, which in turn remains a candidate for later human ancestry (Leakey, 1961; Andrews,

1984; Clarke, 1994; Tattersall, 1997; Tattersall and Schwartz, 2000). Still others argue that the African, Georgian and Asian populations all represent separate species (Gabounia *et al.*, 2002; de Lumley *et al.*, 2006). The more extreme positions posit multiple species (or morphs) even within single '*H. erectus*' sites (Schwartz and Tattersall, 2003; Schwartz, 2004) or place *H. erectus* as a grade within *H. sapiens* (Weidenreich, 1943; Thorne and Wolpoff, 1981; Jelínek, 1982; Tobias, 1991; Wolpoff *et al.*, 1994). These reflect very different interpretations of evolutionary history: a relatively bushy Plio-Pleistocene *Homo* lineage, presumably with numerous terminal species or, conversely, local continuity and extensive gene flow among regional populations of 'archaic' *Homo* and later modern humans.

Weidenreich (1943, 1951) provided the first thorough descriptions of *H. erectus* cranial morphology, and subsequent species definitions have built on his work (e.g., Le Gros Clark, 1955, 1964; Howell, 1978; Rightmire, 1990; Antón, 2003). This fossil sample is linked together by a common cranial shape: a long low neurocranium with a tightly angled occiput and a receding frontal squama. They also share a maximum cranial breadth located at the level of the temporals, usually across the supramastoid crests and the superior border of the temporal squama is straight and positioned relatively low on the vault. Specimens assigned to *H. erectus* exhibit a certain amount of interindividual and interregional variation in the expression of cranial superstructures, but they generally have a prominent, continuous supraorbital torus, transverse occipital torus, midline keeling (on the frontal and / or parietals), marked supramastoid and mastoid crests and an angular torus at the mastoid angle of the parietal bone. More detailed anatomical features of the cranial base have also been identified that further define *H.*

erectus, such as the lack of an articular eminence, small postglenoid processes and thick petrotympanic crests. Though individuals representing *H. erectus* rarely preserve a facial skeleton, those that do share a high and robust zygomatic, prognathic alveolar region, projecting nasal region with a high nasal bridge, wide interorbital breadth and nasal bones, posteriorly located and obliquely oriented incisive canal and ‘sulcus maxillaris’ (also termed a ‘sulcus infraorbitalis’— a furrow like hollowing between the canine jugum and the anterior root of the zygomatic process) (Weidenreich, 1943; Franciscus and Trinkaus, 1988; Rightmire, 1998a; Wolpoff, 1999).

In order to accurately assess intraspecific variation within *H. erectus*, it is necessary to construct a sample which captures the full range of known variation within this species. The 13 *H. erectus* crania utilized here are from sites in East Africa (Koobi Fora, Ileret, Daka and Olduvai Gorge), the Caucasus (Dmanisi), Indonesia (Sangiran, Ngandong and Sambungmacan) and China (Zhoukoudian) (see Table 2.1). The only region excluded from this sample is South Africa. In addition to the fact that SK 847 is too incomplete to be considered here, it is unclear whether its affinities lie with *H. erectus* or with early *Homo* (Walker, 1981; Clarke, 1985; Grine *et al*, 1996). This sample also captures the full time range of *H. erectus* from the Plio-Pleistocene boundary to the Late Pleistocene. The fossil sample includes crania from both the small (e.g., D 2280) and large (e.g., Ngandong 6) end of the size spectrum.

It is equally important that variation in the *H. erectus* sample is not falsely inflated due to the inclusion of non-*erectus* individuals. Although ‘archaic’ *Homo* fossils from middle Pleistocene sites like Bodo, Ndutu, Kabwe, Petralona and Arago and even late Pleistocene sites (Omo II) have sometimes been included in *H. erectus* (Coon, 1963;

Table 2.1: *Homo erectus* sample.

Specimen	Age
Dmanisi 2280	1.7 Ma ¹ ; 1.81 ^{2,3}
KNM-ER 3733*	1.78 Ma ⁴ 1.65 Ma ⁵
KNM-ER 3883	1.57 ⁴
OH 9	1.5 Ma ⁶
Sangiran 17*	1.16-0.71 Ma ⁷ ; < 1.0 Ma ⁸ ~1.25-1.3 Ma ⁹ ; 0.9 – 1.4 Ma ¹⁰
Daka (BOU-VP-2/66)	~1 Ma ¹¹
Zhoukoudian 11 and 12*	418 Ka ¹² , 423 Ka ¹³ >600 Ka ¹⁴ ; 640 Ka ¹⁵
	1 Ma – 100 Ka ¹⁶
	----- Normal polarity corresponding to Jaramillo subchron (~1 Ma) or Brunhes chron (<780 Ka) ¹⁷ for Sm 1 findspot
Sambungmacan 3**	50-35 Ka ¹⁸ for Sm 1 findspot
	Lower Kabuh Formation ¹⁹ (~1 or ~1.5 Ma according to refs. 7 or 9) for Sm 2 findspot
	----- Mid-Pleistocene ²⁰
Ngandong 6, 10, 11 and 12*	100 Ka ²¹ 31 Ka ^{21, 22} ; 50-35 Ka ¹⁸

* Conflicting ages are listed on separate lines.

** Sambungmacan 3 (Sm 3) was described by Delson *et al.* (2001) after it was identified in a New York City natural history store and they considered the age to be essentially unknown, assigning a range of 1 Ma to 100 Ka. Ages for other Sambungmacan hominins are also provided under the dashed line, but these are not necessarily equivalent in age.

1 – Gabunia *et al.* (2000b); 2 – de Lumley *et al.* (2002); 3 – Gabounia *et al.* (2002); 4 – Feibel *et al.* (1989); 5 – Gathogo and Brown (2006); 6 – Delson and van Couvering (2000); 7 – Itihara *et al.* (1994); 8 – Langbroek and Roebroeks (2000); 9 – Larick *et al.* (2001); 10 – Antón (2003); 11 – Asfaw *et al.* (2002); 12 – Huang *et al.* (1991); 13 – Huang *et al.* (1993); 14 – Shen *et al.* (2001); 15 – Zhou *et al.* (2000); 16 – Delson *et al.* (2001); 17 – Jacob *et al.* (1978); 18 – Swisher *et al.* (1996); 19 – Matsu'ura *et al.* (2000); 20 – Santa Luca (1980); 21 – Bartstra and Basoeki (1989); 22 – Bartstra *et al.* (1988)

Hemmer, 1972; Howells, 1974; Clarke, 1976; Stringer *et al.*, 1979; Day and Stringer, 1982; Clarke *et al.*, 1994), they are more often assigned to later species of *Homo* like *H. heidelbergensis* (Stringer *et al.*, 1979; Bräuer, 1984; Clarke, 1990; Rightmire, 1996, 2001; McDougall *et al.*, 2005). An increase in cranial capacity may indicate a cladogenic event leading to *H. heidelbergensis* (Rightmire, 2004). This expansion of the brain is reflected in more vertical parietal walls, parietal bossing, more vaulted frontal squama and a more vertical occipital plane. Certain features of the facial skeleton are also more modern in this group than in *H. erectus*. While a number of ‘*H. erectus*’ features can be identified in these specimens, these are likely plesiomorphies. Therefore, these fossil crania were excluded from the fossil *H. erectus* sample, as was Ceprano (Table 2.1).

While the biological species concept (BSC) and the phylogenetic species concept (PSC) are often contrasted as mutually exclusive models (e.g., Kimbel and Rak, 1993), Jolly (2001, p. 193) has argued that both are “equally valid descriptions of aspects of population structure resulting from evolutionary processes.” Nevertheless, he also recognized that these two approaches can result in quite different alpha taxonomies (e.g., Bilsborough and Wood, 1986). Though most workers agree with the biological species concept in theory (including the related evolutionary species concept and recognition concept), it is difficult if not impossible to directly extrapolate this species category onto the fossil record, as noted by a number of workers (e.g., Mayr, 1942; Simpson, 1951, 1961; Shea *et al.*, 1993; Kimble and Rak, 1993). One option is to utilize an indirect measure: the level and distribution of variation found in a fossil sample is compared with the variation seen in other, better understood taxa, such as extant ones (e.g., Simpson, 1961; Shea *et al.*, 1993; Wood, 1993; Kramer, 1993; Teaford *et al.*, 1993). While this is

the approach adopted here, it is followed with the recognition that different analogs encapsulate diverse sources of variation (e.g., sexual, geographic, climatic) to varying extents, therefore making it difficult to identify a ‘perfect’ model. Fossil taxonomies only partially reflect real-life complexities, and focusing too narrowly on the alpha taxonomy can overshadow more interesting and important evolutionary questions (Jolly, 2001). However, an understanding of diversity within *H. erectus* is a necessary first step toward a more focused examination of the evolutionary history of this species. By examining variation within the expanded *H. erectus* hypodigm relative to various human and non-human primate analogs (including *Papio*, as advocated by Jolly, 2001), it will be possible to formulate hypotheses of *H. erectus* evolutionary history by analogy to these models.

The fundamental question is how likely it is that the degree of variation in the *H. erectus* sample could be found in a single subspecies, a single species or a single genus, as measured by the comparative primate samples. Bootstrapping techniques will be used to create empirical distributions against which to compare the variation in *H. erectus*. In addition, permutation tests will be used to examine the differences in cranial shape between different subsets of *H. erectus* (e.g., African / Georgian vs. Asian).

Although many authors support the use of either (or both) modern humans and African apes as baseline models for taxonomic comparisons in fossil hominins, (Wood *et al.*, 1991; Delson, 1997; Harvati, 2003), other primates are also useful models for early hominins in their ecology and population structure (Jolly, 1970, 2001; Shea *et al.*, 1993). In this analysis, variation within *H. erectus* is assessed relative to a wide range of non-human primates including both apes and papionins.

The great ape members of the family Hominidae are appropriate comparative taxa because they share a close evolutionary relationship with hominins and therefore comparable anatomy and physiology as well as similar evolutionary constraints and patterns of taxonomic variation. Chimpanzees in particular provide an excellent taxonomic model against which to measure *H. erectus* variation, because both intraspecific and interspecific assessments are possible (Harvati, 2003). The degree of sexual dimorphism in *H. erectus* is not well understood, but the large degree of size variation in mandibles found at Dmanisi, Georgia may suggest high levels of dimorphism (Skinner *et al.*, 2006). For this reason, the more sexually dimorphic large-bodied apes and baboons (Swindler, 1976; Phillips-Conroy and Jolly, 1981; Oxnard *et al* 1985; Plavcan, 1990) may also prove informative reference taxa.

It is the case, however, that the limited geographic range of extant apes complicates their use as models for *H. erectus* because morphological variation often correlates strongly with geography (e.g., Howells, 1973, 1989; Albrecht and Miller, 1993; Hennessy and Stringer, 2002). In this respect the large geographic range of modern humans makes them an ideal analog species for *H. erectus*. It is possible that recent humans are comparable to *H. erectus* if the latter is a single polytypic species as suggested by Rightmire (1984; 1990; 1998a) and others. However, modern humans represent only a single species and can not be used to address other taxonomic hypotheses.

Due to the limitations of the available phylogenetic models, it is important to include other ecological and geographic models (Shea *et al.*, 1993). In contrast to the hominines, “African papionins present a complex phylogenetic picture ... (and) baboons

of several genera have shared nonrainforest habitats in sub-Saharan Africa with the hominins ever since their respective lineages emerged” (Jolly, 2001, p. 178). On the basis of mitochondrial and paleontological data it is hypothesized that the *Papio* baboon lineage originated in southern Africa around 1.8 Ma, from where it spread to inhabit its present day distribution across most of Africa (Newman *et al.*, 2004). This is a similar time frame as that seen in *H. erectus*, though *H. erectus* is sampled from an even broader geographic range. In addition, baboons are ecological generalists, allowing them to disperse into different ecological niches across the African continent, a behavior first noted in the human fossil record with the emergence of *H. erectus*. Though the extant *Papio* sample has traditionally been subdivided into five ‘forms’ distinguishable mainly on pelage differences but also exhibiting craniodental differences (anubis, hamadryas, yellow, chacma and Guinea: Jolly, 1965; Hill, 1970; Groves, 2001), a sixth form, *P. h. kindae*, was also recognized by Szalay and Delson (1979) and up to 18 morphs can be diagnosed (Jolly, 2003). While these five (or six) forms are often considered subspecies within a larger *P. hamadryas* species because of their ability (and documented tendency) to interbreed at their boundaries (Jolly, 1993), as well as the clinal nature of their phenotypic characteristics (Frost *et al.*, 2003), they have also been given full species rank in the past (Jolly, 1965; Hill, 1970).

Macaques, in particular members of the *M. fascicularis* species group (*M. fascicularis*, *M. fuscata*, *M. cyclopis* and *M. mulatta*), present another useful geographic and ecological model for *H. erectus* because of their large geographic ranges (*M. mulatta* has the broadest extant non-human primate range – from Afghanistan in the west to China, Laos and Vietnam in the east), their island biogeography (*M. fascicularis*, *M.*

fuscata and *M. cyclopis* all include islands within their distributions) and their adaptations to both tropical and temperate habitats (e.g., *M. mulatta* inhabits both habitat types) (Fooden, 2006).

There is widespread agreement concerning the existence of a *fascicularis* group based on reproductive anatomy and cranial form (Fooden, 1976, 1980, 2006; Delson, 1980) and this is supported by some, but not all, genetic analyses (Hayasaka *et al.*, 1996; Deinard and Smith, 2001; Tosi *et al.*, 2003 but see Morales and Melnick, 1998; Li and Zhang, 2004). However, according to Fooden (1980, p. 8), the assignment of full species rank versus subspecies rank within this species group is more arbitrary than commonly recognized and in fact “borderline subspecific / specific differentiation is the rule, not the exception, within macaque species groups.” The *M. fascicularis* group appears to have diverged before 0.9 Ma (first fossil appearance) and possibly around 2.2 Ma (Hayasaka *et al.*, 1996; Fooden, 2006). Whereas few of the baboon subspecies are geographically isolated, *M. cyclopis* and *M. fuscata*, the Taiwanese and Japanese macaques respectively, diverged from eastern populations of *M. mulatta* around 1-1.2 Ma (Tosi *et al.*, 2003). Both species 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 would be modeled within the *M. fascicularis* species group. In the *fascicularis* group, the ranges of the various species abut but are non-overlapping (Fooden, 1980); baboon distribution can be described as “quasi-continuous...mostly undivided by extrinsic barriers” (Jolly, 1993, p. 67). While hybridization at the

boundaries is better documented in baboons, it may also characterize some macaques where their ranges meet (between *M. fascicularis* and *M. nemestrina* - Bernstein, 1966; 1968; between *M. fascicularis* and *M. mulatta* – Fooden, 1997, 2000; Tosi *et al.*, 2002). In practical terms, therefore, the ‘species’ of macaques are likely to represent a similar degree of biological / ecological differentiation as the numerous ‘subspecies’ of *P. hamadryas*.

In addition to the large geographic range, the long time span of *H. erectus* complicates comparisons of variation within this taxon to other, extant primates with relatively short time spans (Kimbel and White, 1988). Anagenic changes within species are well-documented for primates, including *H. erectus* (e.g., Wolpoff, 1984; Picq, 1990; Bräuer, 1994; Rightmire, 2003; Kaifu *et al.*, 2005), *Paranthropus boisei* (Suwa *et al.*, 1997) and *Theropithecus oswaldi* (Leakey, 1993; Frost, 2001), thus incorporating an additional element of potential variation. While examination of higher taxonomic levels does incorporate shape change that has accumulated since the included taxa diverged, it does not actually sample the entirety of the time range. In addition, fossil and genetic evidence indicates both that modern humans did not originate until 150-200 Ka (Ruvolo, 1996; McDougall *et al.*, 2005; White *et al.*, 2005), and that the modern day distribution of human populations is the result of a rapid dispersal from Africa in the last 100 Ka. While Kimbel and White (1988) have suggested that fossil species may be more variable than extant ones due to temporal variation, an alternative viewpoint has been offered by Delson (1978, 1986, 1997, p. 446), who has suggested that “geographic variation today is broadly comparable to past spatio-temporal variation.” In practice, temporal variation can be modeled by including multiple subspecies or demes within comparative species

samples (Richmond and Jungers, 1995; Lockwood *et al.*, 1996; Lockwood, 1999). From this perspective, modern humans, baboons and macaques would all be excellent models of temporal variation by virtue of their extensive geographic ranges. An alternative is to compare *H. erectus* with an evolutionary species that spans a similar time range. While *P. boisei* has been used in the past and does present an ideal model of temporal change in *H. erectus*, there is an insufficient number of complete crania for inclusion here.

On the other hand, *T. oswaldi* from east and south Africa consists of three chronologically ordered subspecies spanning the late Pliocene through the mid-Pleistocene, a similar time range to *H. erectus* (Leakey, 1993; Frost, 2001; Frost and Delson, 2002). The similarity in species longevity allows variation within *H. erectus* to be assessed relative to a single species composed of several sequential subspecies. This pattern could correspond to a series of temporal subspecies within *H. erectus* displaying shape-related diachronic differences.

Morphometric approaches have been used successfully to address taxonomic questions across primates, including hominins and geometric morphometric methodologies have proven similarly effective in addressing taxonomic issues within both non-human primates and hominins (Frost *et al.*, 2003; Harvati, 2003; Harvati *et al.*, 2004). Geometric morphometrics, like standard morphometrics, allows for the quantification of both the extent and patterning of shape variation in a sample, which is the foundation for the identification of species which is the first step in a phylogenetic analysis (Tattersall, 1992; Harrison, 1993). These techniques allow for the capture and analysis of shape data in the form of three dimensional (3D) landmarks (each landmark is composed of three (x,y,z) coordinates) (Rohlf, 1990; Rohlf and Marcus, 1993;

O'Higgins, 2000; Adams *et al.*, 2004). Once the raw data from the specimens have been superimposed and scaled using generalized Procrustes analysis (Gower, 1975; Rohlf and Slice, 1990) and projected into a Euclidean space tangent to Kendall's shape space (Dryden and Mardia, 1993; Rohlf, 1999), the new coordinates (shape variables) can be analyzed by standard multivariate statistics (Kent, 1994). While the taxonomic status of *H. erectus* has been assessed using standard morphometric techniques, most analyses have not included more recently described specimens (Kramer, 1993; Antón, 2002; Kidder and Durband, 2004; Villmoare, 2005) while others have focused exclusively on the material from Georgia (Macaluso *et al.*, 2004; Lee, 2005; Skinner *et al.*, 2006). This investigation differs from past studies in several ways: 1) it utilizes geometric morphometric methodologies, 2) it incorporates several specimens recently added to the hypodigm and 3) it compares the magnitude of intraspecific variation in *H. erectus* to that found within recent humans and primate taxa, rather than comparing the distance between group means by the use of D^2 , an approach which has been criticized by Ackerman (2003, 2005) and Ahern *et al.* (2005).

Materials

In order to address the alpha taxonomy of *Homo erectus*, it is necessary to assess the degree of variation within this sample relative to other primate taxa. Therefore, several different primate taxa were used to establish a 'yardstick,' against which variation found in *H. erectus* was measured. Extant comparative taxa were chosen to represent both the closest extant relatives of *H. erectus* (modern humans and the great apes) and the

closest ecological and geographic models for *H. erectus* (baboons and macaques). In order to simulate the effect of diachronic change, comparisons were also made to *T. oswaldi*. Using these models also allows variation within *H. erectus* to be evaluated against different taxonomic levels (subspecific, specific and generic) across Primates.

Fossil sample

Thirteen *H. erectus* specimens were analyzed among a total sample of 1250 crania (See Tables 2.1 and 2.2). Due to the incomplete nature of fossils, many members of *H. erectus* had to be excluded, despite analyzing only a small set of landmarks. The 13 *H. erectus* specimens complete enough to be included in this analysis were: Daka (BOU VP-2/66), Dmanisi 2280, ER 3733 and 3883, OH 9, Ngandong 6, 10, 11 and 12, Zhoukoudian 11 and 12, Sangiran 17 and Sambungmacan 3. All attempts were made to collect data on original specimens. However, in some cases this was not possible, and data were collected from casts for four specimens: Zhoukoudian 11 and 12, Dmanisi 2280 and Sangiran 17. The individual fossils included in this analysis provided a representative sampling of the full range of geographic variation from Africa to Java, nearly the full potential temporal variation from ~1.8 Ma to possibly 50 Ka and size variation.

Reference samples

Modern humans: The recent human sample consisted of 372 individuals that could be divided into 11 regional groups. Groups from Africa, Asia, Europe, Australia and North America were selected to cover a wide geographic and climatic range and a variety of subsistence patterns, in order to create a maximally variable sample. For more details and sample sizes, see Table 2.2.

Table 2.2: Samples and sample sizes.

<u>Taxon</u>	<u>Sample size</u>
Total <i>H. erectus</i>	13
Early African / Georgian group	5
Late Asian group	6
<i>H. sapiens</i>	372
Afalou / Taforalt	21
Andamanese	32
Aboriginal Australians	45
Greifenberg, Austria	49
Khoe-San, S. Africa	31
Asian	27
Grand Gulch, Utah	44
Ipiutak, Alaska	46
Lachish, Palestine	27
Mongolians	19
Teita, Kenya	31
<i>Pan</i>	161
<i>P. paniscus</i>	44
<i>P. troglodytes</i>	117
<i>P.t. troglodytes</i>	82
<i>P.t. schweinfurthii</i>	13
<i>P.t. verus</i>	22
<i>Gorilla</i>	98
<i>G. gorilla</i>	74
<i>G.g. gorilla</i>	74
<i>G. beringei</i>	24
<i>G.b. beringei</i>	22

<i>G.b. graueri</i>	2
<i>Pongo pygmaeus</i>	56
<i>P.p. pygmaeus</i>	36
<i>P.p. abelii</i>	20
<i>Papio hamadryas</i>	438
<i>P.h. anubis</i>	155
<i>P.h. cynocephalus</i>	34
<i>P.h. hamadryas</i>	31
<i>P.h. kindae</i>	25
<i>P.h. papio</i>	17
<i>P.h. ursinus</i>	176
<i>Macaca fascicularis</i> species group	99
<i>M. fascicularis</i>	54
<i>M. fuscata</i>	12
<i>M. cyclopis</i>	2
<i>M. mulatta</i>	31
<i>Theropithecus oswaldi</i>	13
<i>T.o. oswaldi</i>	5
<i>T.o. darti</i>	5
<i>T.o. leakeyi</i>	3
Total	1250

Apes: The comparative sample of non-human primates included specimens from all great apes as well as several papionin Old World monkeys. Both chimpanzee species and the three subspecies of the common chimpanzee were included. Following Groves (2003), Stumpf *et al.* (2003) and Grubb *et al.* (2003), two species of *Gorilla* were recognized, *G. gorilla* and *G. beringei*, though only three subspecies were distinguished: *G.g. gorilla*, *G.b. beringei* and *G.b. graueri*. A second subspecies of lowland gorilla is sometimes recognized, the Cross River gorilla from Nigeria and Cameroon, *G.g. diehli* (Groves, 2003; Grubb *et al.*, 2003), but this distinction was not made here. Because the sample size of $n = 2$ for *G.b. graueri* is so small, results were not reported separately for *G. beringei* as they are nearly identical to those for *G.b. beringei*. Both subspecies of

orangutan were also sampled, *Pongo pygmaeus pygmaeus* and *P.p. abelii*. All sample sizes are listed in Table 2.2.

Baboons: The baboon taxonomy here follows Szalay and Delson (1979) and Frost *et al.* (2003) in recognizing the traditional five varieties as subspecies (Guinea, chacma, yellow, anubis and hamadryas), but also according full subspecies status to the Kinda baboons found in Angola and into Zambia where they may grade into ‘typical’ yellow baboons. Kinda baboons are one of the most distinct additional forms noted by Jolly (1993). Sample sizes can be found in Table 2.2.

Macaca fascicularis species group: All species of the *fascicularis* group are included here, though the sample size of two for *M. cyclopis* means that it is not well-represented in analyses. See Table 2.2 for sample details.

Theropithecus oswaldi: One fossil papionin, *Theropithecus oswaldi*, was also included in this analysis because it covers a similar time range as *H. erectus* (~1.5 Myr) (Delson, 1984; Frost, 2001). This species is composed of three chronological forms (commonly recognized as subspecies) that represent an ancestor-descendant pattern from *T.o. darti* to *T.o. oswaldi* to *T.o. leakeyi*. Because sample sizes were small, these subspecies could not be included separately in all analyses. See Table 2.2.

Methods

Geometric morphometrics

For this study, a large number of 3D landmarks were captured with a Microscribe digitizer, in order to cover the overall shape of the neurocranium, base and facial skeleton. 3D data for all members of Hominini were collected by the author. 3D data from comparative non-human primates were generously provided by other members of the NYCEP Morphometrics Group (www.nycep.org/nmg), especially Kieran McNulty (hominoids) and Steve Frost (cercopithecines). Morpheus *et al.* (Slice, 1998) was used for generalized Procrustes analysis as well as for visualization purposes, and statistical analysis was performed in SAS 8 (SAS Institute, 1999-2001).

Out of the initial data collected, a smaller subset of landmarks was chosen for this analysis based on three criteria: (1) they captured overall cranial shape such that the various reference taxa could be differentiated, (2) they were collected by all three researchers and (3) they allowed a representative sample of *H. erectus* to be included in the study. The 16 landmarks chosen were: opisthion, inion, bregma, glabella, frontomale orbitale, frontomale temporale, midtorus inferior, midtorus superior, porion, and postglenoid (See Table 2.3 for definitions and Figure 2.1 for an illustration). The latter six of these landmarks were bilateral, and both left and right antimeres were included in the analysis. These landmarks capture the sagittal profile from glabella to opisthion, cranial breadth at the level of porion and across the supraorbital torus, the overall shape of the supraorbital torus and the position of the posterior

temporomandibular joint. These are the regions of the cranium most often preserved on *H. erectus* remains.

An individual could only be included in the analysis if all landmarks were preserved. In order to maximize sample sizes, bilateral landmarks missing unilaterally were mirrored from the other side for all specimens. For each specimen, its ‘reflection’ is also created – this is a second landmark configuration where the midline landmarks are preserved as in the original but the right and left landmarks are reversed. The original

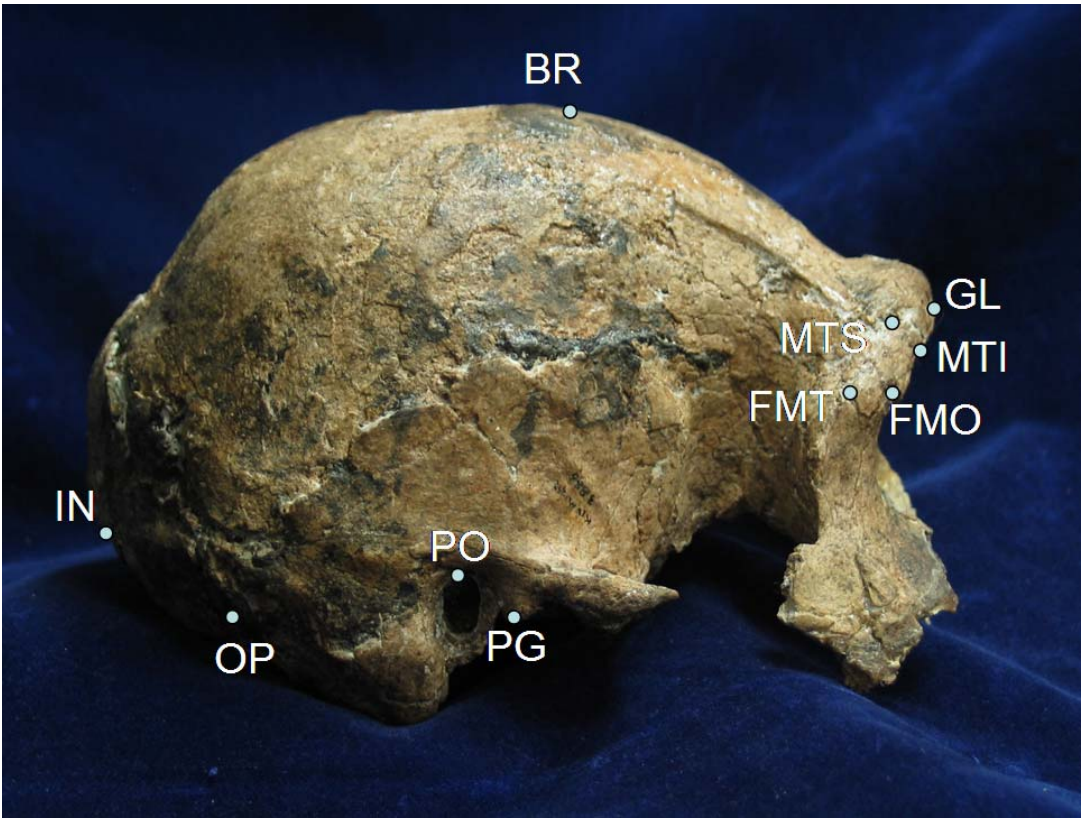
Table 2.3: Landmark definitions and abbreviations.

Landmark	Definition ¹	Abbreviation ²
Opisthion	midline point at the posterior margin of the foramen magnum	OP
Inion	point at which the superior nuchal lines merge in sagittal plane	IN
Bregma	posterior border of the frontal bone in the sagittal plane	BR
Glabella	most anterior midline point on the frontal bone , usually above the frontonasal suture ³	GL
Mid-torus inferior	point on inferior margin of supraorbital torus directly above the center of the orbit	MTS
Mid-torus superior	point on superior aspect of supraorbital torus, directly above mid-torus inferior on the anterior aspect of the torus	MTI
Frontomalarorbitale	point where the frontozygomatic suture crosses the inner orbital rim	FMO
Frontomalartemporale	point where the frontozygomatic suture crosses the temporal line (or outer orbital rim)	FMT
Porion	uppermost point on the margin of the external auditory meatus ³	PR

Postglenoid Process	Infero-lateral-most point posterior to glenoid fossa and anterior to ectotympanic tube (corresponds to postglenoid tuberosity or postglenoid crest)	PG

- 1 – Landmark definitions were modified from the following sources: Howells (1973), White and Folkens (1991), Frost (2001) and McNulty (2003).
- 2 – The abbreviations refer to Figure 2.1.
- 3 – Crania were oriented in Frankfurt Horizontal.

Figure 2.1: Landmarks used to quantify cranial shape. Four midline and six bilateral landmarks were used to explore cranial shape variation in *H. erectus* relative to other human and non-human primate taxa. Both left and right bilateral landmarks were included, though only midline and right-side landmarks are visible here on ER 3883. Landmark definitions and abbreviations are provided in Table 2.3.



Courtesy of National Museums of Kenya

and its reflection are then superimposed by generalized Procrustes analysis (GPA), which permits the right and left landmarks to be reflected as in a mirror image. GPA alignment works by first superimposing centroids at the origin and scaling all configurations to a

unit centroid size. They are then rotated until the residual sum-of-squares can no longer be improved. This fit is accomplished through an iterative approach whereby all specimens are initially aligned to an individual specimen (which acts as a temporary average shape) using a least-squares approach, the average shape is then recalculated and the specimens are realigned to this new average and scaled, and the preliminary residual sum-of-squares is calculated. This least-squares process is repeated until the differences in the residual sum-of-squares falls below a set tolerance level (Gower, 1975; Rohlf and Slice, 1990). The reflected unilateral landmark is then substituted for the missing landmark in the original, creating a more complete landmark configuration. This step is essential in including incompletely preserved fossil specimens. In all cases the bilateral landmarks were averaged with their reflected equivalents (when available) in order to minimize the effects of bilateral asymmetry, especially in fossil specimens (Bookstein, 1996).

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 shy of bregma. I determined that ER 3733 and 3883, D 2700, Ng 5, S 17 and Zkd 3 share a similar trajectory of the mid-sagittal profile with OH 9. A GPA of OH 9 with these six specimens was performed and the mean (x,y,z) coordinates for bregma were calculated. This mean position was then taken as the best available estimate for bregma and was added to the original OH 9 landmark configuration after rescaling by centroid size.

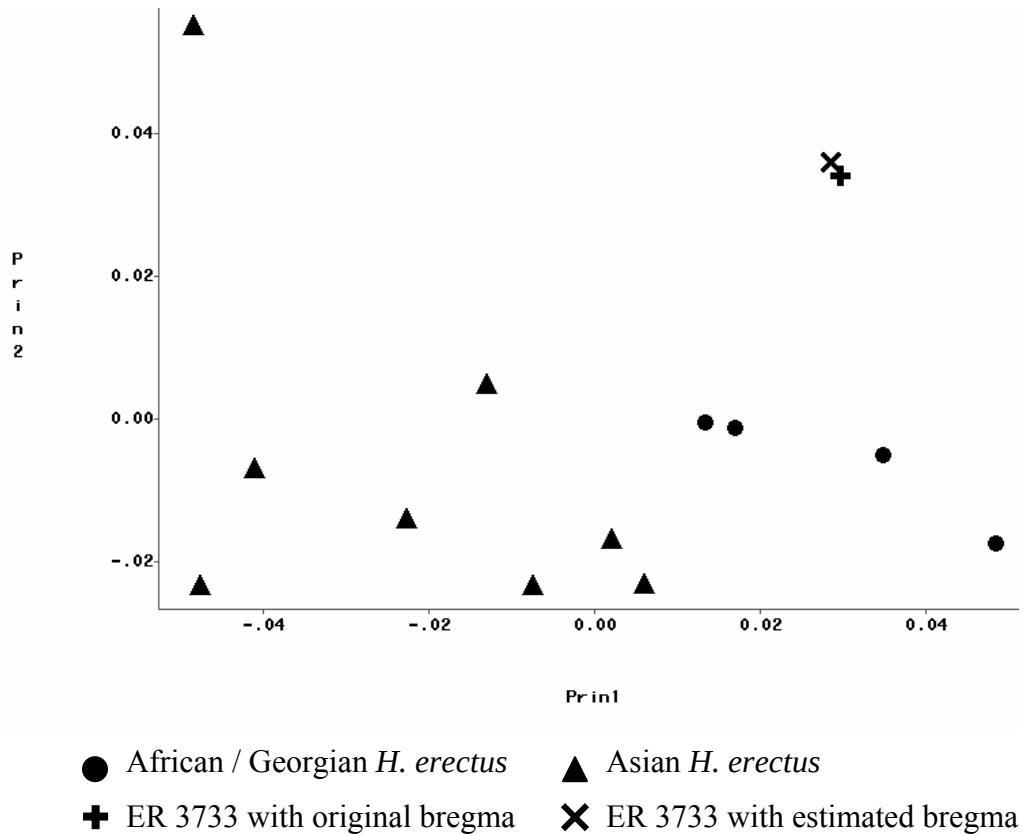
In order to test the reliability of this method, the same procedure was used to estimate bregma for ER 3733. The specimens that were most similar to ER 3733 in this region were ER 3883, Ng 5, S 17, Zkd 3 and 5. Visual inspection indicated that the position of the estimated bregma was nearly identical to the original bregma, falling just posterior to the original landmark. The results of a PCA including two versions of ER 3733, one with the original bregma and one with the estimated bregma, confirm the visual inspection: both fell at the same location in the PCA plot (see Figure 2.2). Based on these results, OH 9 (with a reconstructed bregma) was included in the analysis.

Statistics

The first step was to evaluate whether the 16 landmarks chosen for this analysis captured variation among different taxa and geographic groups. Separate PCAs were performed for each group (modern humans, chimpanzees, gorillas, orangutans, macaques and baboons) and multiple analysis of variance (MANOVA) was used to detect significant group differences on those principal components that accounted for 90% of the total variance. The results for this and later steps are discussed in the Results section below.

The metric used in this study is Procrustes distance, which is the distance between two specimens in Kendall's shape space (the shape space occupied by Procrustes-aligned shape configurations). "True" Procrustes distance is measured as an angle in radians between two specimens. This metric indicates how different two specimens are after they have been aligned using GPA. By looking at pairwise Procrustes distances within a taxon, it is possible to get a measure of inter-individual variation within the group.

Figure 2.2: Principal components analysis illustrating that the procedure used to estimate bregma for OH 9 is accurate. The same procedure used to estimate bregma in OH 9 was applied to ER 3733. This principal components analysis includes ER 3733 with both the original bregma and the estimated bregma. The position of ER 3733 with the original and estimated bregma remains essentially unchanged, supporting the application of this technique for the estimation of bregma in OH 9.



The bootstrapping procedure used in this analysis worked as follows: 13 individuals were selected randomly from a reference taxon sample (equal to the fossil *H. erectus* sample size of 13). Next, pairwise Procrustes distances were calculated for all pairs of those 13 individuals and the sum of squared distances (SSD) was recorded for each sample. This sampling-calculation step was repeated 9,999 times for each analysis in order to create an empirical distribution of SSDs to which the SSD value for the *H. erectus* sample was then compared. The probability of obtaining the SSD associated with

the *H. erectus* sample was determined by comparing this value directly to the distribution of resampled sums of squares. If the *H. erectus* SSD fell outside of the 95% confidence interval, then it was deemed to be significantly more or less variable than that reference sample. However, we are more interested in the taxonomic level to which *H. erectus* compares most closely, so the results are presented in terms of whether the *H. erectus* SSD fell within the 50%, 75% or 95% confidence intervals of the distribution of bootstrapped SSDs for each reference sample. For example, if the *H. erectus* SSD is reported to be within the 95% confidence interval of the *M. fascicularis* distribution, it must fall within the central 95% range of bootstrapped SSDs for *M. fascicularis*.

When sampling at a taxonomic level which 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 chacma baboon has a very large sample size compared to the Guinea baboon (176 versus 17 specimens, respectively). In this case, since 17 was the smallest sample size of the six samples, each of the six forms of baboons were randomly resampled to 17 individuals, and then 13 were chosen (again, randomly) from the resulting 102 specimens. This also applied to within-genus comparisons composed of multiple species. This two step resampling procedure was repeated for each of the 10,000 calculations per sample. Taxa with sample sizes equal to or smaller than 13 were not directly compared to the *H. erectus* sample but were included in larger taxonomic comparisons (e.g., while *H. erectus* was not compared directly to *P.t. schweinfurthii*, this subspecies was incorporated into the *Pan* and *P. troglodytes* samples). In the case of the

fossil cercopithecine *T. oswaldi*, which also had a sample size of 13, analysis of variance (ANOVA) was used to test for differences in average Procrustes distance between the two fossil taxa.

The null hypothesis is that the sample of *H. erectus* used here (Table 2.1) represents a single species; this hypothesis can only be falsified, but not ‘proven’ (Cope, 1993). Although the premise common to most studies is that “fossil species within a restricted geographic area and time span should be about as variable as recent species” (Cope, 1993, p. 235), *H. erectus s.l.* is more widely distributed and has longer time range than most hominin species and thus may violate this supposition. Caution must be exercised in using recent species as analogs and more complex models may be required. It is also necessary to clearly articulate the criteria by which a single species hypothesis for *H. erectus* would be rejected. With regards to living taxa, the *H. erectus* sample would need to be significantly more variable than all single species comparisons (or subspecies in the case of baboons), in order to interpret it as representing more than one species. If the *H. erectus* sample is not significantly more variable than single ‘slice-in-time’ species, even if it is more variable than some single species, then the single species hypothesis cannot be rejected. If, on the other hand, the *H. erectus* sample is more variable than the *fascicularis* species group, the *P. hamadryas* group of subspecies or the genus *Pan*, this would falsify the single species hypothesis. Also, if the *H. erectus* sample was significantly more variable than the fossil *T. oswaldi* sample, then the null hypothesis would be rejected. These predictions follow from the high degree of geographic variation expected from a sample deriving from east Africa, China and Indonesia, as well as the potentially inflated variation due to anagenetic change. Indeed,

many studies have identified both geographic variation and diachronic trends in various aspects of cranial morphology of *H. erectus*, indicating that both sources of variation may have been important factors in the evolutionary history of this species (Weidenreich, 1943; Wolpoff, 1984; Stringer, 1984; Andrews, 1984; Picq, 1990; Bräuer, 1994; Bilsborough, 2000; Antón and Swisher, 2001; Antón, 2002, 2003; Kaifu *et al.*, 2003, 2005; Rightmire, 2004; Kidder and Durband, 2004; Villmoare, 2005).

In addition, permutation tests were used to determine whether the Procrustes distance (in Kendall's shape space) between the means of two (varying) subsets of the *H. erectus* sample was greater than expected by chance ($p < 0.05$). First, the Procrustes distance in radians was calculated between the average shapes of the two *a priori* assigned groups. Using the same specimens, individuals were then assigned randomly to two groups with sample sizes equal to the original subsets. The Procrustes distance between these new group means was calculated and the procedure was repeated 9,999 more times (for a total of 10,000 repetitions). This resulted in an empirical distribution of Procrustes distances against which the original value could be compared and its probability assessed. If 95% or more of the distances generated were smaller than the original Procrustes distance than the null hypothesis that there was no difference between the mean shapes was rejected. These tests were performed for several different subsets of *H. erectus*, including 1) Africa / Georgia vs. Asia, 2) Africa / Georgia vs. Asia minus Ng 11 and 12, 3) the original *H. ergaster* vs. *H. erectus* s.s. samples discussed by Clarke (1990, 2000a) and Wood (1991, 1994), 4) an expanded *H. ergaster* vs. *H. erectus* s.s. which includes additional fossils from Africa, Java and Georgia and, 5) African / Georgian fossils from the Plio-Pleistocene boundary versus all other *H. erectus* fossils..

Details about each of the subsets of *H. erectus* which were contrasted can be found in Table 2.9. For the second contrast (Full African / Georgian vs. Reduced Asian), Ng 11 and 12 were excluded to avoid biasing the Asian sample by including a large proportion of fossils from a single geographically and temporally circumscribed region.

Results

Separate principal components analyses were performed on the Procrustes superimposed coordinates of each comparative primate taxa (chimpanzees, gorillas, baboons, the *M. fascicularis* species group and *H. sapiens*) and separate MANOVAs were performed on the scores along those principal components that accounted for 90% of the total variance within each these taxa. MANOVA indicated significant differences among the majority of species of macaques, species and subspecies of chimpanzees and gorillas, subspecies of baboons and regional groups of humans. See Table 2.4.

Significant results were obtained on the first four principal components (accounting for 69% of the variance) for *T. oswaldi* rather than the first seven (accounting for 90% of the variance), likely due to the smaller sample size (n=13). Pairwise comparisons using a Bonferroni correction indicated that a small number of pairs of regional modern human groups (Lachish – Asian and Lachish – Grand Gulch), one pair of *Pan* subspecies (*P.t. troglodytes* – *P.t. schweinfurthii*) and two pairs of *Gorilla* taxa (*G.b. beringei* – *G.b. graueri* and *G.g. gorilla* – *G.b. graueri*) were not significantly different on those principal components accounting for 90% of the variance. In the case of the gorilla pairs, this may have been related to the small sample size of two *G.g. graueri*. Overall, the

landmark set clearly captures significant taxonomic and geographic variation within the comparative taxa.

Table 2.4: Results of MANOVA for taxonomic differences on those principal components that accounted for 90% of the total variance in each sample. MANOVA was performed on separate PCAs for each taxon listed below.

Taxon	Probability associated with F value for Wilks' Lambda ¹
<i>H. sapiens</i>	<0.0001
<i>Pan</i>	<0.0001
<i>Gorilla</i>	<0.0001
<i>Pongo</i>	0.0056
<i>P. hamadryas</i>	<0.0001
<i>M. fascicularis</i> species group	<0.0001
<i>T. oswaldi</i>	Not significant ²

1 - Separate principal components analyses and MANOVA tests were run for each group listed above. Taxonomic differences refer to regional, subspecific or specific differences, depending on the taxon.

2 - Significant on the first four PCs (0.0252).

Variation in Homo erectus

Recent humans: There is more variation within the *H. erectus* sample than within the diverse recent human sample. All of the 10,000 randomly generated SSDs within single regional groups of recent humans were smaller than that found in *H. erectus* (except the Austrians – 99.9% of the distances within this group were smaller). See Table 2.5. The *H. erectus* SSD falls just within the 95% confidence interval of *H. sapiens* (including both intra- and inter- regional group comparisons). Overall *H. erectus* is more variable than modern humans.

Table 2.5: Comparison of the *Homo erectus* sum of squared Procrustes distances (SSD) with 10,000 bootstrapped SSDs in humans.

Humans	
Reference Taxa	% of SSDs smaller than the Total <i>H. erectus</i> SSD
Ipiutak, Alaska	100.00%
Grand Gulch, Utah	100.00%
Andamanese	100.00%
Mongolians	100.00%
Lachish, Palestine	100.00%
Teita, Kenya	100.00%
Aboriginal Australians	100.00%
Afalou / Taforalt	100.00%
Mixed Asian	100.00%
Bushmen, S. Africa	99.95%
Greifenberg, Austria	99.92%
<i>H. sapiens</i> ³	95.63%

1 – Total *H. erectus* SSD falls within 50% confidence interval.

2 - Total *H. erectus* SSD falls within 75% confidence interval.

3 - Total *H. erectus* SSD falls within 95% confidence interval.

Chimpanzees: The variation seen in this sample of *H. erectus* is higher than that seen in single living subspecies or species of chimpanzee, but comparable to that seen in a single genus composed of two species. Both *P. paniscus* and *P.t. verus* are significantly less variable than the *H. erectus* sample. The *H. erectus* SSD falls just within the 95% confidence interval of *P. troglodytes* but more comfortably within this interval for *P.t. troglodytes*. It would not be difficult to randomly generate the fossil mean from the genus-level sample of *Pan*, as the *H. erectus* SSD falls near the center of the distribution of bootstrapped SSDs for the genus. See Table 2.6.

Table 2.6: Comparison of the *Homo erectus* sum of squared Procrustes distances (SSD) with 10,000 bootstrapped SSDs in apes.

Apes	
Reference Taxa	% of SSDs smaller than the Total <i>H. erectus</i> SSD
<i>P. paniscus</i>	100.00%
<i>P.t. verus</i>	100.00%
<i>P. troglodytes</i> ³	95.48%
<i>P.t. troglodytes</i> ³	89.39%
<i>Pan</i> ¹	60.79%
<i>G.b. beringei</i> ³	9.35%
<i>G. gorilla</i>	1.44%
<i>Gorilla</i>	0.96%
<i>P.p. pygmaeus</i>	0.00%
<i>Pongo pygmaeus</i>	0.00%
<i>P.p. abelii</i>	0.00%

1 – Total *H. erectus* SSD falls within 50% confidence interval.

2 - Total *H. erectus* SSD falls within 75% confidence interval.

3 - Total *H. erectus* SSD falls within 95% confidence interval.

Gorillas and orangutans: For the most part, the models of intraspecific shape variation found in the largest of the ape genera exceeds that seen in *H. erectus*. The *H. erectus* SSD fell within the 95% confidence interval of only one of the subspecies / species of *Gorilla* and *Pongo*: *G.b. beringei* (the same result was obtained for *G. beringei*). *G.g. gorilla* as well as the entire genus *Gorilla* are significantly more variable than *H. erectus*. All SSDs within the two *Pongo* subspecies, as well as the single species / genus of *P. pygmaeus* are larger than the *H. erectus* SSD. See Table 2.6.

Baboons: The variation seen in the *H. erectus* sample generally fell at the high end of intrasubspecific, but low end of intraspecific, variation for *P. hamadryas*. *H. erectus* fell

within the 75% confidence interval of the SSD distributions of *P.h. ursinus* and within the 50% confidence interval of both *P.h. anubis* and *P.h. cynocephalus*. The majority of intrasubspecific bootstrapped SSDs were smaller than the *H. erectus* SSD. The *H. erectus* SSD fell within the 95% confidence interval of *P. hamadryas* (including all six subspecies), but most bootstrapped values for *P. hamadryas* (90%) were smaller than the *H. erectus* value. See Table 2.7.

Table 2.7: Comparison of the *Homo erectus* sum of squared Procrustes distances (SSD) with bootstrapped SSDs in monkeys.

Monkeys	
Reference Taxa	% of SSDs smaller than the Total <i>H. erectus</i> SSD
<i>P.h. papio</i>	100.00%
<i>P.h. hamadryas</i>	98.18%
<i>P.h. kindae</i> ³	96.93%
<i>P.h. ursinus</i> ²	77.30%
<i>M. mulatta</i> ²	77.08%
<i>P.h. anubis</i> ¹	74.03%
<i>M. fascicularis</i> ¹	45.85%
<i>P.h. cynocephalus</i> ¹	30.11%
<i>Macaca fascicularis</i> species group ²	19.00%
<i>Papio hamadryas</i> ³	9.72%

1 – Total *H. erectus* SSD falls within 50% confidence interval.

2 - Total *H. erectus* SSD falls within 75% confidence interval.

3 - Total *H. erectus* SSD falls within 95% confidence interval.

Macaca fascicularis species group: The *H. erectus* SSD fell within the 75% confidence interval for *M. mulatta* and near the center of the distribution for *M. fascicularis*. *H. erectus* variation was also comparable to the *M. fascicularis* species group as a whole,

which included *M. mulatta*, *M. fascicularis*, *M. fuscata* and *M. cyclopis*, falling at the less variable end of the distribution. Neither *M. fuscata* nor *M. cyclopis* were tested individually because of their small sample sizes. The amount of variation in the fossil sample is comparable to that found in either single species of *Macaca* or within the *M. fascicularis* species group. See Table 2.7.

Theropithecus oswaldi: By comparison with *T. oswaldi*, the differences among individuals within the *H. erectus* sample are smaller than expected for a single species with two chronologically ordered subspecies. Because *T. oswaldi* has the same sample size as the total *H. erectus* sample, no bootstrapping was performed, but the average Procrustes distances were significantly different, with the average being higher in *T. oswaldi*. See Table 2.8. ANOVA also indicated significant differences between the fossil *H. erectus* sample and the two sets of chronologically ordered pairs of *T. oswaldi* (*T.o. darti* / *T.o. oswaldi* and *T.o. oswaldi* / *T.o. leakeyi*). In both cases the samples of *T. oswaldi* had significantly higher average Procrustes distances. However, while inter-individual Procrustes distances within *T.o. oswaldi* are significantly higher than those seen in *H. erectus*, this is not the case for *T.o. darti*.

Table 2.8: Results of ANOVA comparing average pairwise Procrustes distances in *Homo erectus* and *Theropithecus oswaldi*. For significant contrasts, bold indicates the taxon with the larger mean pairwise Procrustes distance.

Pair of Taxa		Probability associated with ANOVA F value
Total <i>H. erectus</i>	<i>T. oswaldi</i>	<0.0001
	<i>T.o. oswaldi</i> & <i>T. o. leakeyi</i>	<0.0001
	<i>T.o. oswaldi</i> & <i>T.o. darti</i>	0.0002
	<i>T.o. oswaldi</i>	0.0002
	<i>T.o. darti</i>	0.5406

Comparing subsets of Homo erectus

As described above, permutation tests were also used to test whether the differences between the mean shapes of two *H. erectus* subsamples were statistically significant (as measured by the Procrustes distance between the shapes). The various subsets contrasted in the permutation tests are described in Table 2.9 and the results of the permutation tests are presented in Table 2.10. The results appear to hinge on the assignment of OH 9: when it is grouped with other African fossils (Full African / Georgian) samples, then the difference in mean shape between the African / Georgian and Asian fossils is significant regardless of how many Ngandong fossils are included, but when it is grouped with Asian fossils in *H. erectus* s.s. then the contrasts between this group and *H. ergaster* are not significant.

Table 2.9: The mean shapes of the following subsets of *Homo erectus* were tested using permutation tests of the Procrustes distance between the group means.

Subset 1	Subset 2
Full African / Georgian	Full Asian
ER 3733, 3883, Daka, OH 9, D 2280	Ng 6, 10, 11, 12, Sm 3, S 17, Zkd 11, 12
Full African / Georgian	Reduced Asian
same as above	Ng 6, 10, Sm 3, S 17, Zkd 11, 12
<i>H. ergaster</i>*	<i>H. erectus</i> s.s.*
ER 3733, 3883	S 17, Zkd 11, 12, OH 9
Expanded <i>H. ergaster</i>	Expanded <i>H. erectus</i> s.s.
ER 3733, 3883, D 2280	Ng 6, 10, Sm 3, S 17, Zkd 11, 12, OH 9
Earliest African / Georgian	Later African / Asian
ER 3733, 3883, D 2280	Ng 6, 10, Sm 3, S 17, Zkd 11, 12, OH 9, Daka

**H. ergaster* (= *H. leakeyi*) and *H. erectus* s.s. sensu Clarke (1990, 2000a) and Wood (1991, 1994).

Table 2.10: Results of permutation tests of the Procrustes distance between the average shapes in different subsets of *Homo erectus*. Asterix indicates a statistically significant difference between the mean shapes of each subset. See Table 2.9 for the sample composition of the *Homo erectus* subsamples listed below.

Results of Permutation Tests		
<i>H. erectus</i> subsets	Procrustes distance between group means	Probability that there is no difference between group means
Full African / Georgian vs. Full Asian	0.053	0.01*
Full African / Georgian vs. Reduced Asian	0.049	0.02*
<i>H. ergaster</i> vs. <i>H. erectus</i> s.s.	0.045	0.85
Expanded <i>H. ergaster</i> vs. Expanded <i>H. erectus</i> s.s.	0.039	0.63
Earliest African / Georgian vs. Later African / Asian	0.037	0.77

Discussion

In order to falsify the single species hypothesis, three conditions must be met: 1) linear measurements must discriminate among closely related species, 2) variation present in the biological populations must be well-represented in the sample and 3) “adequate criteria [must] exist for determining the magnitude of variation required to falsify the null hypothesis” (Cope, 1993, p. 232). While these conditions were proposed in regard to use of the coefficient of variation (CV), they are also relevant here, as both the CV and SSD are measures of variation within a sample.

Multivariate methods provide better discriminatory power than examination of single measurements (Albrecht and Miller, 1993), particularly when sample sizes are adequate. There were significant regional, subspecific or specific differences within each genus on the first five principal components (and first four components in *Theropithecus*). This confirmed that the 16 landmarks captured aspects of cranial shape that differed even among closely related taxa. Overall, neurocranial vault shape as captured by these 16 landmarks has high discriminatory power among closely related taxa within Primates, satisfying the first condition.

In terms of both the extant and fossil taxa, samples from a wide range of geographic regions representing the maximum possible subspecies and populations were included, in fulfillment of the second condition.

The third condition requires certain assumptions to be made. As discussed in the methods section, the wide geographic and time span of the *H. erectus* sample means that the usual premise that fossil species diversity is roughly equivalent to neontological

species may not hold. In order to reject the single species hypothesis, the following predictions needed to be fulfilled:

- 1) The intra-individual variation in the *H. erectus* sample exceeds variation seen in all single neontological species.
- 2) The intra-individual variation in the *H. erectus* sample exceeds the variation seen in the *M. fascicularis* species group, *P. hamadryas* or *Pan*.
- 3) The intra-individual variation in the *H. erectus* sample meets or exceeds the variation seen in *T. oswaldi*.

Overall, the predictions for rejecting the single species hypothesis were not met, as is discussed in more detail below.

The *H. erectus* SSD falls within the 95% confidence interval of some single subspecies and species as well as the genus *Pan* and the *M. fascicularis* species group. For simplicity, this discussion will focus on those groups where the *H. erectus* SSD falls closest to the center of the bootstrapped SSDs. The SSD of *H. erectus* falls within the 75% confidence interval of the *M. fascicularis*, *M. mulatta*, *P.h. cynocephalus*, *P.h. anubis* and *P.h. ursinus* distributions in addition to the *Pan* and *fascicularis* species group distributions.

The amount of variation within the *H. erectus* sample is similar to that seen in some single species of *Macaca* and subspecies of *P. hamadryas*. As discussed in the introduction, subspecies of *P. hamadryas* and species of *Macaca* may reflect the same underlying biological / ecological reality. Both groups consist of a patchwork-like distribution of taxa with a certain amount of gene flow between subspecies of *P. hamadryas* and between species of the *M. fascicularis* species group. This is supported

by descriptions of these taxa (Jolly, 1993; Fooden, 1980). There is overlap in the amount of intrasubspecific or intraspecific variation displayed by baboons and macaques, respectively (see Table 2.7). *H. erectus* variation is also comparable to that in the multiple species models of *Pan* and the *M. fascicularis* species group. It seems that *H. erectus* variation is in or near the zone of overlap between intraspecific and interspecific variation. This result may explain why there is widespread support for both a single species and a multiple-species status for this fossil taxon.

It is in this zone of overlap between taxonomic levels that the differences between species concepts like the BSC and the PSC are most apparent. For example, despite the extensive morphological, behavioral, ecological and genetic data available, there is not perfect agreement on how many distinct baboon forms should be recognized and whether they should be regarded as species or subspecies. In the absence of much of the same data, there is also unlikely to be consensus concerning *H. erectus* taxonomy. However, because the variation in the *H. erectus* sample does not exceed that found in single ‘slice-in-time’ species or subspecies like *M. fascicularis*, *M. mulatta*, *P.h. anubis*, *P.h. ursinus* and *P.h. cynocephalus* and all species of *Gorilla* and *Pongo*, we cannot reject the single species hypothesis for *H. erectus*.

Following the arguments that temporal variation can be modeled by geographic variation (as represented by multiple subspecies or populations within reference species) (Delson, 1978, 1986, 1997; Richmond and Jungers, 1995; Lockwood *et al.*, 1996; Lockwood, 1999), the comparisons with the *M. fascicularis* species group (four species) and *P. hamadryas* (six subspecies) are perhaps most relevant for a long-lived species like *H. erectus*. *H. erectus* variation fell within the 75% confidence interval for the *M.*

fascicularis species group and the 95% confidence interval for *P. hamadryas*, albeit at the low end of the distributions. The variation in *H. erectus* was similar to that found in the genus *Pan*, which encapsulated two species within a constricted geographic range. It was also considerably less variable than any two chronologically ordered subspecies of *T. oswaldi* or the total *T. oswaldi* sample (all three subspecies) which spanned a similar time interval. Based on the second and third predictions discussed above, the single species hypothesis cannot be rejected.

When the average shape of varying subsets of *H. erectus* s.l. were compared, it was clear that there were statistically significant differences between the early African / Georgian vs. later Asian subsamples but not between the classic *H. ergaster* vs. *H. erectus* s.s. (sensu Clarke, 1990, 1994, 2000a; Wood, 1991, 1994) subdivisions. This apparently contradictory finding was tied closely to whether OH 9 and Daka were assigned to the African / Georgian group or to *H. erectus* s.s.. This is probably related to the fact that the neurocranium of OH 9 in particular resembles that of the other early African fossils and not the Asian fossils (Baab, chapter 4). It is clear that the *H. ergaster* vs. *H. erectus* s.s. division proposed by Clarke (1990; 2000a) and Wood (1991, 1994) is not tenable and the difference between these two “species” is no greater than that of randomly generated groups of specimens. Based on the results of these analyses, there is greater support for the recognition of a more inclusive *H. ergaster* species which incorporates all African (and possibly Georgian) fossils. However, the statistically significant difference between the African / Georgian and Asian fossils is not unexpected given the greater age of the African and Georgian fossils compared to the Asian fossils. In fact, the only two specimens from these groups which overlap in time are Daka (~1

Ma) and S 17 (~1.3 Ma). These results are compatible with either: 1) a single species exhibiting anagenetic and/or geographic variation between the earlier (African / Georgian) fossils and the later (Asian) fossils or 2) two closely related and morphometrically similar species, one in Africa and Georgia and one in Asia. A more thorough evaluation of the patterns of variation within this sample appear to support the first scenario as there is overlap among the geographic subsamples of *H. erectus* (Baab, chapter 4).

From these observations, it is clear that *H. erectus* populations maintained a consistent cranial shape across a wide geographic, temporal and size range, albeit with some geographic and/or temporal partitioning of variation. The conservation of this basic *Bauplan* across time and space with variation most comparable to single neontological species leads to the conclusion that this fossil sample represents a single species. While it is likely that *H. erectus* exhibited significant (temporo-) geographic population substructure similar to that seen in the *M. fascicularis* species group or in *P. hamadryas*, it was generally less variable than these taxa. Although the temporo-geographic ‘populations’ (e.g., Zhoukoudian or Ngandong) within the fossil sample are not biologically equivalent to the neontological subdivisions of *Papio* or *Macaca* because of the additional temporal element, they may result in similar phenostructure (sensu Jolly, 1993) within the samples. As has been advocated by several researchers, temporo-geographic populations could be recognized as either subspecies or paleodemes (Delson, 1990; Howell, 1999; Jacob, 2001; Asfaw *et al.*, 2002).

Choice of reference taxon will clearly influence perception of variation within *H. erectus*. *H. erectus* was more variable than single species of *Pan* and modern humans,

while in comparison to *Gorilla* or *Pongo* it is a was not more variable than single subspecies. A persuasive argument has been made that *P. hamadryas* and the *M. fascicularis* species group are more relevant geographic, ecological and evolutionary models for *H. erectus* (Jolly, 2001). However, individual subspecies or species within monophyletic clades are not equally variable. This confirms the importance of taking a *Gestalt* approach by using multiple reference taxa.

This approach supplements more comparative morphological approaches. Several workers have concluded that the Asian (plus OH 9) hypodigm is derived relative to the early African (East Turkana) and possibly Georgian samples, suggesting that *H. erectus* be restricted to the former set of fossils (Stringer, 1984; Andrews, 1984; Wood, 1984; 1991; 1994; Villmoare, 2005). However, the issue is far from settled as some of the ‘Asian’ features appear to have a broader distribution (Rightmire, 1984; 1990; Bräuer, 1990; 1994; Bräuer and Mbua, 1992) and some of the African fossils, including OH 9 and Daka, may exhibit the more derived traits seen in the Asian fossils (Wood, 1991; Asfaw *et al.*, 2002). While the results here support the view that *H. erectus* was a geographically widespread species that maintained phenotypic (and therefore genetic) continuity throughout its time range, a better understanding of the patterning of variation within the recently expanded *H. erectus* sample will further our understanding of the taxonomic status and evolutionary history of this taxon. Future research must address the relative influence of time, geography and size on cranial morphology in *H. erectus* in order to confirm the results of this analysis.

Conclusions

Cranial shape variation at single taxonomic levels (e.g., subspecific or specific) was not comparable across a range of hominin and non-hominin primate taxa. For example, modern humans and chimpanzees were much less variable than gorillas and orangutans despite their close phylogenetic relationship. Therefore, multiple primate analogs were needed to model the geographic and temporal variation present in the *H. erectus* sample. In addition to modern humans, both *Papio* and the *M. fascicularis* species group provide good geographic models while the fossil species *T. oswaldi* has a similar time span to *H. erectus*. Taking a comprehensive approach, the 3D cranial shape variation found in the *H. erectus* sample did not exceed the variation expected for a single, long-lived, widely distributed species. Populations of *H. erectus* maintained remarkable shape continuity across the Old World throughout the Pleistocene epoch. While geographic differences and temporal changes have been observed within *H. erectus*, these are best interpreted as intraspecific variation.

Chapter 3:

Homo erectus Cranial Shape in Perspective: A Comparative Approach

Introduction

Recent additions to the *H. erectus* hypodigm from Asia, Africa and the Caucasus require a reassessment of the definition and composition of *H. erectus*. While general descriptions of this species have incorporated both discrete and shape-based characters (e.g., Weidenreich, 1943, 1951; Le Gros Clark, 1964; Howells, 1978; Howell, 1980; Rightmire, 1990), arguments in favor of the recognition of multiple species within the *H. erectus* s.l. sample have focused more on non-metric traits (Andrews, 1984; Wood, 1984, 1991, 1994; Stringer, 1984; Manzi *et al.*, 2001; de Lumley *et al.*, 2006; Villmoare, 2005). However, continuing disagreements about the meaning and significance of discrete traits have yet to be resolved (Hublin, 1986; Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992), leaving the taxonomic and phylogenetic status of *H. erectus* in doubt. Considerable debate surrounds the relationship of *H. erectus* to later species of *Homo*, to modern humans in the Far East, and to the hominin population from Flores, Indonesia. Cranial shape offers an alternative source of data with which to address unresolved questions surrounding *H. erectus* evolutionary history.

Perhaps because phylogeny has been reconstructed using discrete traits, less attention has been paid to how cranial shape has changed over speciation events in the genus *Homo*. Because cranial shape is strongly influenced by brain growth and development, clarifying the details of shape change along the *Homo* lineage can shed

light on the chronology of brain evolution. A careful examination of cranial shape evolution on the *Homo* lineage can also identify reversals along a given tree.

Background

Defining *Homo erectus*: Previous studies have concluded that there are few to no autapomorphies which can be used to define *H. erectus* (Delson *et al.*, 1977; Hublin, 1986; Kennedy, 1991) or that the few autapomorphies present were restricted to the Asian part of the hypodigm (Andrews, 1984; Wood, 1984; Stringer, 1984). The latter observation has led some workers to propose the presence of at least one additional species, *H. ergaster*, to accommodate some of the less derived African fossils. This has also resulted in the removal of Asian *H. erectus* (and possibly OH 9) from the ancestry of later *Homo* species. However, the mere presence of autapomorphies does not automatically signify a separate species as unique traits may also be the result of intraspecific variation. At the same time, it is not clear that autapomorphies are an essential component of a species definition (Wood, 1984; Strasser and Delson, 1988; Kimbel and Rak, 1993). An alternative to definitions based on unique character traits are ‘combination’ species definitions (i.e., a polythetic classification), which incorporate a unique combination of primitive and derived features. Several such definitions have been proposed for *H. erectus* (Wood, 1984; Turner and Chamberlain, 1989; Rightmire, 1990; Kimbel and Rak, 1993).

Standard descriptions of *H. erectus* have always included references to both discrete cranial traits as well as metrical aspects of the shape of the neurocranium and

sometimes the facial skeleton (e.g., Weidenreich, 1943, 1951; Le Gros Clark, 1955, 1964; Howell, 1978; Howells, 1980; Rightmire, 1984, 1990; Antón, 2003). However, the most conservative list of possible *H. erectus* autapomorphies, compiled by Andrews (1984), included only discrete characters: the presence of an angular torus, midline keeling on the frontal and parietal bones, the vertical separation of inion and endinion, and fissures between both the entoglenoid and the tympanic tube and the petrosal crest and the mastoid process. However, the widespread disagreement concerning the definition, distribution and significance of discrete traits within *H. erectus* (Hublin, 1986; Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992; Villmoare, 2005) has led to a stalemate.

Previous studies have highlighted several aspects of cranial shape which characterized *H. erectus*: a long, low vault that was widest at the level of the supramastoid crests; parietals that converged superiorly above the supramastoid crests; a receding frontal bone; angulation of the occipital bone in the sagittal plane; and a prominent and strait supraorbital torus with marked postorbital constriction. While certain of these features of cranial shape were also seen in later ‘archaic’ *Homo* fossils, it is unclear whether all of these features were found simultaneously outside of *H. erectus*.

Traditionally, *H. erectus* has been compared to modern humans or to Neanderthals, but very few comparisons have been made to either earlier *Homo* species (*H. habilis* and *H. rudolfensis*) or other later *Homo* taxa (e.g., *H. heidelbergensis* and *H. mauritanicus* / *antecessor*). However, *H. erectus* overlaps several of these groups in time and likely shares either an ancestor-descendant or a sister-group relationship with some of these taxa. Indeed, many individuals now assigned to later *Homo* species, such as Narmada, Petralona and Ndutu, were initially considered to be *H. erectus* because they

share many aspects of cranial shape with *H. erectus* (Hemmer, 1972; Clarke, 1976; Stringer *et al.*, 1979; Sonakia, 1984, 1985). For example, both Kabwe and *H. erectus* exhibit a receding frontal bone with a prominent supraorbital torus, but the parietals are more parallel in Kabwe than in *H. erectus*.

Composition of *Homo erectus*: The relatively recent addition of numerous fossils to *H. erectus* from sites like Dmanisi, Georgia; Bouri, Ethiopia; Olorgesailie and Ileret, Kenya; and Ceprano, Italy has broadened the potential geographic, temporal and morphological range of *H. erectus* (Ascenzi *et al.*, 1996; Vekua *et al.*, 2000; Gabounia *et al.*, 2002; Asfaw *et al.*, 2002; Leakey *et al.*, 2003; Potts *et al.*, 2004). This expansion has not been met with universal agreement (Schwartz, 2000, 2004; Manzi *et al.*, 2001; Gabounia *et al.*, 2002; Mallegni *et al.*, 2003; Schwartz and Tattersall 2003; de Lumley *et al.*, 2006), however, and it is unclear whether all of the more recent additions to *H. erectus* exhibit the same cranial morphology as the remainder of the species.

Some specimens recently attributed to *H. erectus* have not been described in detail, such as the calvariae from Bouri, Ethiopia (Daka), the subadult / young adult from Ileret, Kenya (ER 42700) and the partial cranium from Olorgesailie, Kenya (OL 45500). ER 42700 has not yet been fully described but it has been linked to *H. erectus* by a few discrete features and its general vault shape (Leakey *et al.*, 2003; Spoor *et al.*, 2005). However, its small size and early age (~1.5 Ma) leave open the possibility that this specimen represents another species of early *Homo*. Another small African specimen compared favorably to *H. erectus* on the basis of several discrete traits is OL 45500, which was younger (0.9 Ma) than ER 42700. OL 45500 consists of several fragments of

a single cranium, the largest of which are the left temporal and the frontal bone; its incomplete nature makes it difficult to evaluate its overall cranial form.

In other instances, questions still remain even after complete descriptions and comparative analyses have been performed. This is the case for the fragmentary cranium from Salé, Morocco, the calvarium from Ceprano, Italy and the numerous fossils from Dmanisi, Georgia. Similarities to *H. erectus* but also to Middle Pleistocene ‘archaic’ *Homo* have been observed for both the Salé (Jaeger, 1975; Laitman and Crelin, 1980; Hublin, 1985, 2001; Rightmire, 1990, 2004; Picq, 1990; Bräuer *et al.*, 1997; Wolpoff, 1999) and Ceprano fossils (Ascenzi *et al.*, 1996, 2000; Clarke, 2000a,b; Manzi *et al.*, 2001; Mallegni *et al.*, 2003; Rightmire, 2004). If these specimens are not attributable to *H. erectus*, then one hypothesis is that Ceprano represents the last common ancestor of *H. sapiens* and Neanderthals (*H. antecessor* or *H. mauritanicus*) (Manzi *et al.*, 2001; Bruner and Manzi, 2005, 2006), while Salé was a member of *H. rhodesiensis*, a species ancestral to *H. sapiens* (Hublin, 2001). In contrast to the more advanced features exhibited in Salé and Ceprano, the less derived cranial morphology of the Dmanisi population has led to the erection of a new species of early *Homo*, *H. georgicus*, to accommodate these fossils. Variation in the size and morphology of the Dmanisi craniodental remains could also support the presence of more than one species within the sample (Schwartz, 2000; Skinner *et al.*, 2006).

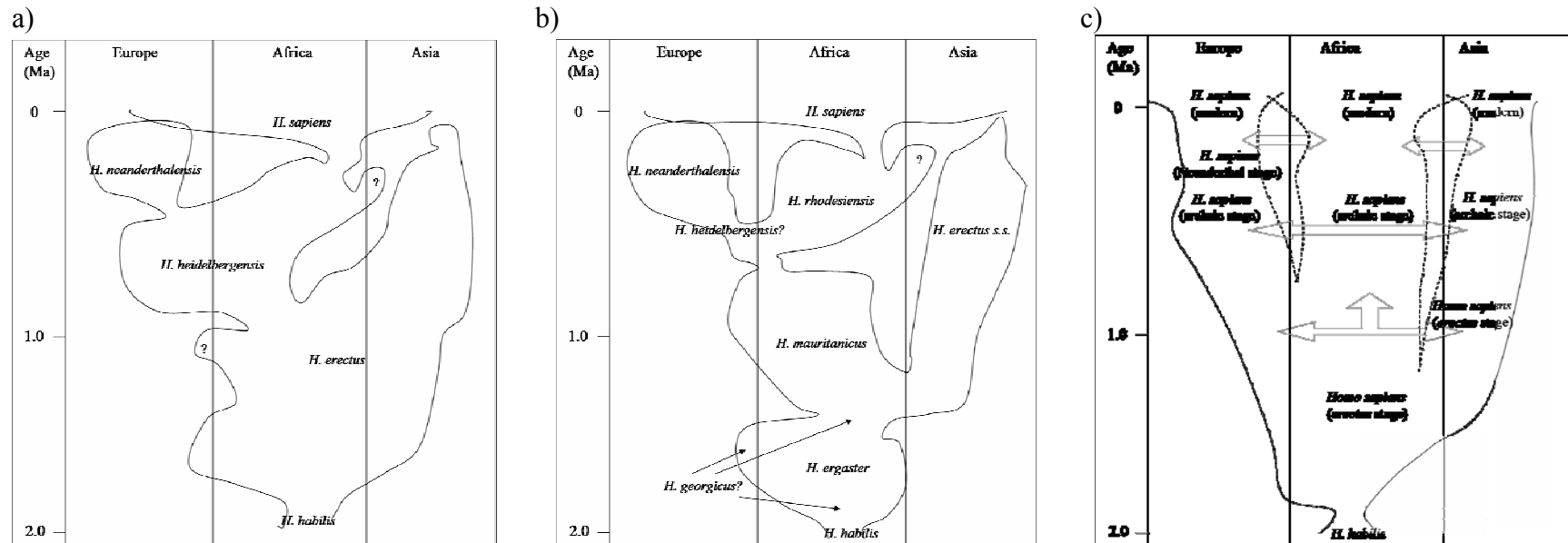
Origins of *Homo erectus*: Although most workers place *H. habilis* as the most likely ancestor of *H. erectus* (Kimbel *et al.*, 1997; Strait *et al.*, 1997; Foley, 2002), a close relationship was recently proposed between *H. rudolfensis* and the Dmanisi hominins (de

Lumley *et al.*, 2006), which may in turn be ancestral to later populations of *H. erectus* (Lordkipanidze *et al.*, 2006). The relative paucity of few well-preserved early *Homo* specimens and the wide range of craniodental variation encompassed by these specimens (McHenry and Coffing, 2000) have contributed to the uncertainty surrounding the origins of *H. erectus*. The results of cladistic studies reflect this ongoing ambiguity, with conflicting studies supporting either a sister relationship between *H. erectus* and *H. habilis* (Chamberlain and Wood, 1987; Stringer, 1987; Lieberman *et al.*, 1996) or between *H. erectus* and *H. rudolfensis* (Wood, 1992; Skelton and McHenry, 1992; Strait *et al.*, 1997; Wood and Collard, 1999)

Relationships among later *Homo* species: Even less clear are the relationships among later species of *Homo*. While numerous scenarios have been advanced in regard to the later evolutionary history of the genus *Homo*, most of these can be subdivided into three major categories. As these scenarios are well-known, only the basics will be reviewed here and illustrated in Figure 3.1. In the first scenario, African *H. erectus* (or *H. ergaster*) gave rise to another species (*H. heidelbergensis*) which was the last common ancestor of Neanderthals and *H. sapiens*. *H. heidelbergensis* was spread throughout Africa, Europe and Asia, and included Middle Pleistocene specimens like Bodo, Kabwe, Arago, Petralona and Dali (Rightmire, 1998b, 2001).

There is continuing debate concerning the phylogenetic relationships among mid-Pleistocene *Homo* specimens, a topic which is outside of the scope of this thesis. For simplicity, fossils assigned to a variety of taxa (e.g., *H. heidelbergensis*, *H. antecessor*, *H. rhodesiensis* and *H. mauritanicus*) are here referred to as mid-Pleistocene *Homo*, with the

Figure 3.1: Three major phylogenetic trees of genus *Homo*. These trees are based on Rightmire (1998b, 2001) (a), Hublin (2001) (b) and Frayer *et al.* (1993) and Wolpoff (1999) (c). Tree (b) represents the most speciose tree whereas (c) recognizes only one post-*habilis* species, *H. sapiens* and (a) is intermediate in terms of recognized species diversity. The arrows in tree (c) signify the presence of significant genetic exchange between geographic regions.



recognition that this likely masks some meaningful taxonomic variability. In order to address this possibility, the implications of a second phylogenetic / taxonomic scenario are also explored.

The second scenario recognizes a far more speciose later *Homo* phylogeny. In its most basic form, the second scenario argues that *H. ergaster* gave rise to a species, *H. mauritanicus* / *H. antecessor* (Gran Dolina, Tighenif and Ceprano), which was the last common ancestor of *H. sapiens* and *H. neanderthalensis*. *H. rhodesiensis* (e.g., Kabwe, Bodo, Ndutu, Salé) then diverged from *H. mauritanicus* and was in turn ancestral to *H. sapiens*. In this scenario, most European Middle Pleistocene fossils were part of the Neanderthal lineage and are either included in *H. neanderthalensis*, or the less derived (and older) fossils from sites such as Sima de los Huesos (Atapuerca), Arago and Petralona are given their own species designation, *H. heidelbergensis* (Carbonell *et al.*, 1995; Arsuaga *et al.*, 1997). Numerous variations on this scenario exist, a reflection of the wide range of opinions regarding the taxonomy and inter-relationships among later *Homo* species (e.g., Arsuaga *et al.*, 1997; Bermúdez de Castro *et al.*, 1997, 2004; Lahr and Foley, 2004).

H. erectus does not exist as a separate species in the third scenario, but rather represents a grade within *H. sapiens*. In this scenario (the multiregional model), *H. sapiens* originated in Africa around 2 Ma and evolved as a series of interconnected geographic groups into present day modern humans (Thorne and Wolpoff, 1981; Frayer *et al.*, 1993; Wolpoff, 1999). Supporters of multiregional evolution have made the clearest case for *H. erectus* genetic contribution to regional modern human populations in

Australasia (Pope, 1991, 1992; Frayer *et al.*, 1993; Hawks *et al.*, 2000; Wolpoff *et al.*, 2001).

A major point of disagreement between the multiregional and recent African origin models of modern human origins concerns the ultimate evolutionary fate of *H. erectus*, particularly in Southeast Asia / Australia. Proponents of the multiregional model posit that early modern humans in Southeast Asia / Australia exhibit numerous cranial and dental features which were inherited from recent populations of *H. erectus* from Ngandong (Weidenreich, 1945; Thorne and Macumber, 1972; Thorne and Wolpoff, 1981; Wolpoff *et al.*, 1984, 2001; Frayer *et al.*, 1993; Hawks *et al.*, 2000).

However, these supposed 'regional' features may be plesiomorphies and not unique to Indonesia and Australia, or they may be the result of hybridization between late-surviving *H. erectus* populations in Indonesia and early modern humans that originated in Africa (Stringer, 1992a,b; Bräuer, 1992; Lahr 1994). A second issue is the chronology of the populations in this region of the world. Although ESR dating of bovid teeth pointed to an age as young as ~50-30 ka for the Solo High Terrace deposits in which the Ngandong crania were found (Swisher *et al.*, 1996), earlier U-series dates on some of the fauna provided a greater range of 100-30 ka for the Ngandong fossils (Bartstra *et al.*, 1988). The younger dates were criticized on methodological grounds (Grün and Thorne, 1997), and several workers questioned whether the Ngandong fossils were intrusive into the Solo High Terrace layers (Santa Luca, 1980; Grün and Thorne, 1997; Dennell and Roebroeks, 2005). A further complication is the uncertain age of most Pleistocene / early Holocene modern humans from Indonesia and Australia. However it does appear that the Ngandong populations likely predated all three of the modern

humans from Kow Swamp, Wajak (=Wadjak) and Willandra Lakes used in this study which were ~22 to <10 ka in age (Thorne and Macumber, 1972; Storm, 1995; Simpson and Grün, 1998; Stone and Cupper, 2003) although older dates were reported for Willandra Lakes Hominid 50 (WLH-50) (~30 ka, Caddie *et al.*, 1987).

Previous analyses that have addressed this question by analyzing cranial shape or morphometric data have produced conflicting results (Stringer, 1992a; Hawks *et al.*, 2000). A major weakness in the Stringer (1992a) dataset was the absence of any late Indonesian *H. erectus* fossils. The Hawks *et al.* (2000) analysis included only one modern human specimen, WLH-50, the use of which was criticized on numerous grounds by Bräuer *et al.* (2004). Perhaps the most serious problem with this specimen is the pathological hyperostosis of the cranial bone (observed by Brown, 1989, 1992; Webb, 1990) which likely inflated the measure of cranial vault thickness used by Hawks *et al.*, 2000. Regardless of these controversies, the fossils from Wajak, Kow Swamp and particularly Willandra Lake are central to the debate over modern human origins (Thorne and Wolpoff, 1981; Wolpoff *et al.*, 1984; Stringer and Andrews, 1988; Bräuer, 1989; Stringer, 1992b; Wolpoff, 1992; Frayer *et al.*, 1993; Hawks *et al.*, 2000; Wolpoff *et al.*, 2001; Bräuer *et al.*, 2004).

There is further uncertainty surrounding the hypothesized *H. erectus* ancestry of the recently described Flores hominins. Liang Bua 1 (LB1) is a fairly complete skeleton found in the Liang Bua cave on the Indonesian island of Flores. This population was given the species nomen *H. floresiensis* (Brown *et al.*, 2004). The evolutionary position of the Liang Bua cave hominin fossils has proven contentious. There are three major hypotheses regarding this population: 1) it represents a lineage of dwarfed *H. erectus*

(Brown *et al.*, 2004; Falk *et al.*, 2005, 2007), 2) it was a dwarfed form of a yet unidentified small-bodied hominin from the mainland (Brown *et al.*, 2004) or 3) it was a microcephalic from a population of small-bodied modern humans (Jacob *et al.*, 2006; Martin *et al.*, 2006). The presence at Liang Bua of additional postcranial remains of several individuals spanning 95-74 to 12 ka, as well the mandibular specimen LB6\1 (which is smaller than the LB1 mandible), supports the argument that LB1 was part of a small-bodied population with both unique and *erectus*-like morphological features (Morwood *et al.*, 2005).

Questions addressed by this study

Unique aspects of the craniofacial shape of *H. erectus* were identified through comparisons of the three dimensional (3D) shape of the *H. erectus* cranium with other species of *Homo*. Rather than comparing *H. erectus* only to modern humans and Neanderthals, the comparative sample also included African, Asian and European Middle Pleistocene specimens that are known to share a similar cranial shape to *H. erectus*. Using this shape-based species definition, it was then possible to evaluate the affinities of those specimens which are less certainly assigned to *H. erectus*, such as ER 42700, Ceprano and the Dmanisi fossils.

By examining the cranial shapes of various *Homo* taxa in the context of proposed phylogenetic trees, it was possible to explore the implications of different evolutionary scenarios for cranial evolution in terms of the timing of evolutionary events and the polarity of cranial shape features. The implications of cranial shape evolution along two

different trees are presented (see Figure 3.1a, b), that of Rightmire (1998b, 2001) and a more speciose tree proposed by Hublin (2001, p. 117, Figure 8.10c).

A careful examination of different regions of the cranium will also highlight patterns of mosaic evolution in cranial shape. For example, the hypothesis that frontal bone morphology underwent evolutionary changes in Ceprano before the shape of the cranium as a whole changed will be assessed through side-by-side comparisons of the taxonomic patterns evident in both overall cranial shape and frontal bone shape.

Although 3D geometric morphometric data likely capture synapomorphic characters pertaining to cranial shape, these data also include plesiomorphic and autapomorphic aspects of shape. This fact, in addition to a lack of discrete characters, means that this dataset cannot be analyzed using standard cladistic methods. However, it was possible to generate trees using several tree building techniques that were rooted with an outgroup. These trees were then compared to phylogenetic trees found in the literature. Lockwood *et al.* (2004) were able to recover the molecular phylogenetic tree for humans and African apes using 3D landmarks from the temporal bone and suggested that this region of the skull may be particularly useful for recovering the true phylogenetic relationships among fossil hominins, as well. A number of the landmarks in the landmark protocol used here were collected from the temporal bone, particularly the temporal base, and it will be possible to test whether the expected relationships are recovered for Plio-Pleistocene *Homo* using this landmark set.

The affinities of early modern humans from both Indonesia and Australia (Wajak 1, WLH-50 and Kow Swamp 17 [KS 17]) were assessed relative to recent Indonesian fossil hominins, early modern humans from Africa and the Levant and a geographically

diverse recent human sample. Both principal component and canonical discriminant analyses were utilized and the latter was compared to the discriminant function analysis on linear measurements reported by Hawks *et al.* (2000). The pathology associated with WLH-50 (cranial vault hyperostosis) is not expected to affect the overall cranial shape of this specimen.

The resemblances in cranial shape of the LB1 cranium to a range of *Homo* species were first explored through principal components analysis. The possibility that LB1 represents a dwarfed population of *H. erectus* was also addressed more specifically. While there are no examples of endemic dwarfism in primates / hominoids, it was possible to test the compatibility of LB1 with a scaled down *H. erectus* by performing analyses in the “size-shape space” described by Mitteroecker *et al.* (2004), which allows analysis of both size and shape data simultaneously.

Materials

3D landmark data were acquired from original cranial fossils representing *H. erectus*, *H. habilis*, *H. rudolfensis* and several later *Homo* taxa and from a geographically widespread sample of recent human crania. Data were collected from institutions in Africa, Europe, the United States and Indonesia. While all efforts were made to collect data on original *H. erectus* specimens, this was not always possible and casts were used for the Zhoukoudian and Dmanisi samples as well as S 17 and Ngawi. Casts were used for more of the non-*erectus* fossils, although originals were used for many of the best-preserved fossils. High quality casts were used from the American Museum of Natural

History and the Musée de l'Homme. See Table 3.1 for sample details. The reconstruction of a Zhoukoudian male by Tattersall and Sawyer (1996) was used only in the analysis of facial morphology as there are no complete faces in the Zhoukoudian sample. This specimen is an amalgam of the neurocranium (including the supraorbital torus) of Zkd 12 and facial fragments from several other individuals. Zkd 12 is one of the larger specimens from the Zhoukoudian collection, and all facial fragments used in the reconstruction were also relatively large (Tattersall and Sawyer, 1996).

Table 3.1: Fossil *Homo* sample.

Region	Specimen ¹	Taxon ²	Cast	Region	Specimen	Taxon	Cast
Africa	ER 1813	H.h. ³		Indonesia	S 2	H.e.	
	ER 1470	H.r. ²			S 4	H.e.	
	ER 1805	U			S 12	H.e.	y
	OH 24	H.h. ³			S 17	H.e.	y
	ER 3733	H.e.			Sm 1	H.e.	
	ER 3883	H.e.			Sm 3	H.e.	
	ER 42700	U			Ng 1	H.e.	
	WT 15000	H.e.			Ng 6	H.e.	
	OL 45500	H.e.			Ng 7	H.e.	
	OH 9	H.e.			Ng 10	H.e.	
	Daka	H.e.			Ng 11	H.e.	
	Kabwe	mP.H.			Ng 12	H.e.	
	Bodo	mP.H.			Ngawi	H.e.	y
	Omo Kibish 2	mP.H.			Wajak	Recent H.s.	
	LH 18	mP.H.		Europe	Ceprano	U	
	ES 11693	mP.H.			Petralona	mP.H.	
	Ndutu	mP.H.			Arago XXI	mP.H.	
	Salé	U			Saccopastore 1	H.n.	
	Omo Kibish 1	Early H.s.			Saccopastore 2	H.n.	
	Jebel Irhoud 1	Early H.s.	y		La Ferrassie	H.n.	y
	Jebel Irhoud 2	Early H.s.	y		La Chapelle	H.n.	y
	Fish Hoek	Recent H.s.			Cro Magnon 1	H.n.	y
Georgia	D 2280	H.e.	y		Abri Pataud	Recent H.s.	y
	D 3444	H.e.	y				

China	Zkd 3	H.e.	y	Israel	Skhul 5	Early H.s.	
	Zkd 5	H.e.	y		Jebel Qafzeh 6	Early H.s.	y
	Zkd 11	H.e.	y		Jebel Qafzeh 9	Early H.s.	y
	Zkd 12	H.e.	y	Australia	WLH-50	Recent H.s.	y
	Dali	mP.H.	y		KS 17	Recent H.s.	y
	Liujiang	Recent H.s.	y				

1, ER = East Rudolf, OH = Olduvail Hominid, WT = West Turkana, OL = Olorgesailie, LH = Laetoli Hominid; ES = Eliye Springs, D = Dmanisi, Zkd = Zhoukoudian, S = Sangiran, Sm = Sambungmacan, Ng = Ngandong, WLH = Willandra Lake Hominid, KS = Kow Swamp

2, H.e. = *H. erectus*, H.h. = *H. habilis*, H.r. = *H. rudolfensis*, mP.H. = mid-Pleistocene *Homo*, Early H.s. = Early *H. sapiens*, Recent H.s. = Recent *H. sapiens*, H.n. = *H. neanderthalensis*, U = unknown

3, In some analyses the H.h. and H.r. fossils were combined into one category, Early *Homo* (E.H.)

For the comparative recent *H. sapiens* sample, four individuals each were randomly selected from 11 recent human populations. The resulting sample of 44 recent humans had approximately the same number of males and females and represented a wide geographic and climatic range from Africa, Europe, Asia, Australia and North America. Additional Late Pleistocene modern humans listed in Table 3.1 were utilized from Africa, China, Europe and Australia.

Very young individuals (i.e., Mojokerto) were not included in any analysis. Age estimates for WT 15000 initially ranged from 10.5 to 13.5 years based on dental and skeletal indicators of maturity, respectively (Smith, 1993). Several studies have found both dental and skeletal indicators of age to be problematic, but it was unclear whether the estimates were likely to be too old (Smith, 1993) or too young (Clegg and Aiello, 1999). A more recent estimate of age at death for WT 15000 was eight years based on enamel formation and estimated molar emergence times (Dean *et al.*, 2001). Despite the subadult status of WT 15000, it represents one of only three well-preserved crania often

assigned to *H. ergaster*, and analyses were therefore performed both with and without this specimen when available. The occipital synchondrosis of ER 42700 was nearly fused, and this fossil likely represents an older subadult or young adult (Leakey *et al.*, 2003) and was treated similarly to WT 15000. The age of Zkd 3 is unclear. It may be a young subadult (8-9 years of age) (Weidenreich, 1943), an older subadult (Black, 1929, 1931; Antón, 2001) or an adult (Mann, 1971). Analyses of intraspecific variation presented in Chapter 4 indicated that Zkd 3 was within the range of shape variation present in the adult Zhoukoudian fossils (e.g., Zkd 5, 11 and 12) and it was therefore included in analyses when possible.

A priori groups were necessary to test for significant taxon effects and to perform canonical discriminant analysis to examine the affinities of specimens with less certain taxonomic attributions. For the sake of clarity, the following species / groups were recognized: *H. habilis*, *H. rudolfensis*, *H. erectus* (sensu Rightmire, 1990), mid-Pleistocene *Homo*, *H. neanderthalensis* and *H. sapiens*. Table 3.1 indicates which specimens were assigned to each of these species. *H. sapiens* included both early (i.e., Skhul, Jebel Qafzeh, Jebel Irhoud) and recent (Upper Paleolithic through the present) members of the species. Only the early *H. sapiens* specimens were incorporated into the “fossils only” analyses. The two earliest species of *Homo*, *H. habilis* and *H. rudolfensis*, were sometimes treated as a single group, “early *Homo*.” The group assignments of individual early *Homo* fossils were explicitly addressed for each analysis in the Results section. ER 42700, Ceprano and Salé were treated here as *H. sp. incertae sedis*, and their species status was addressed in this study. These individuals were generally treated both as separate ‘groups’ and placed within the most likely taxon or taxa for the purposes of

significance testing. The treatment of these taxonomically ambiguous cases is also addressed in the Results section.

Methods

Geometric morphometrics

Data collection: 3D Landmark and curve data were acquired from each specimen with a Microscribe 3D-X digitizer. 11 midline and 66 bilateral landmarks (143 total), as well as semilandmarks from the MFP, SFT and MOP curves were analyzed; definitions and abbreviations can be found in Table 3.2. Each curve is a series of landmarks (termed semilandmarks) taken along a cranial contour like the midsagittal plane or along the temporal squama. Each curve was resampled to an identical number of evenly spaced semilandmarks for each specimen using weighted linear interpolation. The landmark protocol included landmarks and curves from all regions of the vault, face and base and was similar to landmark sets employed by Frost *et al.* (2003), Harvati *et al.* (2004) and McNulty *et al.* (2006). In addition to the landmarks recorded directly with a digitizer, four landmarks (metopion, the mid-parietal and the mid-temporal squama left and right), were calculated as midpoints along the ‘curves’ taken between glabella and bregma (MFP), bregma and lambda (MPP) and along the temporal squama suture (TSP), respectively.

Table 3.2: Landmarks and curves: definitions and abbreviations.

<i>Landmarks / Curves</i>	Abbr.	Definition	Ref.
<i>Dorsal Landmarks</i>			
Inion	IN	point at which the superior nuchal lines merge in the external occipital protuberance (or linear tubercle)	2
Opisthocranion	OPC	the most posterior midline ectocranial point	6
Lambda	LA	the apex of the occipital bone at its junction with the parietals, in the midline	1
Bregma	BR	posterior border of the frontal bone in the midline;	1
Midline post-toral sulcus	PTS	minima of concavity on midline post-toral frontal squama	6
Glabella	GL	most anterior midline point on the frontal bone, usually above the frontonasal suture	2
Nasion	NA	the intersection of the fronto-nasal suture and the median plane	1
Alveolare	AL	midline point at the inferior tip of the bony septum between the upper central incisors	2
Alare	ALR	the most lateral point on the margin of the nasal aperture	2
Zygoorbitale	ZO	point where the orbital rim intersects the zygomaticomaxillary suture	2
Supraorbital notch	SON	point of greatest projection of notch into the orbital space, taken on the medial side of the notch	6
Frontomale temporale	FMT	point where the frontozygomatic suture crosses the temporal line (or outer orbital rim)	2
Frontomale orbitale	FMO	point where the frontozygomatic suture crosses the inner orbital rim	2
Mid-torus inferior	MTI	point on inferior margin of supraorbital torus roughly at the middle of the orbit (on superior margin of orbit)	3

Mid-torus superior	MTS	point on superior aspect of supraorbital torus, directly above mid-torus inferior on anterior aspect of torus	3
Anterior pterion	AP	where coronal suture intersects sphenofrontal or sphenoparietal suture	
Jugale	JG	the point in the depth of the notch between the temporal and frontal processes of the zygomatic	2
Porion	PO	uppermost point on the margin of the external auditory meatus	2
Auriculare	AU	a point vertically above the center of the external auditory meatus at the root of the zygomatic process	2
Malar root origin	MR	point where malar root arises from the maxilla (often a point of convexity between malar juga and malar root)	6
Frontotemporale	FT	the point where the temporal line reaches its most anteromedial position on the frontal	2
Parietal notch	PN	on posterosuperior border of the temporal where the squamosal and parietomastoid sutures meet	2
Asterion	AS	the common meeting point of the temporal, parietal, and occipital bones, on either side	1
Posterior Temporal Line	PT	point where superior temporal line crosses the parieto-mastoid suture	
<i>Ventral Landmarks</i>			
Opisthion	OP	midline point at the posterior margin of the foramen magnum	2
Tympanomastoid junction	TM	point where tympanic tube and mastoid fissure meet laterally	
Medial petrotympanic crest	MPT	most medial point of petrotympanic crest at level of carotid canal	5

Lateral petrotympanic crest	LPT	lateral origin of petrotympanic crest	5
Stylomastoid foramen	SF	posterior border of stylomastoid foramen	4
Postglenoid	PG	Infero-lateral most point posterior to glenoid fossa and anterior to ectotympanic tube (corresponds to postglenoid process)	3
Entoglenoid	EG	most inferior point on the entoglenoid pyramid	4
Lateral articular fossa	LAF	deepest point on the lateral margin of the articular eminence	4
Center of mandibular fossa	CMF	the intersection of the perpendicular axes through the longest and widest parts of the mandibular fossa	
Medial squamo-tympanic fissure	MST	intersection of squamotympanic fissure with medial edge of mandibular fossa	
Lateral squamo-tympanic fissure	LST	Intersection of squamotympanic fissure with lateral edge of mandibular fossa	
Foramen spinosum	FS	point on posterior margin of foramen spinosum	
Temporosphenoïd suture	TS	point where temporosphenoïd suture passes from squama to cranial base (often on infratemporal crest)	
Lingual canine margin	LC	most lingual aspect of canine alveolar process	6
M1-M2 contact	M1-2	point of contact projected onto buccal alveolar margin	3
M2-M3 contact	M2-3	point of contact projected onto buccal alveolar surface	6
Metopion	ME	point midway between glabella and bregma in midline, calculated <i>a postieri</i>	2
Mid-parietal	MP	Point midway between bregma and lambda in the midline, calculated <i>a postieri</i>	
Mid-temporal squama	MT	Point midway along the temporal squama, calculated <i>a postieri</i>	

Curves

Midsagittal Frontal Profile	MFP	from bregma to glabella along midline
Midsagittal Parietal Profile	MPP	from lambda to opisthion along midline
Temporal Squama Profile	TSP	from temporo-sphenoid suture to parietal notch along temporal suture
Superior Frontal Torus	SFT	from frontomalarotemporale to the midline along the supero-anterior edge of the frontal torus
Midsagittal Occipital Profile	MOP	from lambda to opisthion along midline

¹ Howells, 1973 ² White and Folkens, 2000 ³ Frost, 2001 ⁴ Harvati, 2001 ⁵ Harvati, 2003 ⁶ McNulty, 2003

Landmark mirroring: While most *H. erectus* calvaria and crania preserve the cranial vault and the lateral basicranium (particularly the mastoid and temporomandibular regions), the exact structures preserved vary among individuals. Due to the constraints of the current software packages, individual analyses could only be run without any missing data. One strategy which maximized the number of specimens available for analyses was to mirror missing bilateral landmarks.

Bilateral landmarks missing unilaterally were mirrored to the other side for all specimens. The procedure is straightforward. First, a ‘reflection’ is created for each specimen – this is a second landmark configuration where the midline landmarks are preserved as in the original but the right and left landmarks are reversed. In the second step the original and its reflection are superimposed by generalized Procrustes analysis (GPA; explained below) which permits the right and left landmarks to be reflected as in a mirror image. The reflected bilateral landmark is then substituted for the missing landmark in the original, creating a more complete landmark configuration. This step is

essential in including incompletely preserved fossil specimens. The remaining bilateral landmarks were then averaged with their reflected configurations in order to minimize the effects of bilateral asymmetry, especially in fossil specimens (Bookstein, 1996; McNulty *et al.*, 2006).

Because landmark mirroring does assume a high degree of symmetry in the original specimens, adjustments to fossils exhibiting marked asymmetries due to taphonomic processes were necessary. In the case of WT 15000, plastic deformation of the cranium has resulted in a misalignment of the midline of the upper face, palate and the midsagittal plane of the neurocranium (Walker and Leakey, 1993). Therefore the right lateral supraorbital torus landmarks as well as right PN, AS and PT were removed so that the landmarks included in the GPA and subsequent mirroring steps were reasonably symmetrical. The final result was a relatively complete neurocranium where the removed bilateral landmarks were replaced with those from the opposite side. Similarly, ER 3883 suffered from plastic deformation (Wood, 1991), resulting in asymmetries of the left and right temporal and occipital bones. The left basal landmarks, as well as left PO, PN, AS and PT were deleted and mirrored from the right side.

Taphonomic processes have resulted in misalignments between the vault and the face in several specimens including WT 15000 and ER 1813. Because the mirroring process assumes symmetry, these misalignments can create problems during the superimposition step in the process of mirroring missing bilateral landmarks. To avoid introducing this artificial error, facial landmarks were mirrored and analyzed separately from the neurocranium for all specimens; for those specimens with clear misalignments between the face and the vault, the facial landmarks were removed before mirroring

neurocranial landmarks as well. Unfortunately, the lack of alignment between face and neurocranium meant that the facial landmark set had to be analyzed separately from the remainder of the cranium.

Landmark reconstruction: There were a few important *H. erectus* specimen which were missing a single key landmark. In order to include these specimens, these landmarks were reconstructed, but only when it was possible to use preserved morphology from the original fossils as a guide, as described below.

Kabwe was missing the outer table and some of the diploë in the region of inion but did preserve the occipital squama superior to this landmark. Visual examination of other fossil *Homo* specimens indicated that La Ferrassie and Saccopastore 1 exhibited very similar occipital curvature, so the average of inion for these specimens was used for Kabwe. A slightly different procedure was used to reconstruct bregma in Zkd 5. Portions of both temporal bones were recovered in the mid-1930s and described by Weidenreich (1935, 1936/37, 1943). In 1966, members of the Institute of Vertebrate Paleontology and Paleoanthropology recovered both a frontal and an occipital bone that also belong to Zkd 5 (Qiu *et al.*, 1973; but see Schwartz and Tattersall, 2003). Together these form a nearly complete cranium lacking its superior aspect. While most of the frontal squama is present, the posterior border is not complete. This specimen has been reconstructed with plaster in the area of bregma. The midsagittal curve was recorded from glabella to the general region of bregma along the reconstructed region, and Zkd 2, 3, 10, 11 and 12 were used only to estimate the position of bregma along this curve.

In order to include a European representative of mid-Pleistocene *Homo* in those analyses addressing the position of Ceprano, the tympanomastoid landmark was estimated for Petralona. Because there was no curve which incorporated this landmark, tympanomastoid was estimated as the average of all fossil *Homo* in the no opisthocranion, no mid-parietal landmark set. Using the average position for all *Homo* avoided biasing the analysis in the direction of any particular taxon, but this method of landmark estimation was judged inferior to those approximations discussed above because it was not possible to use the original morphology of Petralona as a guide. Hence, analyses were run both with and without Petralona.

Initial analyses highlighted the very anterior position of lambda in ER 1813. As noted by Wood (1991), this landmark was difficult to locate due to a complicated pattern of sutures and accessory ossicles in the lambdoid region of this fossil. Positioning lambda at the posterior end of the sagittal suture (the anterior end of the lambdoid ossicles) (Wood, 1991), resulted in a particularly long occipital plane, in addition to affecting the relative position of the mid-parietal landmark. To examine the effect of this single landmark, a second (alternative) position for lambda was estimated along MFP in ER 1813 using the height of lambda in five other early *Homo* specimens (ER 1470, 1805, OH 13, 16 and 24) as a guide. This resulted in a more inferiorly and posteriorly positioned lambda. The original landmark configuration for ER 1813 continued to be used in all analyses, but analyses were also re-run with this alternative landmark configuration for comparative purposes.

Landmark superimposition: Before statistical analysis was undertaken, landmark configurations for all specimens were superimposed using GPA which removes variation due to location and orientation of the original specimens during data collection, as well as differences in scale among individuals (Rohlf, 1990; Rohlf and Marcus, 1993; O'Higgins, 2000; Adams *et al.*, 2004). GPA alignment works by first superimposing centroids at the origin and scaling all configurations to a unit centroid size. They are then rotated until the residual sum-of-squares can no longer be improved. This fit is accomplished through an iterative approach whereby all specimens are initially aligned to an individual specimen (which acts as a temporary average shape) using a least-squares approach, the average shape is then recalculated and the specimens are realigned to this new average and scaled, and the preliminary residual sum-of-squares is calculated. This least-squares process is repeated until the differences in the residual sum-of-squares falls below a set tolerance level (Gower, 1975; Rohlf and Slice, 1990).

The superimposed landmarks were then treated as variables (termed Procrustes shape variables) in standard multivariate statistical analyses. Geometric morphometrics is theoretically comparable to traditional morphometrics, but has the advantage of including additional information about the original geometry (i.e., shape) of the organism. In addition, landmark data allow visual comparisons of individual or mean shapes, another improvement over traditional morphometrics. While GPA does remove scale, it does not remove shape correlated with size (i.e., allometric shape). TpsSmall (Rohlf, 2003) was used to test the correspondence between this dataset in Kendall's shape space and the Euclidean space which is tangent Kendall's shape space at the mean configuration (Marcus *et al.*, 2000). The very tight correlations ($R^2 = 0.99999 - 1.0$)

between the pairwise Procrustes distances (calculated in Kendall's shape space) and the pairwise Euclidean distances for all landmark sets described in Table 3.3 permitted statistical analyses to be carried out in GPA space (sensu Slice, 2001). For two-dimensional objects, GPA space is a hyper-hemisphere (Rohlf, 1999). For 3-D landmark configurations the shape space is likely to be considerably more complex (Slice, 2001; 2005).

Study design

The 'standard landmark set' used in the first several analyses consisted of landmarks that captured the sagittal profile, the widths of the posterior, anterior and mid-vault as well as the orientation and shape of the supraorbital torus and the basic shape and position of the temporomandibular joint. In order to accommodate individuals missing one or more of these landmarks, analyses were also re-run without some landmarks (the no-metopion landmark set and the no-opisthion/no-mid-parietal landmark set). Table 3.3 provides a list of the landmarks and sample composition for each analysis. Figure 3.2 illustrates the location of landmarks in the standard landmark set on Ng 12.

Three additional landmark sets were used to examine more limited regions of the cranium: the face, the frontal bone, the temporal base and the occipital bone as described in Table 3.3. In addition to standard landmarks, the frontal and occipital bone analyses also incorporated semilandmarks from the MFP, SFT and MOP curves (defined in Table 3.2). Landmarks from each of these analyses were illustrated in Figures 3.3-3.6.

Table 3.3: Composition of landmark sets and samples.

Analysis	Landmarks ¹	# Landmarks	Sample ²	# Specimens
Standard landmark set, all-specimens	IN, LA, MP, BR, ME, PTS, GL, SON, FMT, FMO, PO, AU, FT, PN, AS, AP, MTP, OP, TM, PG, EG, TS	36	<u>H. erectus</u> : ER 3733, 3883, Daka, D 2280, 3444, S 17, Sm 3, Ng 6, 11, 12, Zkd 11 and 12 <u>H. habilis</u> : ER 1813 <u>H. neanderthalensis</u> : La Chapelle and La Ferrassie <u>mid-Pleistocene Homo</u> : Kabwe and Dali <u>Early H. sapiens</u> : Skhul 5 <u>Recent H. sapiens</u> : 47 ³	65
Standard landmark set, fossils only	Same as above	36	Same as above, without 47 recent <i>H. sapiens</i>	18
No-metopion set, all-specimens	Same as standard landmark set - ME	35	+ <u>Unknown</u> : ER 42700	66
No-metopion set, fossils only	Same as above	35	Same as above	19
No-opisthion/no-mid-parietal set, all-specimens	Same as standard landmark set - OP, MP	34	Same as standard landmark set + <u>H. erectus</u> : Zkd 3 and 5 <u>Early H. sapiens</u> : Jebel Irhoud 1 <u>Unknown</u> : Ceprano	68
No-opisthion/no-mid-parietal set, fossils only	Same as above	34	Same as above, without 47 recent <i>H. sapiens</i>	22

In the temporal base analysis one *H. habilis* fossil and one probable early *Homo* specimen (ER 1805) were analyzed as part of the larger sample. Although the majority of workers have treated ER 1805 as a member of *H. habilis* (i.e., Wood, 1991; Skelton and McHenry, 1992; Lieberman *et al.*, 1996; Strait, *et al.* 1997; Miller, 2000), previous taxonomic allocations of ER 1805 have ranged from australopith to *H. ergaster* (e.g., Groves and Mazák, 1975; Tobias, 1980) and the most recent review of this fossil concluded that it does not belong in *H. habilis* (Prat, 2002). Due to this uncertainty, this specimen was treated as early *Homo* only if its morphological pattern corresponds closely to OH 24. Otherwise it was treated as *incertae sedis*.

H. erectus species definition: While most previous comparisons of *H. erectus* were explicitly or implicitly made with modern humans, it is important to also compare *H. erectus* to both contemporaneous species as well as to the taxa which bracket it chronologically. Principal components analysis (PCA) and canonical variates analysis (CVA) were used to examine shape differences between *H. erectus* and other *Homo* taxa, particularly those species which were thought to share either an ancestor-descendant or sister-taxon relationship with *H. erectus*. Multiple analysis of variance (MANOVA) was used to test for group differences in principal component (PC) scores on the first four components, and a Bonferroni correction was applied to the *post hoc* contrasts among groups on each of these PCs. A limited number of PCs were used due to the limited degrees of freedom available as the result of small fossil sample sizes. In addition to PCA, comparisons were

Figure 3.2: Illustration of standard landmark set on Ng 12. Abbreviations refer to Table 3.2, where definitions for all landmarks can be found. Those landmarks shown in black and white stripes (i.e., EG and OP) are not visible in this view and their position is approximated. The wireframe connecting landmarks is for visualization purposes only and does not represent actual data.

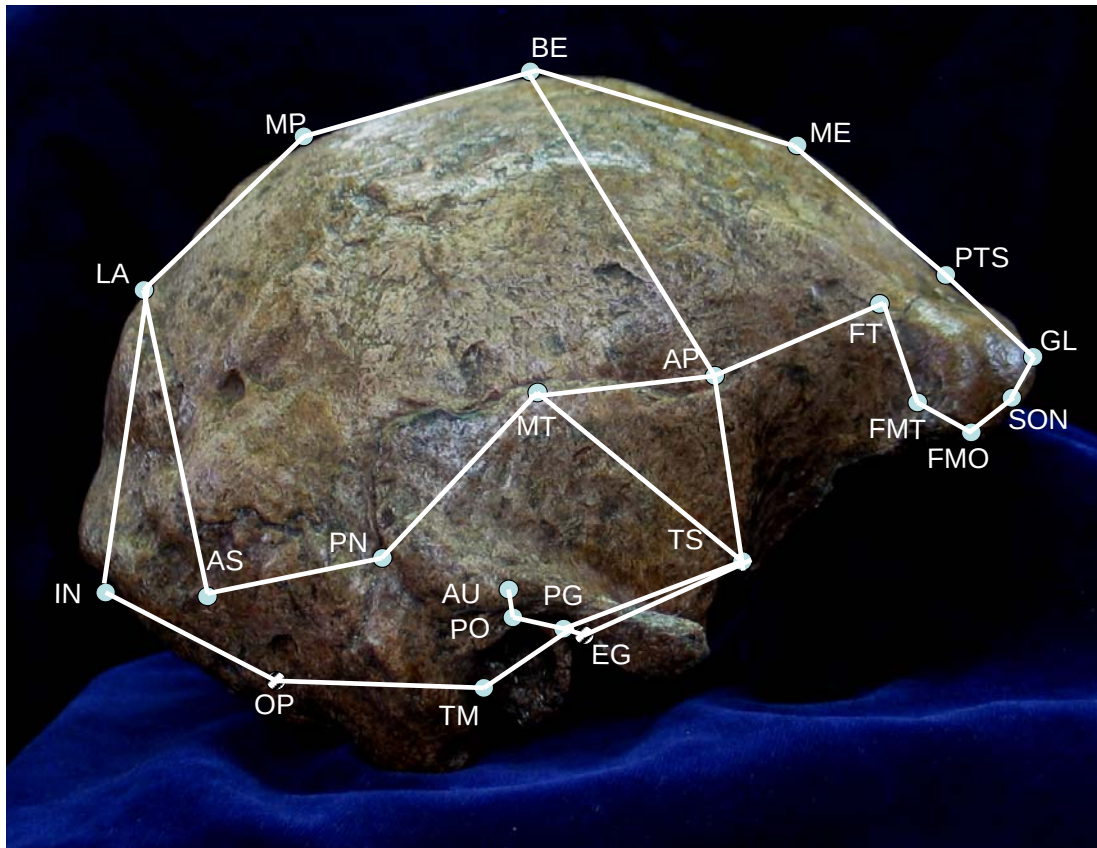
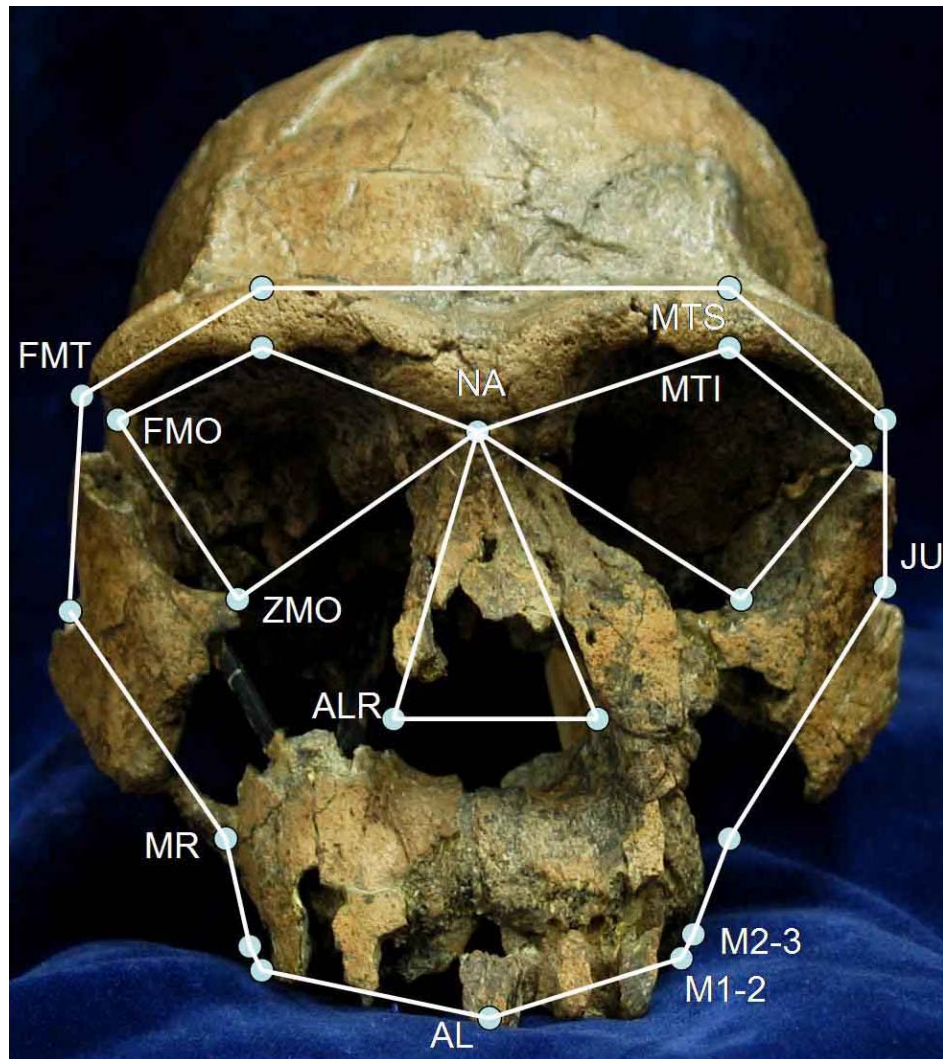


Figure 3.3: Illustration of facial landmark set on ER 3733. Abbreviations and definitions of landmarks are found in Table 3.2. The wireframe connecting the landmarks is for visualization purposes only and does not represent actual data.



Courtesy of National Museums of Kenya

Figure 3.4: Illustration of frontal bone landmark set on Sm 1. The blue circles are landmarks (abbreviations and definitions provided in Table 3.2) and the yellow circles are semilandmarks. The wireframe connecting the landmarks and semilandmarks is for visualization purposes only and does not represent actual data.

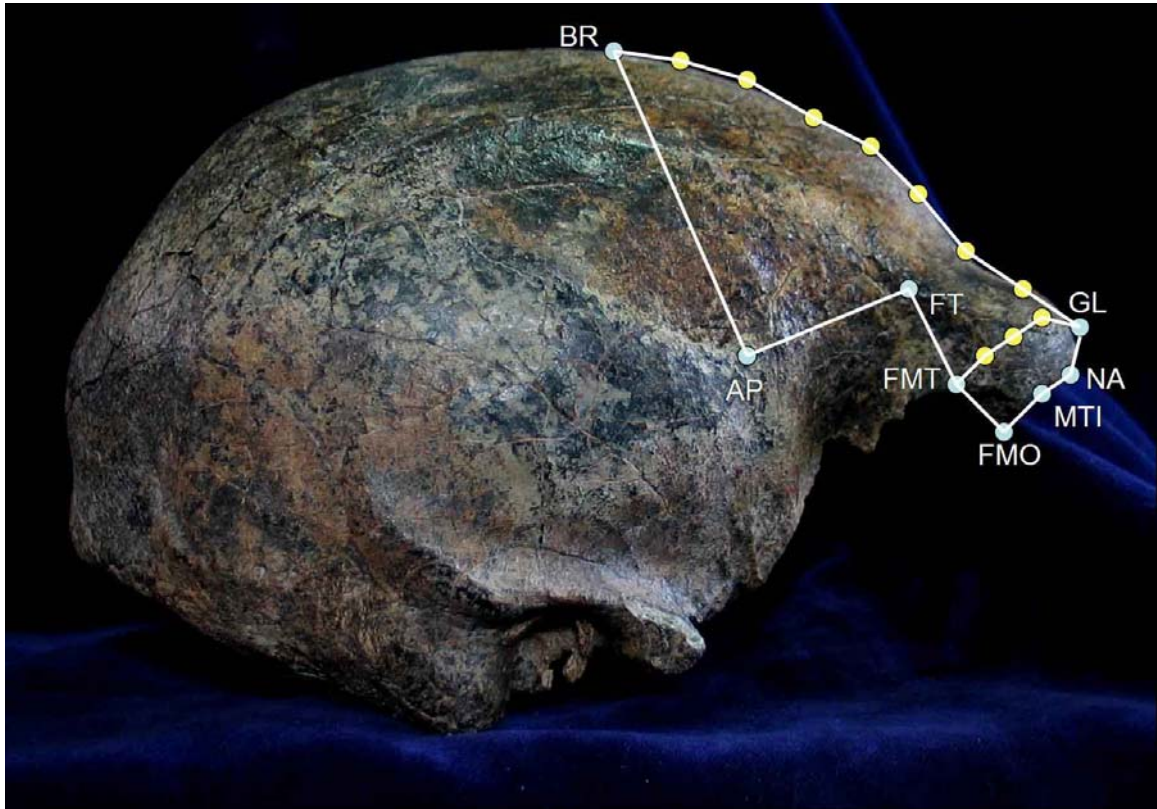
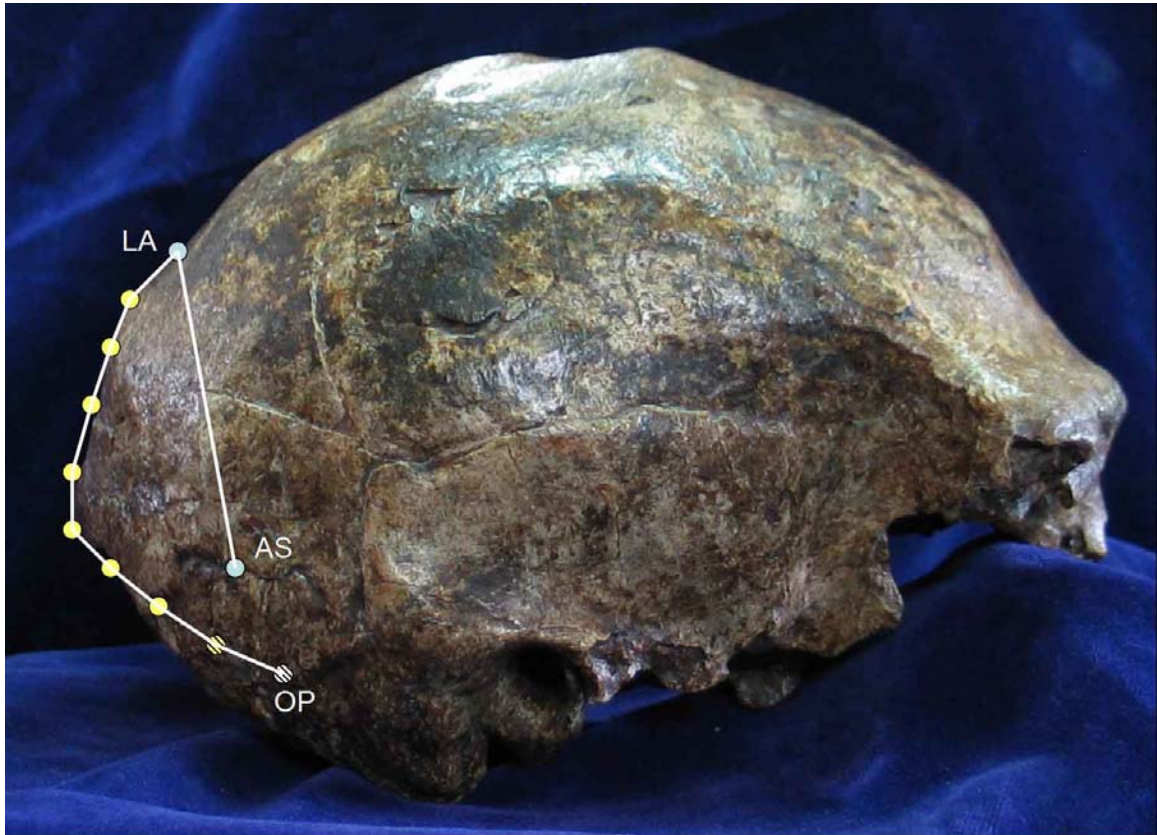


Figure 3.5: Illustration of the temporal base landmark set on S 4. The landmark abbreviations and definitions are available in Table 3.2. The wireframe connecting the landmarks is for visualization purposes only and does not represent actual data.



Figure 3.6: Illustration of occipital bone landmark set on Ng 7. The blue circles are landmarks (see Table 3.2 for abbreviations and definitions) while the yellow circles are semilandmarks. Striped circles indicates that the landmark positions are approximate as they are not visible in lateral view. The wireframe connecting the landmarks and semilandmarks is for visualization purposes only and does not represent actual data.



made between the mean shape configurations of *H. erectus* and all other taxa for the standard, frontal bone and occipital bone landmark sets. In the neurocranial and frontal bone comparisons, some slightly less complete specimens were also included in order to increase the sample sizes of the comparative species, because when only one specimen was available the idiosyncrasies of that particular fossil tended to dominate the comparisons. *H. habilis*, however, was represented by only ER 1813 because the shape of the next most complete specimen, OH 24, was affected by plastic deformation. By incorporating fossil specimens which were missing only five or fewer unique landmarks

(counting each bilateral landmark once) for the neurocranial analysis and only one unique landmark for the frontal bone analysis, it was possible to increase the sample size of each species (with the exception of *H. habilis*) to at least two individuals. This also had the added advantage of increasing the sample size of the *H. erectus* samples in these comparisons.

Homo erectus species composition: There are several specimens which have been assigned to *H. erectus* but which have also been placed within other species of *Homo*. Among the most complete specimens that are potentially *H. erectus* are ER 42700, a young adult specimen from Kenya, and the calvarium from Ceprano, Italy. In addition to visual assessment of affinities in PCAs, canonical discriminant analysis (CDA, also known as multiple discriminant analysis) was performed to assign these specimens of uncertain species status to their proper taxon.

CDA determines the linear combination of predictors (dependent variables, here PC scores on any PC which accounted for 5% or more of the total variance of the sample), called canonical axes, that provides maximum separation of (*a priori*) group means. The canonical axes can then be used to 1) classify individuals of unknown group membership into one of these groups, and 2) calculate the posterior probability associated with this classification for each specimen. The classification is based on the Mahalanobis distance between the individual specimens to each *a priori* group centroid. In all cases the CDA was run with three *a priori* groupings: *H. sapiens* (including both early and recent specimens), *H. erectus* and mid-Pleistocene *Homo* / *H. neanderthalensis*. mid-Pleistocene *Homo* and *H. neanderthalensis* were combined into a single unit in the CDA

because of their very small sample sizes. A jackknife validation procedure was used to evaluate the effectiveness of the canonical roots to correctly classify individual specimens. The jackknife procedure removes each specimen sequentially from the sample, performs the CDA without this specimen, and then classifies it into a group based on the new canonical axes. The results of both the jackknife procedure and the posterior probabilities associated with the classification of each unclassified specimen (i.e., ER 42700, Ceprano and Salé) to a taxon were reported.

As a final approach to evaluating the affinities of these fossils in regards to overall cranial shape, the landmark configurations of each of these specimens was compared to the average landmark configurations of several other *Homo* species. These comparisons allowed for a more detailed assessment of similarities and differences between these specimens and other *Homo* taxa. As discussed previously, the mid-Pleistocene *Homo* “group” likely encompasses more than one species. However, due to the uncertainties surrounding the taxonomic assignments of individual mid-Pleistocene fossils, and the small sample size of this sample, they were all incorporated into the mid-Pleistocene *Homo* mean landmark configuration.

Phylogeny and cranial shape in *Homo*: Distance trees were generated using true Procrustes distances among individuals or group means (when available) from several of the landmark sets in Table 3.3. These trees were created using PHYLIP 3.57c (Felsenstein, 2007) and visualized in TreeEditor 2.12 (Tamura, 2007). The results of several tree building methods were presented below: both ordinary and weighted least-squares (WLS) (Cavalli-Sforza and Edwards, 1967; Fitch and Margoliash, 1967),

neighbor joining (NJ) (Saitou and Nei, 1987), and minimum evolution (ME) (Kidd and Sgaramella-Zonta, 1971; Rzhetsky and Nei, 1993). All trees were rooted using *H. habilis* as the outgroup. These methodologies were similar to those employed by Lockwood *et al.* (2004).

Distance trees were generated based on two different taxonomies, which were designed so that the distance trees were comparable to the phylogenetic trees proposed by Rightmire (1998b, 2001) and Hublin (2001, p. 117, Fig. 8.10c). These comparisons served to test the ability of 3D cranial shape data to recover those relationships which were supported by shared derived characters. The less speciose taxonomy used by Rightmire recognizes four species of later *Homo*: *H. erectus*, *H. heidelbergensis* (equivalent to the mid-Pleistocene *Homo* grouping used here), *H. neanderthalensis* and *H. sapiens* (Table 3.1), whereas the more speciose taxonomy of Hublin recognizes six post-*habilis* species of *Homo*: *H. ergaster*, *H. erectus*, *H. mauritanicus* / *H. antecessor*, *H. neanderthalensis*, *H. rhodesiensis* and *H. sapiens* (Table 3.4). Hublin (2001) considered the early European fossils, such as Petralona and Arago, to be early members of the Neanderthal lineage and are therefore included in this species in the more speciose model.

Table 3.4: Alternative, more speciose *Homo* taxonomy based on Wood (1991), Hublin (2001) and Manzi *et al.* (2001).

<i>H. ergaster</i>	<i>H. mauritanicus</i> / <i>antecessor</i>
East Rudolf (ER) 3733, 3883	Ceprano
West Turkana (WT) 15000	<i>H. neanderthalensis</i>
Dmanisi (D) 2280, 3444	La Ferrassie
<i>H. erectus</i>	La Chapelle

Zhoukoudian (Zkd) 3, 5, 11, 12	Saccopastore 1 and 2
Sangiran (S) 2, 17	Gibraltar
Sambungmacan (Sm) 1, 3	Petralona
Ngandong (Ng) 6, 10, 11, 12	Arago 21
Ngawi	<i>H. sapiens</i>
Olduvai Hominid (OH) 9	Jebel Irhoud 1, 2
Olorgesailie (OL) 45500	Skhul 5
Daka	Jebel Qafzeh 6, 9
<i>H. rhodesiensis</i>	Unknown taxon
Kabwe	ER 42700
Bodo	
Omo Kibish 2	
LH 18	
Eliye Springs (ES) 11693	
Salé	
Dali	

A weakness in this analysis was the absence of European representatives of mid-Pleistocene *Homo* in the less speciose phylogeny. Therefore, Petralona with the estimated tympanomastoid landmark (as described above) was used to test whether the inclusion of European specimens in the mid-Pleistocene *Homo* group affected the distance trees.

In order to examine the broader implications of this dataset for cranial evolution in the genus *Homo*, the shape transitions associated with each node on these two phylogenetic trees were visualized using the no-opisthion/no-mid-parietal landmark set. The sample compositions for each species average are listed in Table 4.9. I will address the assignment of taxonomically ambiguous specimens in more detail here. *H. ergaster* was restricted to the earliest and smallest fossils from Africa and Georgia. Therefore, OH 9 and Daka were assigned to *H. erectus* s.s. in the more speciose phylogeny. Because

Rightmire (2004) includes Ceprano in *H. erectus*, it is treated as such in the less speciose scenario, but it is included in *H. mauritanicus* in the more speciose model (Hublin, 2001). While Dali is included in the fairly inclusive *H. heidelbergensis* in Rightmire's (2001) phylogeny, it is not addressed explicitly by Hublin (2001). Here it is included in *H. rhodesiensis* in this model based on its overall morphology, geological age (~270 Ka, Xiao *et al.*, 2002) and the fact that it does not show any derived Neanderthal features (Wu, 1981; Wu and Poirer, 1995). It is worth noting that excluding this specimen from *H. rhodesiensis* did not change the average landmark configuration in a meaningful way. Whereas Petralona was included in *H. heidelbergensis* in the less speciose phylogeny (Rightmire, 1998b, p. 224), it was assigned to *H. neanderthalensis* on the more speciose tree because Hublin (2001, p. 115) argued that all European fossils showing even incipient Neanderthal features be included in this species. As with the comparison of the average *H. erectus* shape to the mean configurations of each of the other *Homo* species, some nearly complete specimens were included in the averages to increase the sample sizes of the comparative taxa.

Contribution of *Homo erectus* to modern human ancestry: In order to address one of the fundamental differences between the multiregional and recent African models of modern human origins, the affinities of three early modern specimens from Indonesia and Australia were tested (WLH-50, KS 17 and Wadjak 1). PCA was used to compare them with both early and recent *H. sapiens* and other fossil *Homo* including the Indonesian hominins from Ngandong. If the three modern humans inherited certain features from the Ngandong hominins, then we might expect to see both sets of specimens separate out

together on one PC because of the covariance of those inherited features in these individuals.

CDA was also used to assess the similarities in cranial shape between the three modern humans and the Ngandong hominins on one hand and early *H. sapiens* on the other. This CDA was designed to approximate, as closely as possible, that performed with linear measurements in Hawks *et al.* (2000). The measurements used in their discriminant function were maximum cranial length, glabella-bregma chord, bregma-asterion arc, medial supraorbital height and central parietal thickness. The landmarks used in this analysis include (among others) bregma, opisthocranium, glabella and asterion as well as the superior and inferior mid-supraorbital torus landmarks as described in Table 3.3 and illustrated in Figure 3.7. The only one of Hawks *et al.*'s measurements not incorporated into this landmark set is the thickness of the parietal bone, a trait expected to be adversely affected by pathological hyperostosis observed on WLH-50 (Brown, 1989, 1992; Webb, 1990). However, my samples for early *H. sapiens* from the Middle East and North Africa were smaller than those used by Hawks *et al.* (2000) and had to be combined here. Recent modern humans were also included in the CVA as it is equally likely that the early Australian *H. sapiens* would resemble this group, and the larger sample size of this sample provided a better estimate of the within group covariance matrix. The CDA was thus performed with the following *a priori* groupings: early *H. sapiens*, recent *H. sapiens* and the Ngandong hominins.

The CDA was run twice, once including glabella and asterion (but excluding Wajak 1) and once without these three landmarks but with Wajak 1. The second CDA did not correspond as closely in its landmark configuration to the measurements used by

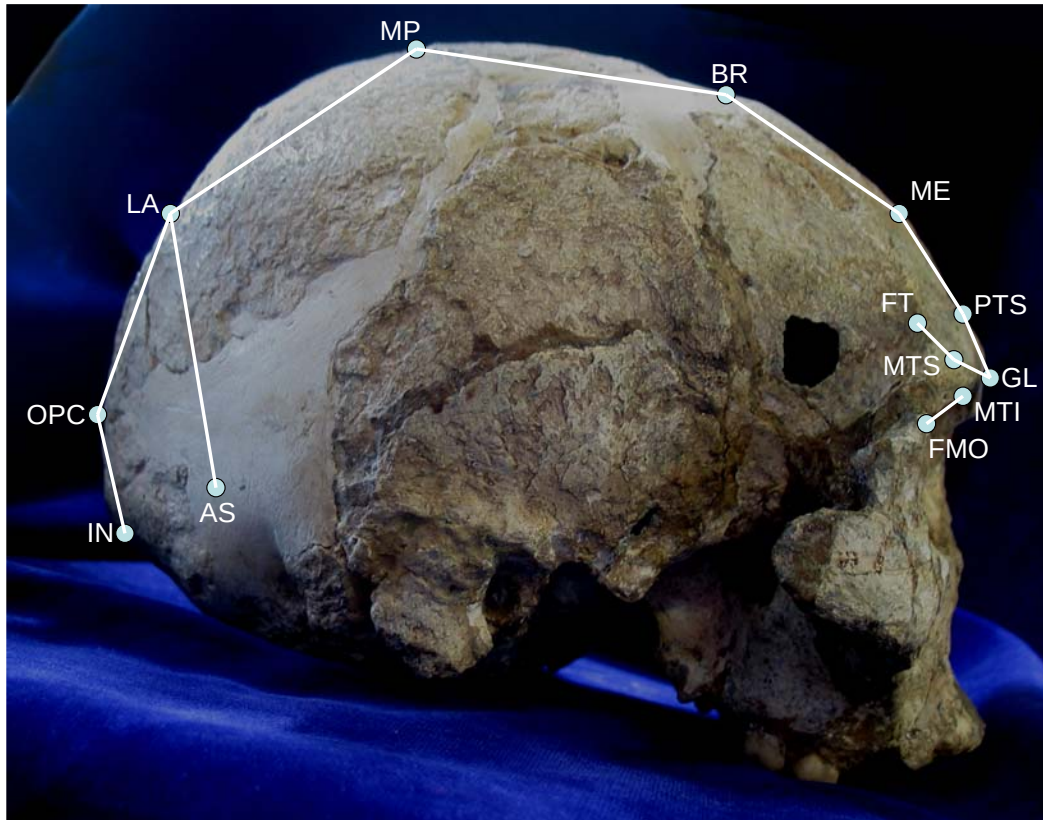
Hawks *et al.* (2000). Glabella was missing in WLH-50 but its location was estimated using clay without any depression, as suggested by Hawks *et al.* (2000).

Position of Liang Bua 1: PCA was conducted in both GPA space (as above) and in size-shape space (Mitteroecker *et al.*, 2004; also called form space: Gunz *et al.*, 2007) which, in addition to Procrustes shape variables, also includes $\ln(\text{centroid size})$ as an additional variable. This has been shown to be an effective analytical method for analyzing allometry (Mitteroecker *et al.*, 2004). While it is not known whether dwarfing in *Homo* would follow a simple allometric relationship, this does present a straightforward size – shape model against which to examine the relationship of cranial form in LB1 to both modern humans and *H. erectus*.

During excavation, LB1 was damaged in the region of the anterior frontal bone centrally (Brown *et al.*, 2004). As has been documented by other workers (Brown *et al.*, 2004; Jacob *et al.*, 2006), there was also obliteration of most cranial vault sutures. As a result, the landmark set used to examine the shape affinities of LB1 resembled the standard landmark set but was lacking the post-toral sulcus, metopion and glabellar landmarks from the frontal bone due to damage, and asterion, parietal notch and mid-temporal squama due to the inability to confidently identify these sutures (Table 3.3).

While there was some damage at bregma, this landmark was estimated using the mid-sagittal plane and the patent coronal suture as a guide.

Figure 3.7: Australians only landmarks illustrated on the mirror image of Wajak 1. Abbreviations and definitions of landmarks can be found in Table 3.2.



Results

Homo erectus species definition

PCA standard landmark set, all-specimens: As seen in Table 3.5, MANOVA ($\alpha < 0.05$) performed on scores from the first four PCs indicated significant group differences.

Posthoc pairwise comparisons indicated that *H. erectus* differed significantly from modern humans on PC 1 and 2 and from *H. habilis* (represented only by ER 1813) on PC

2 (Table 3.5). *H. erectus* did not differ significantly from either the mid-Pleistocene *Homo* group (Kabwe and Dali) or the Neanderthals, although both groups (but especially mid-Pleistocene *Homo*) scored higher on PC 1 than any *H. erectus* specimens. As seen in Figure 3.8a, taxa were generally positioned along PC 1 from the negative to positive ends in a chronological sequence. However, both Kabwe and Dali scored higher (closer to *H. sapiens*) than the geochronologically younger Neanderthals and Asian *H. erectus* fossils (i.e., Ngandong and Sambungmacan). Despite the extensive geographic and temporal range encompassed by the *H. erectus* sample, it occupies only a limited portion of both PCs 1 and 2, confirming the morphometric homogeneity of this species.

Figure 3.8b illustrates that higher scoring individuals on PC 1 have a more globular neurocranium (accomplished through an expansion along the midsagittal plane, especially around the mid-parietal), a steeper frontal squama with a reduced supraorbital torus and a more superiorly positioned and narrower anterior cranial base. In addition, the occipital squama is longer and less posteriorly projecting. The cranial vault was wider across the frontal bone (especially across frontotemporale) and the temporal squamae but narrower posteriorly. The mid-temporal squama was higher whereas asterion and the parietal notch were relatively inferiorly positioned. The entoglenoid process was also less inferiorly projecting.

Ln(centroid size) explained only a small percentage of variation (13%) in PC 2 scores (Table 3.5) and Figure 3.9 clearly shows that ER 1813 fell well above the regression line while most *H. erectus* individuals fell below the line. This suggests that the differences in shape between ER 1813 and *H. erectus* on PC 2 cannot be attributed

Table 3.5: Results of principal components analysis of neurocranial, facial, frontal, occipital and temporal base landmark sets. MANOVA was used to test for significant group differences on the first four principal components and significant group differences were then determined for each component using a Bonferroni correction (with those comparisons involving *H. erectus* in **bold**). For example, in the first analysis (Standard landmarks, all specimens), *H. sapiens* differs from all other species and mid-Pleistocene *Homo* differs from *H. habilis* on PC 1 while there are significant group differences between *H. habilis* and *H. erectus*, *H. sapiens* and mid-Pleistocene *Homo*, and between *H. erectus* and *H. sapiens* on PC 2.

Analysis	% of Variance on PC1–PC4	Regression on size R ² value ($\alpha < 0.05$)				MANOVA Wilks' Lambda P value	Pairwise Group differences (Bonferroni correction at $\alpha < 0.05$) ¹			
		1	2	3	4		1	2	3	4
Standard landmarks, all specimens	0.60	-	.13	-	-	< 0.0001	H.s.- All MP.H.- H.h.	H.h.- H.e. , H.s. & MP.H. H.e. - H.s.	-	-
Standard landmarks, fossil specimens	0.62	.46	-	-	-	< 0.0001	H.h.- All H.e. - MP.H. & H.s.	H.e. - H.n.	-	-
No metopion, all specimens	0.59	-	.09	-	-	< 0.0001	H.s.- All mP.H.- H.h.	H.h.- H.e. , H.s. & mP.H. H.e. - H.s.	-	-
No metopion, fossil specimens	0.60	-	.25	-	-	< 0.0001	H.h.- All H.e. - mP.H. & H.s. ²	-	-. ²	-
No opisthion, no mid-parietal, all specimens	0.57	.13	.12	-	-	< 0.0001	H.s.- All mP.H.- H.h.	H.h.- H.e. , mP.H. & H.s. H.e. - H.s. ³	-	-

No opisthion, no mid-parietal, fossils only	0.60	.44	-	-	-	< 0.0001	H.h.- All H.e. - H.s. & mP.H. ⁴	-	-	-
Face, all specimens	0.62	.15	.25	.12	-	< 0.0001	-	H.s.- All	-	-
Face, fossils only	0.73	-	-	-	-	0.8930	-	-	-	-
Frontal, all specimens	0.77	-	-	.19	-	< 0.0001	H.s.- All	H.e. - H.s., mP.H. & H.n.	E.H. ⁵ - mP.H.	E.H. ⁵ - mP.H.
Frontal, fossils only	0.70	-	.28	.19	.19	< 0.0001	H.e. - mP.H.	H.s. – H.e. & E.H.	-	E.H.- H.e. & mP.H.
Temporal base, all specimens	0.53	.11	-	.08	-	< 0.0001	H.s.- H.e. , H.h. & H.n. mP.H.- H.n. ⁶	ER 1805- H.e. , H.h. & mP.H.	H.e. - H.s., H.n., H.h. & mP.H.	-
Temporal base, fossils only	0.56	-	-	.13	-	0.0062	-	-	H.e. - H.n. ⁷	-
Occipital, all specimens	0.91	-	.12	.18	-	< 0.0001	H.e. - H.s., H.n & mP.H. H.s.- H.h. & mP.H. ⁸	-	-	-

Occipital, fossils only	0.88	.21	.19	-	-	0.0002	H.e.- H.n. & mP.H. ⁹	H.e.- H.s.	-	-

1, H.e. = *H. erectus*; H.h. = *H. habilis*; H.n. = *H. neanderthalensis*; H.s. = *H. sapiens*; mP.H. = mid-Pleistocene *Homo*

2, The results were reported with ER 42700 as its own taxon. If ER 42700 is included in H.e. then the differences with mP.H. and H.s. on PC 1 are not significant but it does differ from H.n. on PC 3. Also, the Wilks' lambda p value is 0.0004.

3, Results are reported with Ceprano as either H.e. or as mP.H.. When Ceprano is treated as its own group, then the H.e.- H.s. contrast is no longer significant.

4, Results reported when Ceprano is assigned to either H.e. or mP.H. (although the p value associated with Wilks' lambda is 0.0003 when Ceprano is assigned to H.e.). When Ceprano is assigned to its own taxon, an additional contrast is significant (H.e.- Ceprano on PC 3).

5, E.H. = Early *Homo* which includes both *H. habilis* (ER 1813) and *H. rudolfensis* (ER 1470).

6, In the temporal base analysis results reported here, both Salé and ER 1805 are treated as separate groups. Alternatively, ER 1805 was classified as H.h. and Salé was classified as mP.H. (all combinations were tested and were significant at $p < 0.0001$). Whenever Salé was considered to be in the mP.H. group, then the mP.H. – H.e. contrast on PC 1 was significant, and whenever ER 1805 was considered to be H.h., then there were no significant contrasts on PC 2.

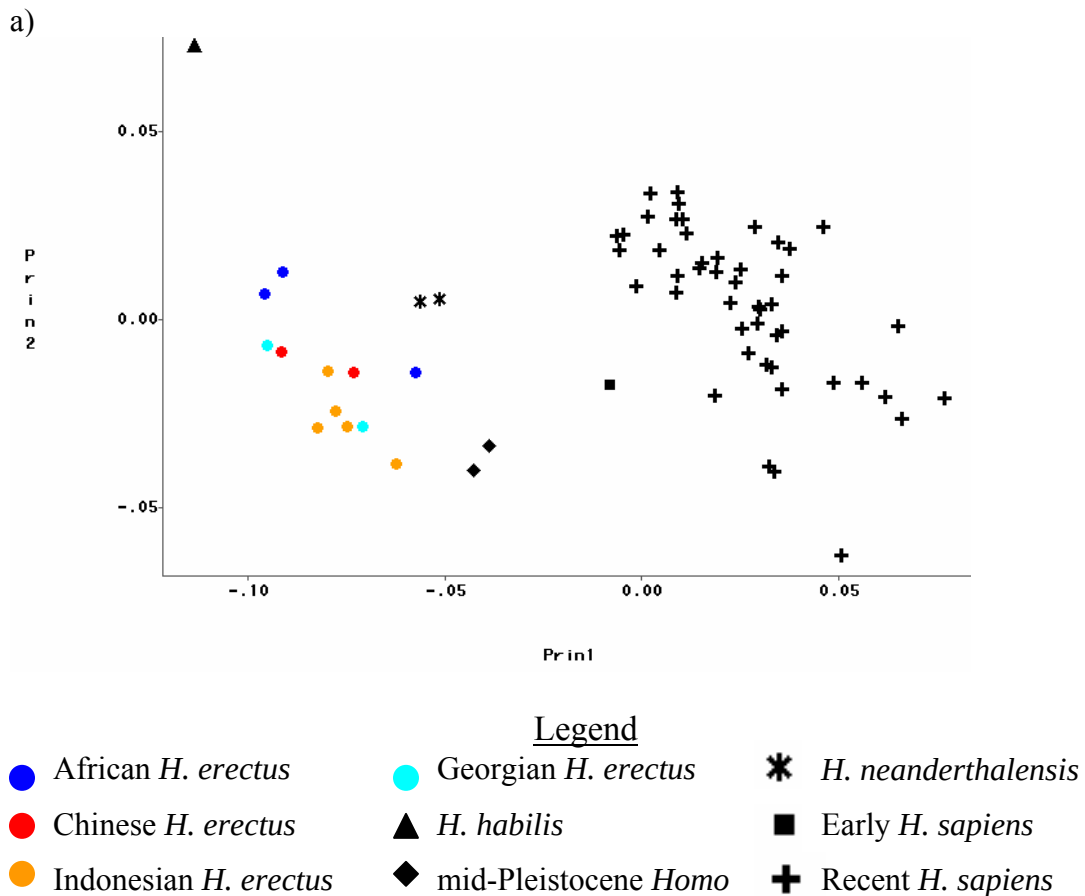
7, The results are reported for the case when Salé and ER 1805 are each treated as separate groups. When Salé is grouped as mP.H., the Wilks' lambda p value is 0.0017, but the significant contrasts remain unchanged. When Salé is considered mP.H. and ER 1805 is considered to be H.h., then the Wilks' lambda p value is 0.0022 and both H.h. and H.n. differ significantly from H.e. on PC 3.

Similarly, when Salé is placed in its own group and ER 1805 is grouped with OH 24 in H.h., H.e. differs from H.h., H.n. and mP.H. on PC 3 (Wilks' lambda p value is 0.0084).

8, The results are reported for ER 42700 as its own group. When it is classified as H.e., there is an additional significant contrast: H.e. and mP.H. on PC2.

9, The results are reported for ER 42700 as its own group. When it is classified as H.e., then the p value for Wilks' lambda is 0.0007 but the significant contrasts remain unchanged.

Figure 3.8: a) PCA of the standard landmark set, all-specimens. PC 1 versus PC 2 is shown below. *H. erectus* differs significantly from the modern human specimens on PC 1 and from ER 1813 on PC 2. While not significant, *H. erectus* is also separated from Kabwe and Dali (mid-Pleistocene *Homo*) on PC 1. Significant differences discussed here and in subsequent figures are based on the results of MANOVA on PCs 1-4, as summarized in Table 3.5. Shape differences from the negative (black solid line) to positive ends (red dashed line) of PC 1 (b) and PC 2 (c) are shown in lateral and superior views.



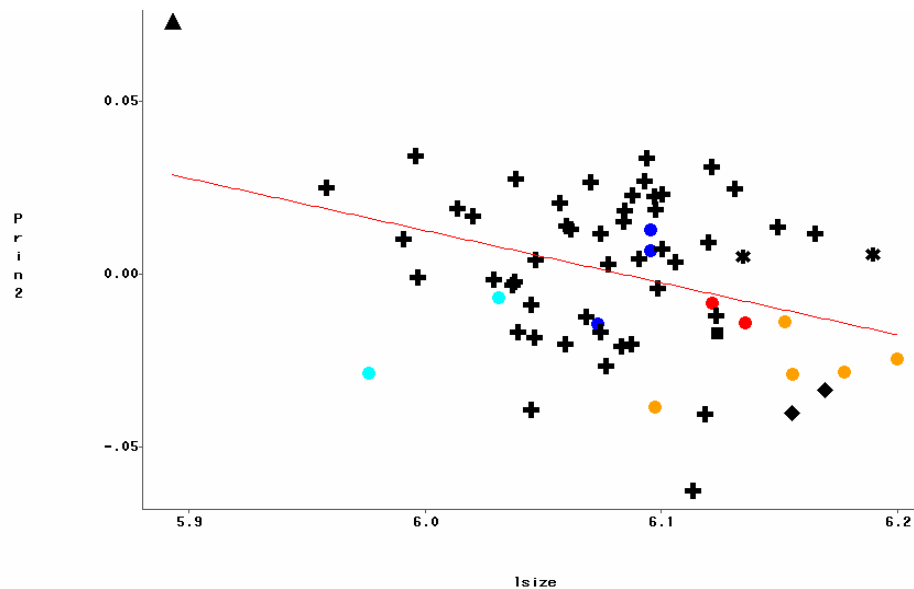
simply to allometry. These shape differences, seen in Figure 3.8c, include a shorter frontal squama; a more anteriorly positioned lambda; superior expansion at mid-parietal, bregma and metopion; and inferior extension of the base in higher scoring individuals like ER 1813. The entoglenoid was slightly more inferiorly projecting relative to the rest

of the base and there was greater constriction across frontotemporale. Higher scoring individuals also had an overall narrower neurocranium.

This PC analysis was re-run with the alternative ER 1813 landmark configuration described in the “Methods” section. This alternative configuration differed from the original in having more posteriorly and inferiorly positioned lambda and mid-parietal landmarks. Figure 3.10a demonstrates that the PC plots were very similar (as were the eigenvalues of the components) to those described in the original analysis, but ER 1813 was not as separated from the other fossils on PC 1 and particularly on PC 2. Some of the significant differences involving *H. habilis* were no longer significant (in particular the *H. habilis* – mid-Pleistocene *Homo* contrast on PC 1 and the *H. habilis* – *H. sapiens* contrast on PC 2). The *H. erectus* – *H. sapiens* contrast on PC 2 was also no longer significant. The shape differences on PCs 1 and 2, illustrated in Figure 3.10b and c, were similar to those described in the original analysis, but those differences involving the relative position of lambda, particularly along PC 2, were less noticeable.

Therefore, although the original position of lambda for ER 1813 was consistent with that used by Wood (1991), the postero-inferior repositioning of lambda based on its location in other early *Homo* fossils did result in a cranial shape for ER 1813 which was more similar to that of other fossil *Homo* specimens. While the original position recorded for lambda was used in subsequent analyses, this issue should be borne in mind.

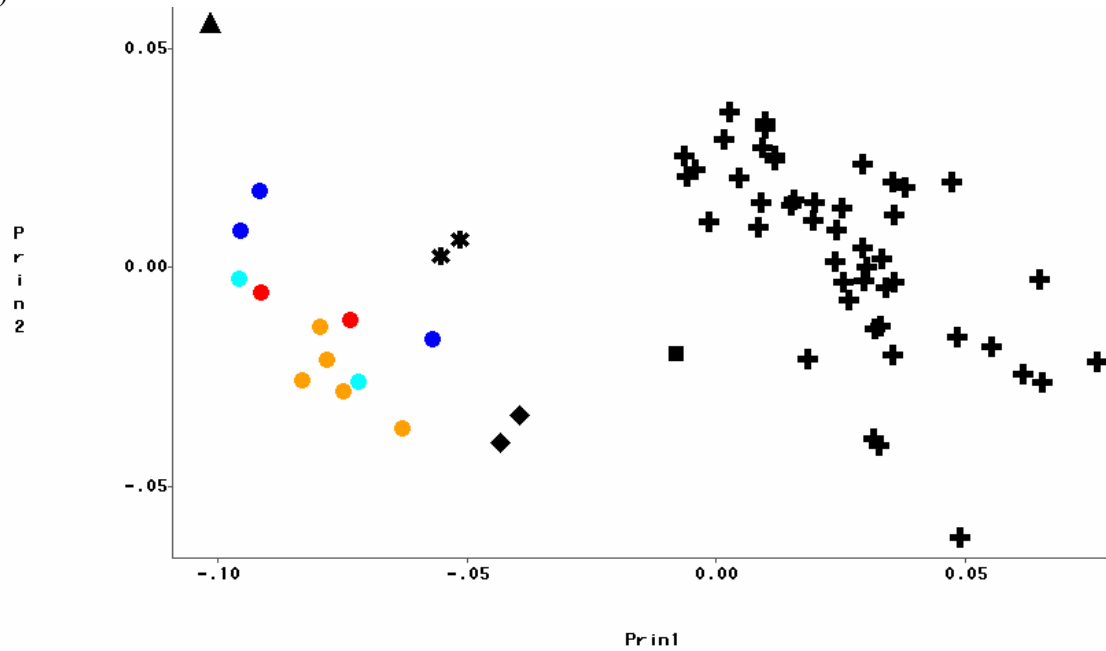
Figure 3.9: The relationship between $\ln(\text{centroid size})$ and PC 2 scores ($R^2 = 0.13$, $\alpha < 0.05$) in the standard landmark set, all specimens analysis. The symbols used here and in subsequent figures are the same as in Figure 3.8. While ER 1813 (*H. habilis*) falls well above the regression line, most *H. erectus* specimens fall below the line. This implies that the shape differences between ER 1813 and *H. erectus* do not reflect allometry. When ER 1813 is excluded from the regression analysis, the result is no longer significant. See legend in Figure 3.8.



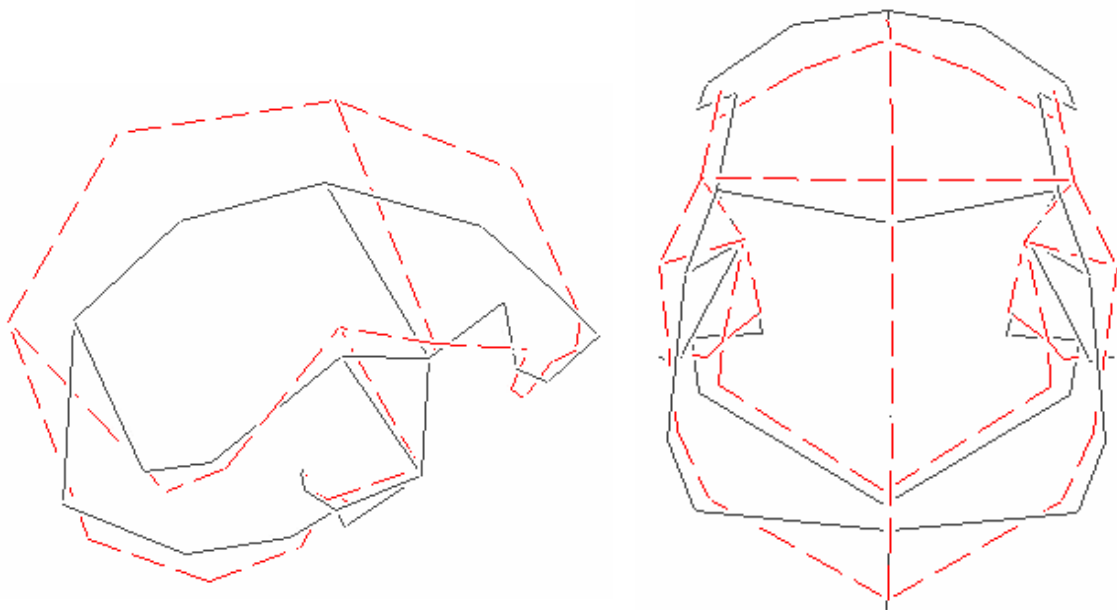
PCA standard landmark set, fossils only: A PCA was also run with only the fossil individuals, excluding the recent (including Late Paleolithic) modern humans. This reduced the sample size to 18 individuals (Table 3.3). The relative positions of the species along PC 1, seen in Figure 3.11a, were very similar to that seen in the all-specimens PCA. Significant differences were detected between *H. erectus* and *H. habilis*, *H. sapiens* and mid-Pleistocene *Homo* on PC 1 and from the Neanderthals on PC 2. Thus, using the standard landmark set, *H. erectus* could be differentiated from all other Plio-Pleistocene species of *Homo* represented in this analysis. *H. habilis* also differed from all other groups on PC 1 (Table 3.5).

Figure 3.10: a) PCA of standard landmark set, all-specimens using the alternative ER 1813 with the height of lambda estimated from other early *Homo* specimens. Shape differences from the negative (black solid line) to the positive (red dashed line) of PC 1 (b) and PC 2 (c) are shown below in lateral and superior views. See legend in Figure 3.8.

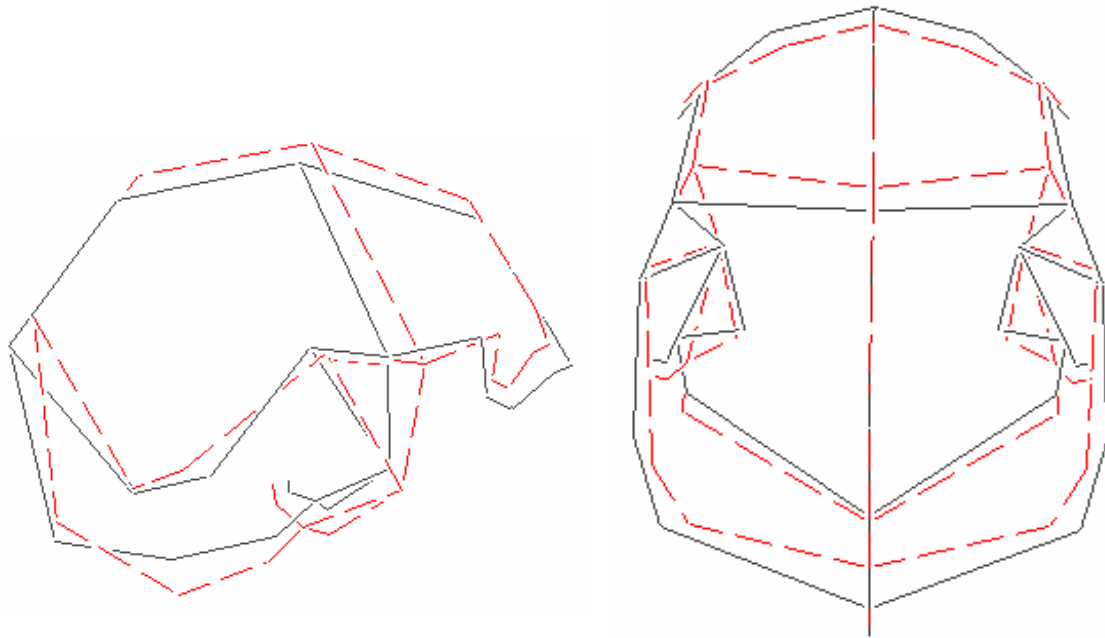
a)



b)



c)



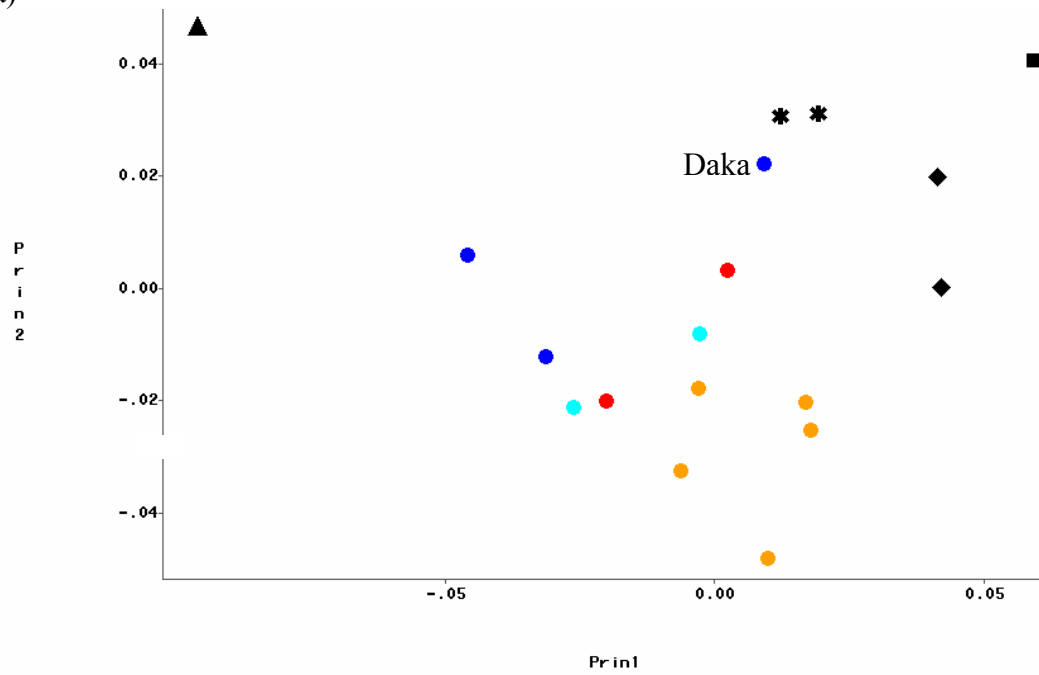
As illustrated in Figure 3.11b, the shape differences along PC 1 were similar but not identical to those described for the all-specimens analysis. Expansion along the mid-sagittal plane was less marked and the occipital plane did not increase in length. Also, there was no increase in the steepness of the supraorbital torus nor a reduction in the supraorbital region. The Indonesian *H. erectus* all score low on PC 2, reflecting the similar cranial shape of these specimens, while the African fossils, particularly Daka, scored higher. The shape changes associated with the negative end of PC 2 are illustrated in Figure 3.11c and include a long frontal squama with a well-developed supraorbital torus and no supratotal sulcus, a lower mid-sagittal profile and greater width across the temporal base and the posterior cranium. Within the African *H. erectus* sample, Daka, the youngest of the African fossils (~1 Ma, labeled in Figure 3.11), resembles later *Homo* taxa more so than do the older African specimens from East Turkana. This may reflect a temporal trend towards greater modernity in some populations of African *H. erectus*.

About half of the variation in the position of individual specimens along PC 1 was related to the size of the fossils ($R^2 = 0.46$, $\alpha < 0.05$) as seen in Figure 3.12. This relationship is driven in large part by the small size and unique shape of ER 1813 on PC 1; removal of ER 1813 from the regression analysis results in a non-significant relationship. However, the small size of ER 1813 clearly accounts for some of the shape differences between *H. erectus* and ER 1813 on PC 1.

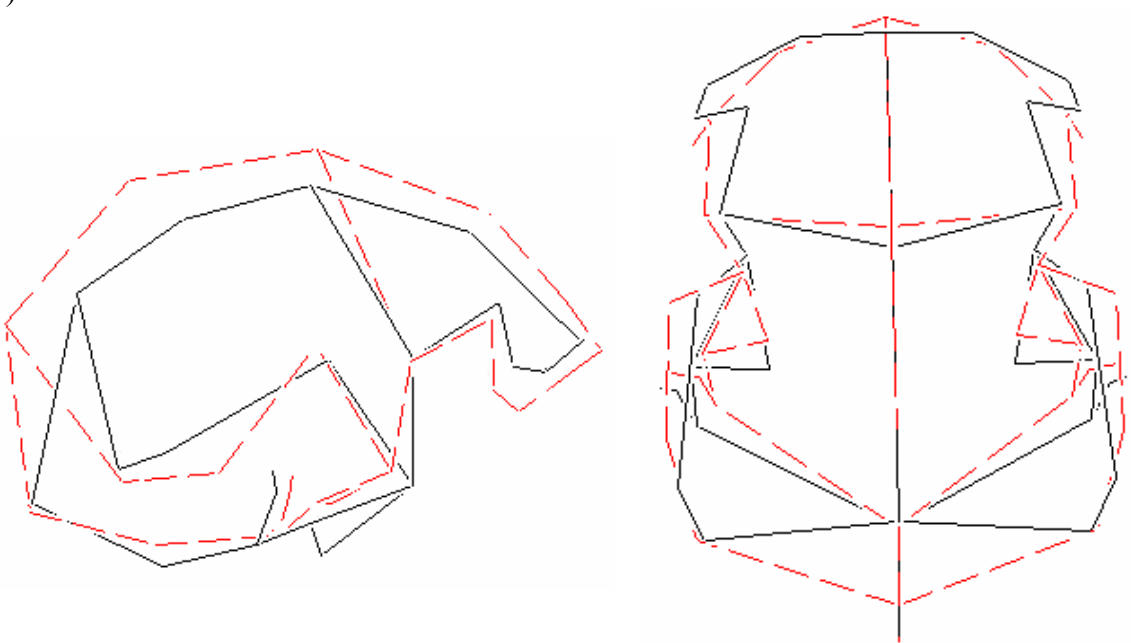
PCA no-metopion landmark set, all-specimens: By excluding metopion from the standard landmark set, it was possible to evaluate the affinities of ER 42700, a specimen allocated to *H. erectus* but which is not yet fully described (Leakey *et al.*, 2003; Spoor *et al.*, 2005). As seen in Figure 3.13, this specimen did not group with other *H. erectus* fossils on either of the first two components. On PC 1, ER 42700 exhibited a cranial shape which was similar to mid-Pleistocene *Homo* and the early *H. sapiens* specimen, Skhul 5 (Figure 3.9), despite its much older age and smaller cranial size. The changes in cranial shape along PC 1 are similar to those described for the first component in the “standard landmark set, all-specimens” PCA. *H. erectus* differed from modern humans on PC 1 and 2 and from ER 1813 on PC 2. Ln(centroid size) explained only a small proportion of variance in PC 2 scores (9%).

Figure 3.11: a) PCA of standard landmark set, fossils only. PC 1 vs. PC 2 plotted below. The results of MANOVA on the scores on PCs 1-4 indicated significant group differences as described in Table 3.5. The shape differences along PC 1 (b) and PC 2 (c) are shown below. See legend in Figure 3.8.

a)



b)



c)

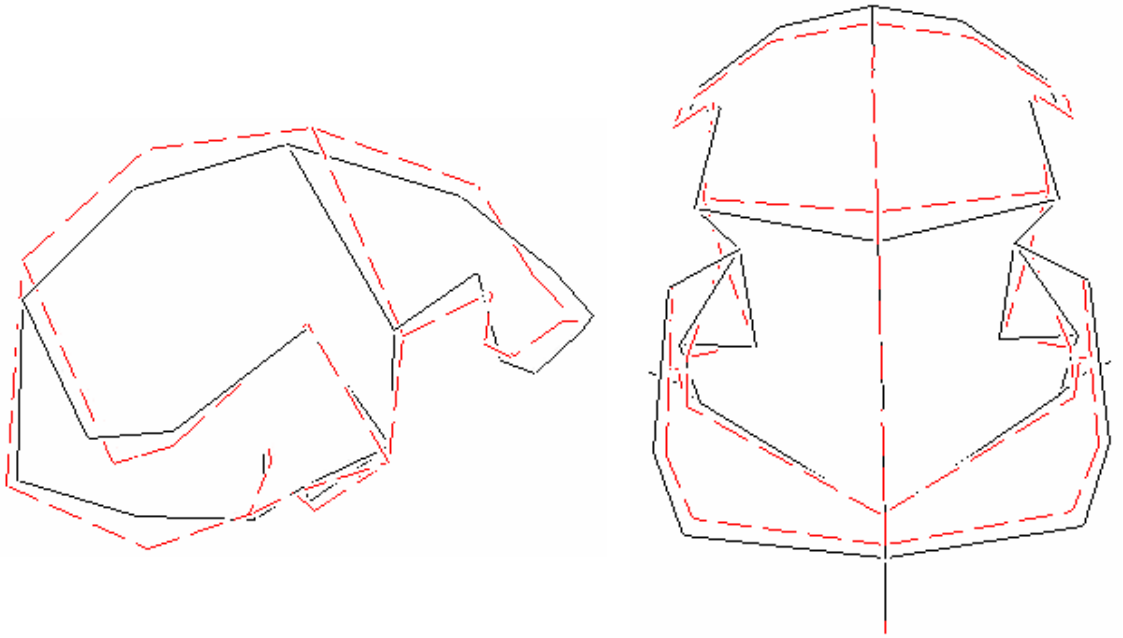


Figure 3.12: Regression of PC 1 scores from standard landmark set, fossils only PCA on $\ln(\text{centroid size})$ ($R^2 = 0.46$, $\alpha < 0.05$). The small size of ER 1813 is driving this regression and by removing it from the regression analysis, the relationship becomes non-significant. See legend in Figure 3.8.

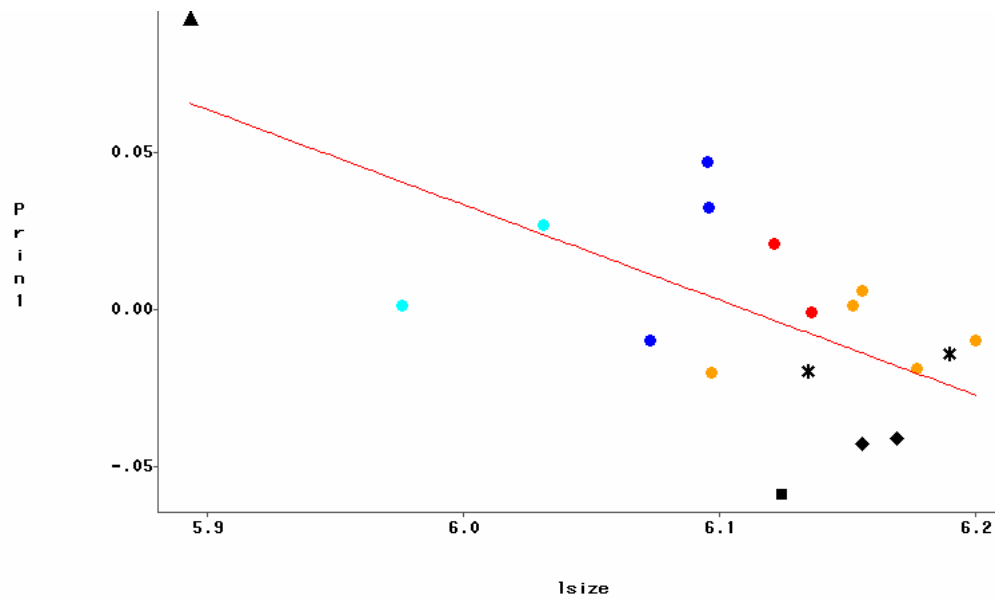
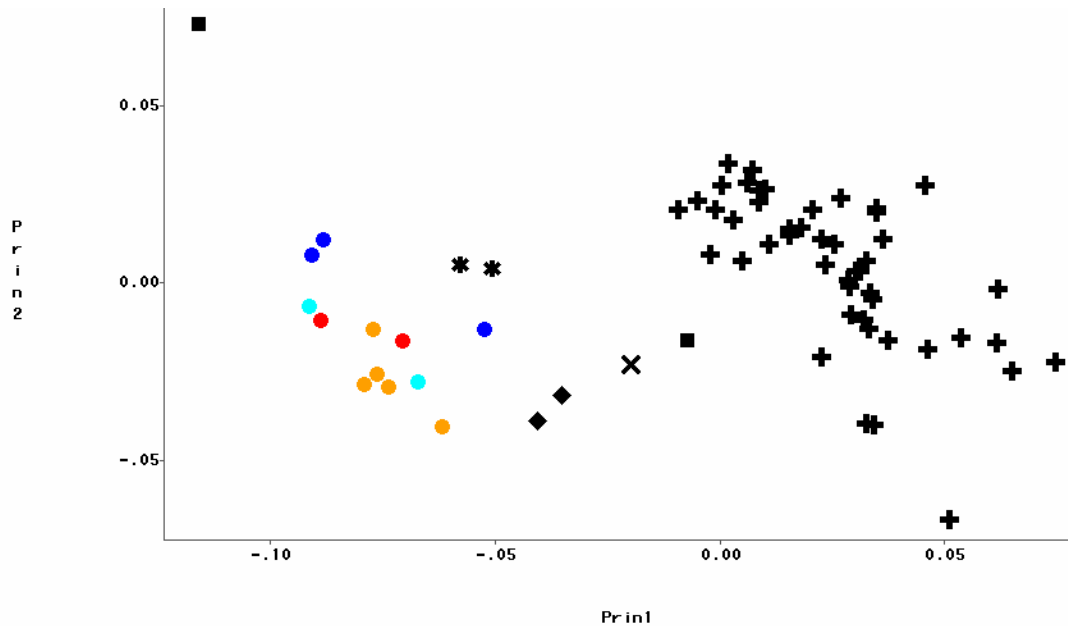
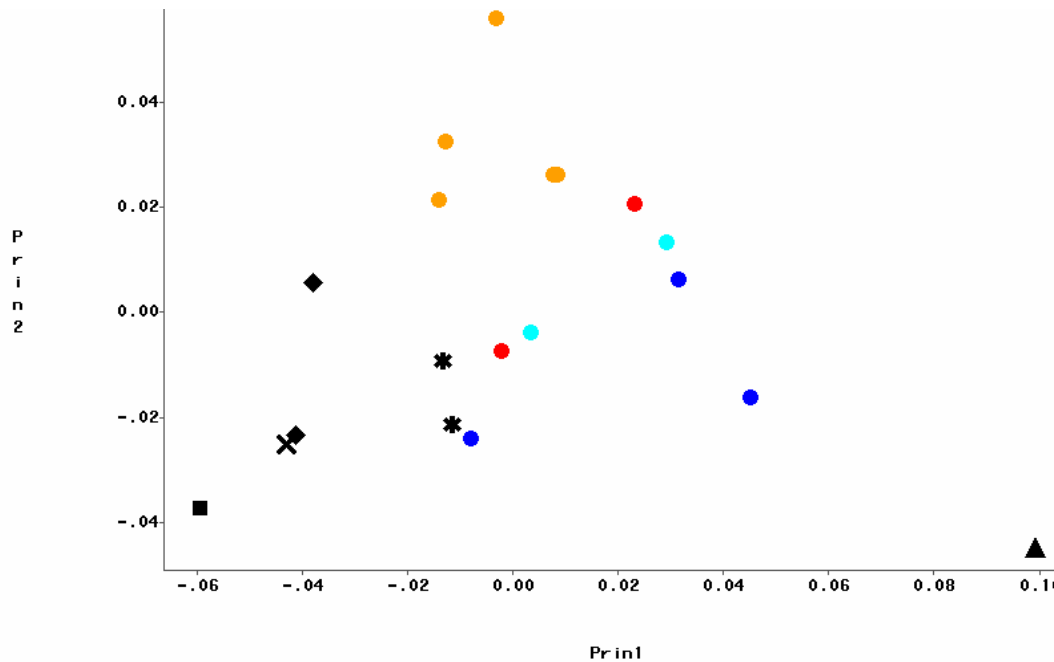


Figure 3.13: PCA of no-metopion landmark set, all-specimens. PC 1 vs. PC 2 plotted below. ER 42700 (X) is a potential member of *H. erectus* but did not group with other members of this species. Despite its small size, its cranial shape was more similar to that of mid-Pleistocene *Homo* or early *H. sapiens* like Skhul 5. See legend in Figure 3.8.



PCA no-metopion landmark set, fossils only: When the modern humans were removed and the PCA was re-run using the no-metopion landmark set, ER 42700 appeared nearly identical in cranial shape to Kabwe on the first three PCs (Figure 3.14). Shape differences were similar to those described for the standard landmark set, fossils only. In contrast to ER 42700, Daka scored within the *H. erectus* range on PC 1 and just outside of the range on PC 2. As summarized in Table 3.5, when ER 42700 was considered its own taxon, the significant differences among groups were between *H. habilis* and all other groups on PC 1. In addition, there were significant differences detected between *H. erectus* and mid-Pleistocene *Homo* and early *H. sapiens* on the first component. If ER 42700 was instead considered a member of *H. erectus*, then this species differed significantly from *H. habilis* on PC 1 and Neanderthals on PC 3. Overall, ER 42700 did

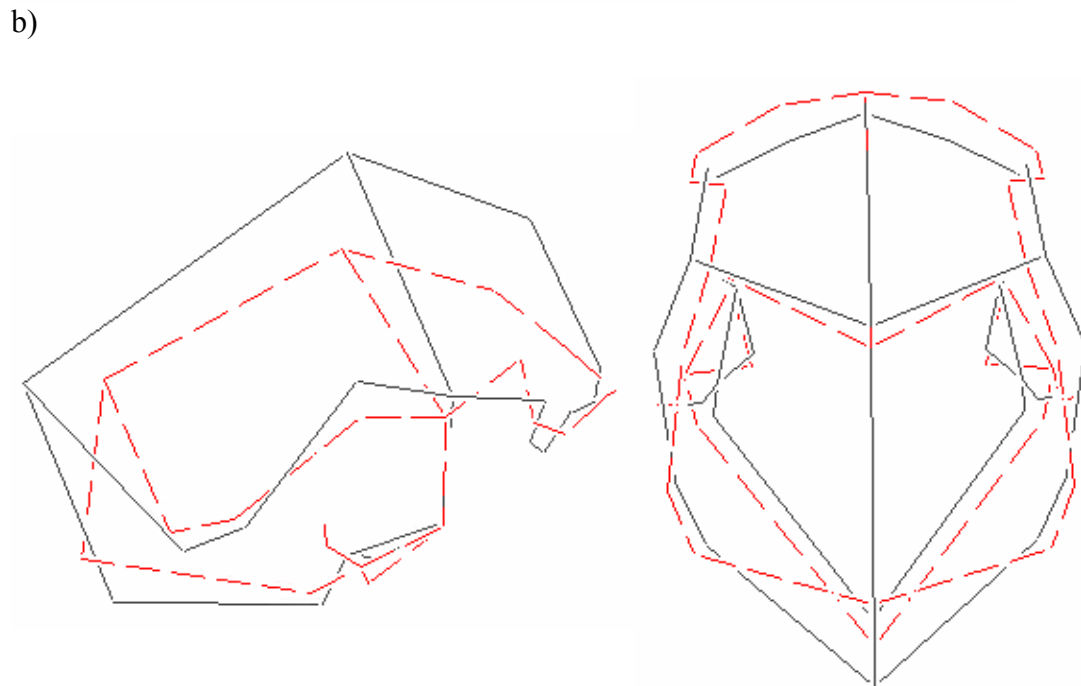
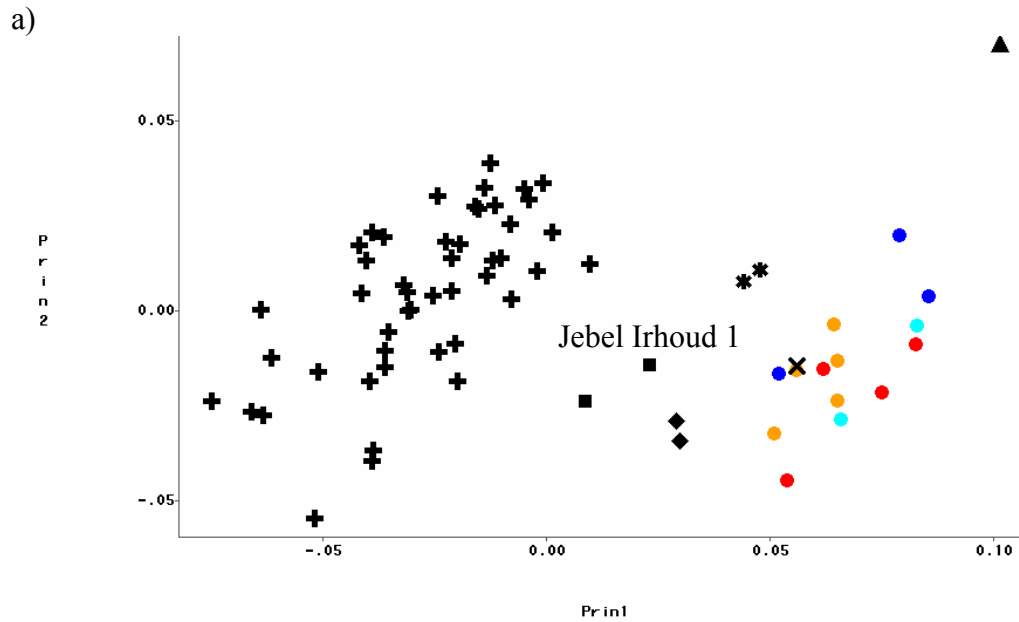
Figure 3.14: PCA of no-metopion landmark set, fossils only (PC 1 vs. PC 2 plotted below). ER 42700 (X) appears nearly identical to Kabwe on PCs 1-3 (PC 3 not shown here). *H. erectus* and *H. habilis* have significantly different mean scores on PC 1. If ER 42700 is not included in *H. erectus* then this species also differs from the Neanderthals and mid-Pleistocene *Homo* on the first component. See legend in Figure 3.8.



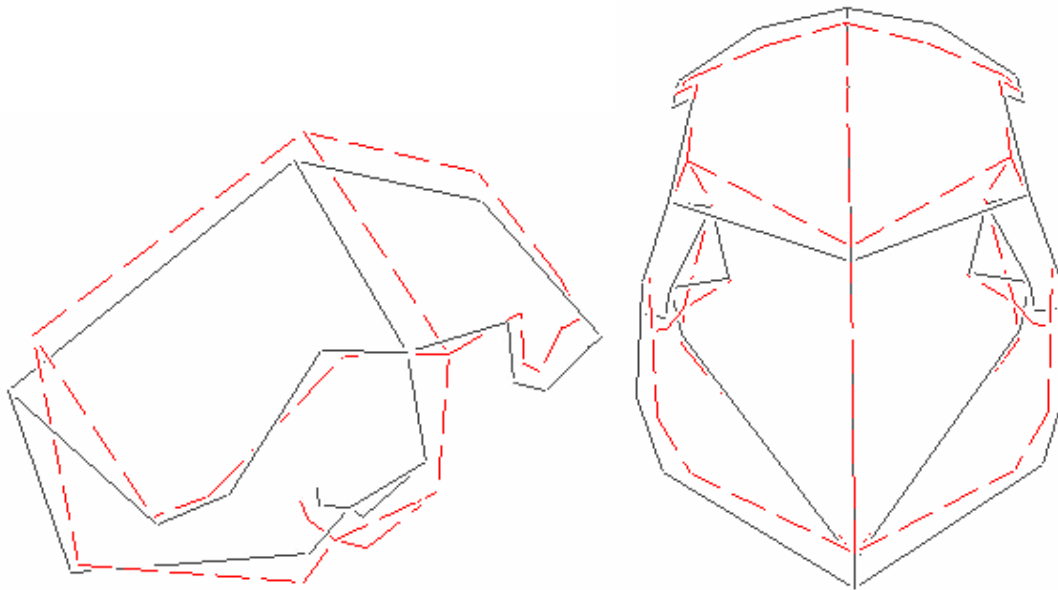
not fit the *H. erectus* neurocranial cranial shape pattern, which may indicate that there was greater taxonomic diversity at 1.5 Ma than previously recognized.

PCA no opisthion, mid-parietal landmark set, all-specimens: Several specimens, namely Ceprano, Jebel Irhoud 1, Zkd 3 and Zkd 5, were included in the PCA by excluding both opisthion and the mid-parietal landmark. As illustrated in Figure 3.15, Ceprano fell among the *H. erectus* sample on the first four components (though it was at the edge of the *H. erectus* distribution on PCs 3 and 4) and well beyond the *H. erectus* sample on PC 5. Therefore, it seems that Ceprano does share the basic cranial architecture of *H. erectus*, as noted by Manzi *et al.* (2001), but that it differs in more detailed aspects of neurocranial shape from this sample, as well. Jebel Irhoud 1 (labeled in Figure 3.15) was

Figure 3.15: a) PCA of no-opisthion/no-mid-parietal landmark set, all-specimens. Ceprano (X) grouped with *H. erectus* on PCs 1 and 2 (shown below), but it scored higher than all other *H. erectus* specimens on PC 5 and at the edge of the *H. erectus* distributions on PCs 3 and 4. The shape differences associated with PC 1 (b) and PC 2 (c) are shown below. See legend in Figure 3.8.



c)



positioned just between mid-Pleistocene *Homo* and early *H. sapiens* on the first PC. Both Zhoukoudian specimens fell within the *H. erectus* range on PC 1 although Zkd 5 has the lowest score of all *H. erectus* on PC 2. The shape differences on PC 1, illustrated in Figure 3.15b, were similar to those described in the standard landmark set, all-specimens analysis, although the excluded landmarks made it difficult to judge the height of the posterior cranial vault. The shape differences in PC 2 (Figure 3.15c) were also similar to those described in the original analysis, but the frontal bone breadth did not vary along this component.

When Ceprano was assigned to either *H. erectus* or to mid-Pleistocene *Homo*, then *H. erectus* differed significantly from *H. sapiens* on the first two components and from *H. habilis* on PC 2 (Table 3.5). When Ceprano was assigned to its own group, then the *H. erectus* – *H. sapiens* contrast on PC 2 was no longer significant. Only a small proportion of the variation in both PC 1 and 2 scores (13% and 12%, respectively) was explained by differences in $\ln(\text{centroid size})$.

In order to explore the possibility that Ceprano resembled European (rather than African and Asian) mid-Pleistocene *Homo*, Petralona was also included in this analysis using the estimated tympanomastoid landmark as described in the “Methods” section. Figure 3.16a shows that the relative positions of individual fossils along PC 1 were very similar to the original analysis. Petralona, like Ceprano, fell within the *H. erectus* distribution on PCs 1 and 2. In fact, the scores of Petralona and Ceprano on PC 1 (reflecting overall cranial expansion, basicranial narrowing and supraorbital torus projection) were nearly identical. Petralona separated out on PC 3 (Figure 3.16a) based on its relatively shorter cranium antero-posteriorly (due to the more anterior positions of inion and lambda), its less marked post-toral sulcus and wider frontal and temporal squamae (Figure 3.16b). The European hominins as a whole (including Petralona, Ceprano, La Chapelle and La Ferrassie) did not group together to the exclusion of non-European fossils, but all four did score fairly high on the second component. It is interesting that the European mid-Pleistocene hominins had a neurocranial shape which was more similar to *H. erectus* on PC 1 while the neurocranial shape of the African mid-Pleistocene fossils was more intermediate between *H. erectus* and *H. sapiens*.

PCA no-opisthion/no-mid-parietal landmark set, fossils only: When a PCA was performed with the no-opisthion/no-mid-parietal landmark set but limited to fossil *Homo* only, the results were slightly clearer. Ceprano fell between the *H. erectus* / *H. neanderthalensis* and the mid-Pleistocene *Homo* / early *H. sapiens* samples on PC 1 and was very distinct on PC 3 (significantly different from *H. erectus*) (Figure 3.17a, c). The results of the MANOVA, summarized in Table 3.5, indicated that regardless of what

Figure 3.16: PCA of no-opisthion/no-mid-parietal landmark set, all-specimens including *Petalona* with the tympanomastoid landmark estimated. a) PC 1 vs. PC 3 is plotted below. *Petalona* is the highest scoring individual on PC 3. b) Shape change on this third component is illustrated in lateral and superior views. See legend in Figure 3.8.

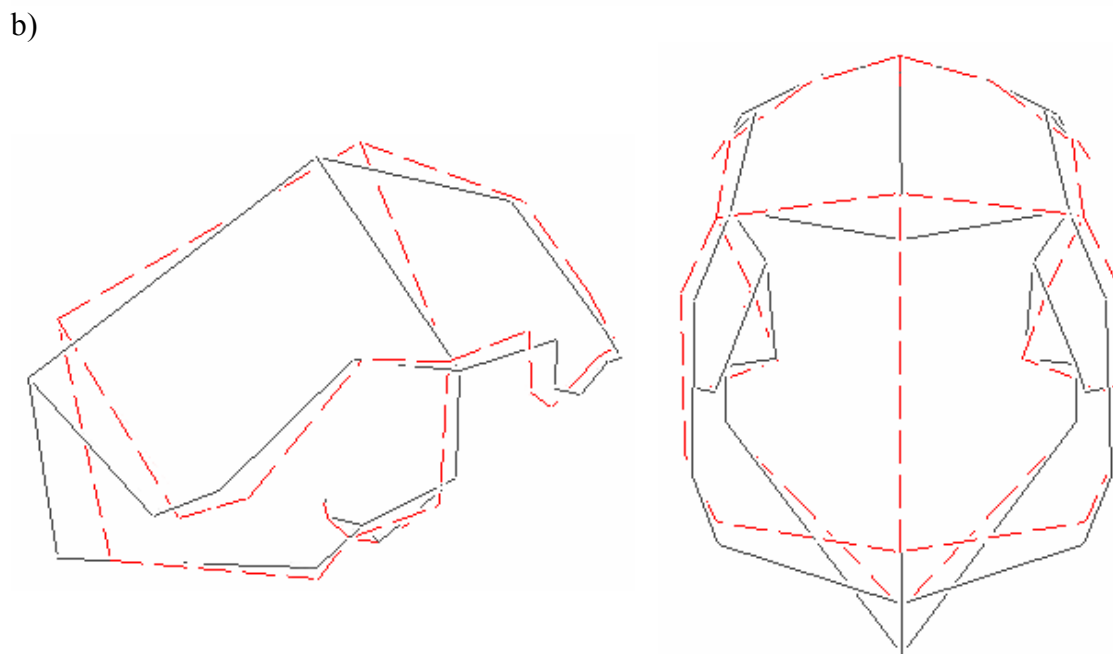
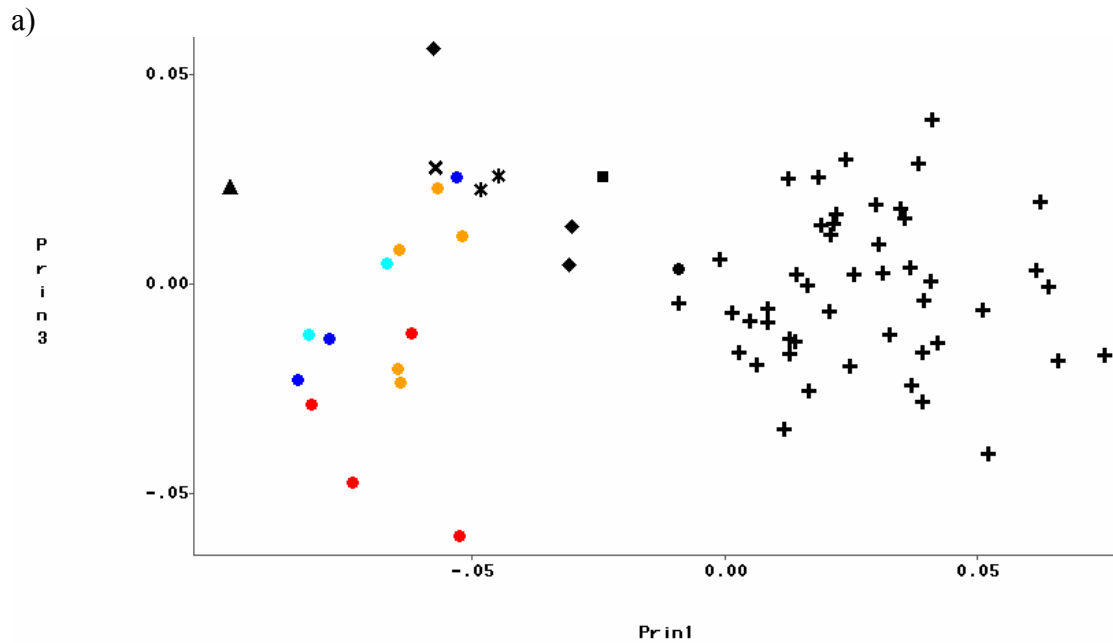
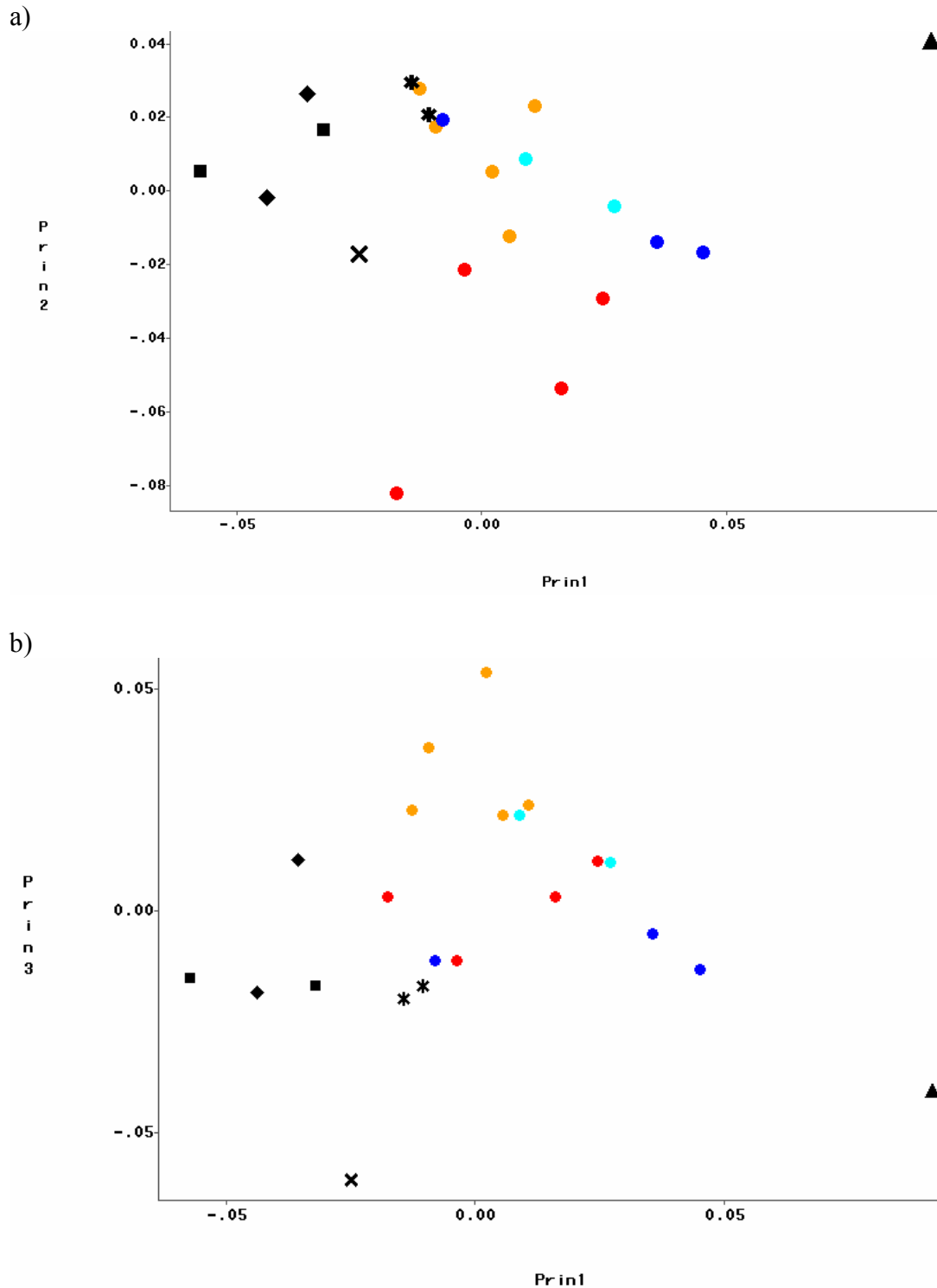
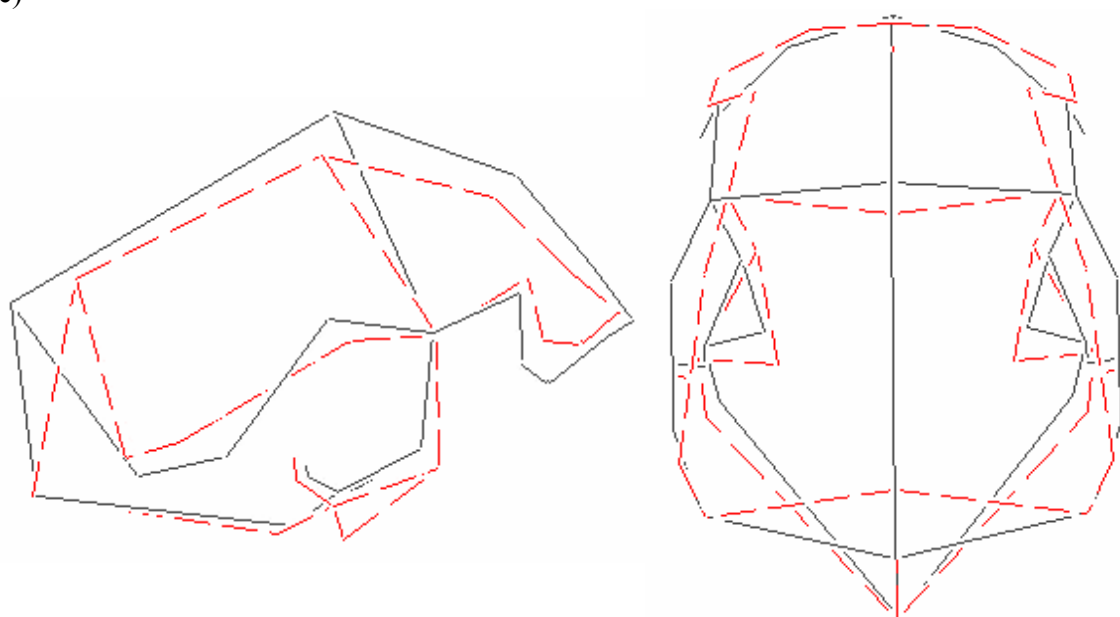


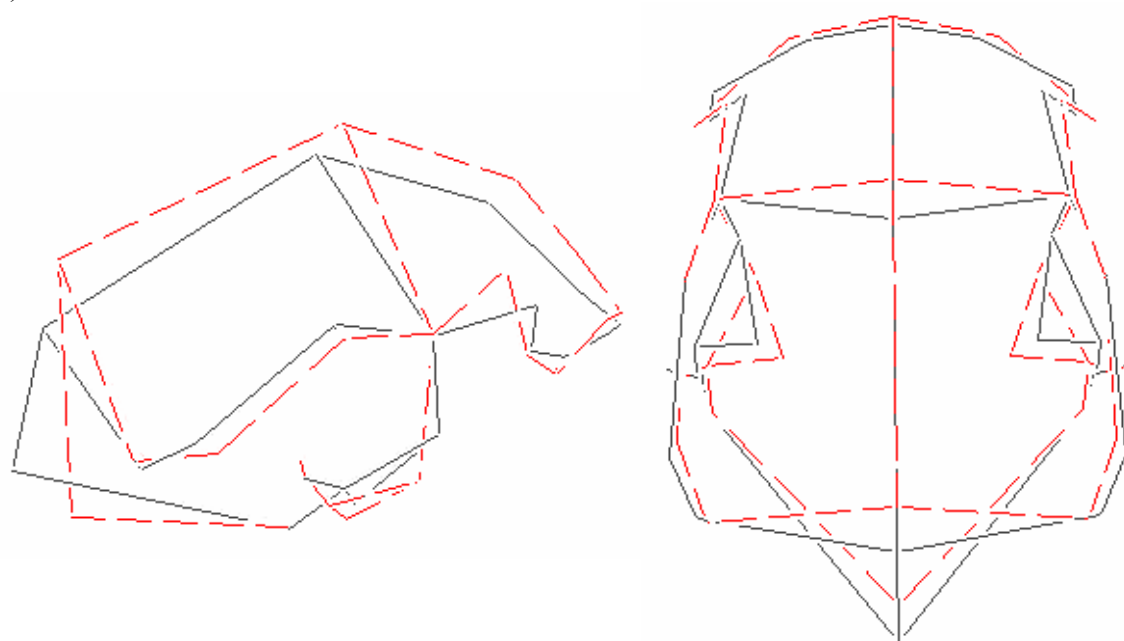
Figure 3.17: PCA of no-opisthion/no-mid-parietal landmark set, fossils only. a) PC 1 vs. PC 2 and b) PC 1 vs. PC 3 are shown below. *H. erectus* was significantly different from *H. habilis*, *H. sapiens* and mid-Pleistocene *Homo* on PC 1, regardless of how Ceprano (X) was classified. Shape changes along PC 1 (c), PC 2 (d) and PC 3 (e) are shown below. See legend in Figure 3.8.



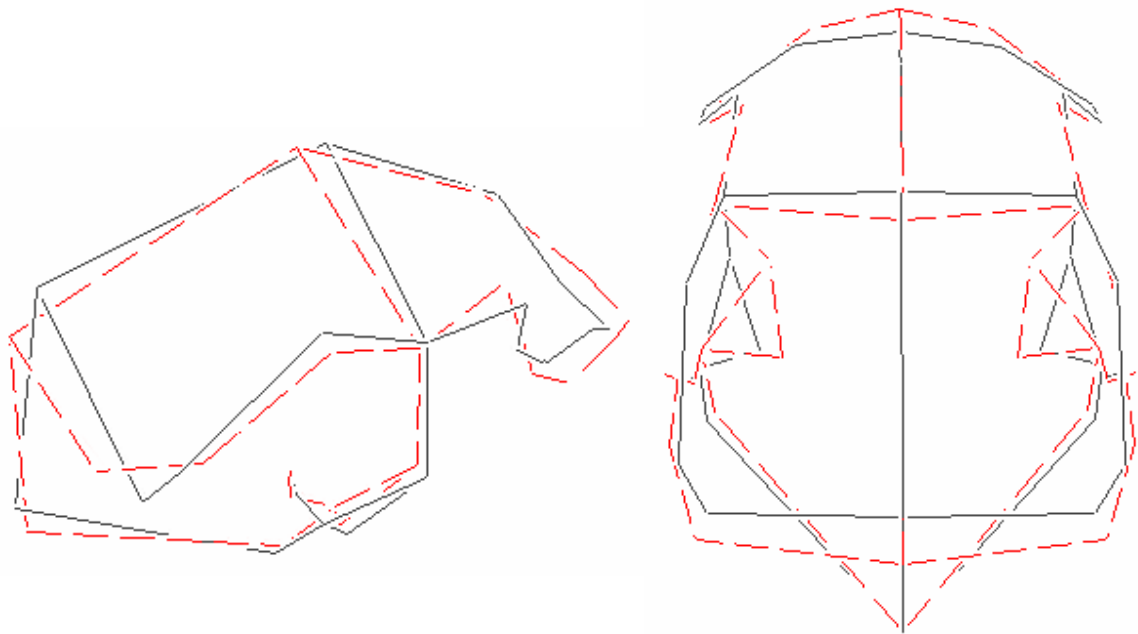
c)



d)



e)



group Ceprano was assigned to (*H. erectus*, mid-Pleistocene *Homo*, or its own group), *H. erectus* differed from all other groups on the first PC with the exception of the Neanderthals. Daka grouped with *H. erectus* on the first three components. Jebel Irhoud 1 scored lower than Skhul 5 and overlapped the mid-Pleistocene hominin sample (Kabwe, Dali, Petralona and Ceprano). Neither Ceprano nor Petralona overlaps *H. erectus* on the first component, and Petralona is more similar to Skhul 5 than are any of the other mid-Pleistocene *Homo* fossils.

The shape differences on PC 1 were very similar to those described in the standard landmark set, fossils only analysis and are illustrated in Figure 3.17c. The shape changes associated with the negative end of the third component (Figure 3.17e) included a much shorter frontal squama with a smaller supraorbital torus and a more marked supraglabellar depression. The posterior cranium was wide, the temporal squama was high while asterion was quite low. Also the anterior base was more inferiorly positioned

and both the inferior entoglenoid and the temporosphenoid suture were much more laterally positioned. In these aspects of cranial shape, Ceprano differed most strongly from the Asian and Georgian *H. erectus* fossils.

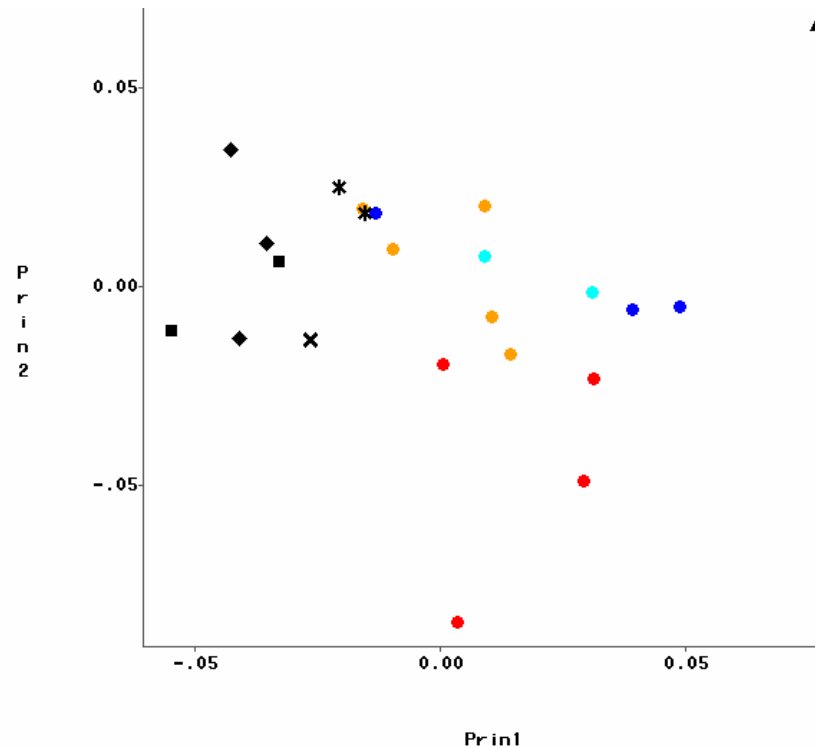
On PC 2, the Zhoukoudian fossils scored low in general and Zkd 5 scored especially low due to their very low cranial outline with an exaggerated posterior projection of the occipital bone and deeper supratral sulcus relative to metopion (a reflection of their frontal tuberosity) (Figure 3.17d). Zkd 5 is the youngest of the Zhoukoudian hominins and may have become more derived through either drift or isolation. The Neanderthals, particularly La Chapelle, scored low on PC 4, overlapping only Zkd 11. This difference was not significant, however.

When the PCA was re-run with Petralona (Figure 3.18), this specimen grouped with other mid-Pleistocene *Homo* fossils along PC 1. Although Petralona did not separate out on any component, it did score slightly higher than the other mid-Pleistocene *Homo* fossils on PC 2. Petralona did not group with the Neanderthals who scored low on PC 3.

PCA face landmark set, all-specimens: A PCA of facial landmarks was also performed using landmarks from the supraorbital torus, the alveolar region and the mid-face as described in Table 3.3 and illustrated in Figure 3.3. Only a limited number of fossils have facial skeletons which are sufficiently well-preserved to be included in this analysis, but the landmark set was chosen to maximize the number of specimens and species represented.

There was no consistent grouping of *H. erectus* individuals on any component. Interspecific variation accounted for the most variable aspect of facial shape (seen on PC 1 in Figure 3.19a). Shape variation along this component was related to width and depth of the mid-face, height of the supraorbital torus and the antero-posterior position of the malar root as illustrated in Figure 3.19c. As seen in Table 3.5, *H. sapiens* specimens scored significantly lower than any other species of *Homo* on PC 2, although S 17 and the Zhoukoudian reconstruction are at the edge of the *H. sapiens* distribution. The higher scoring individuals (non-*sapiens*) displayed greater alveolar prognathism, a narrower mid- and upper- face, a wider nasal aperture and a supraorbital torus which was taller at mid-orbit and thicker laterally (Figure 3.19d). As seen in the regression plot (Figure 3.20), about a quarter of the shape variation along PC 2 was explained by

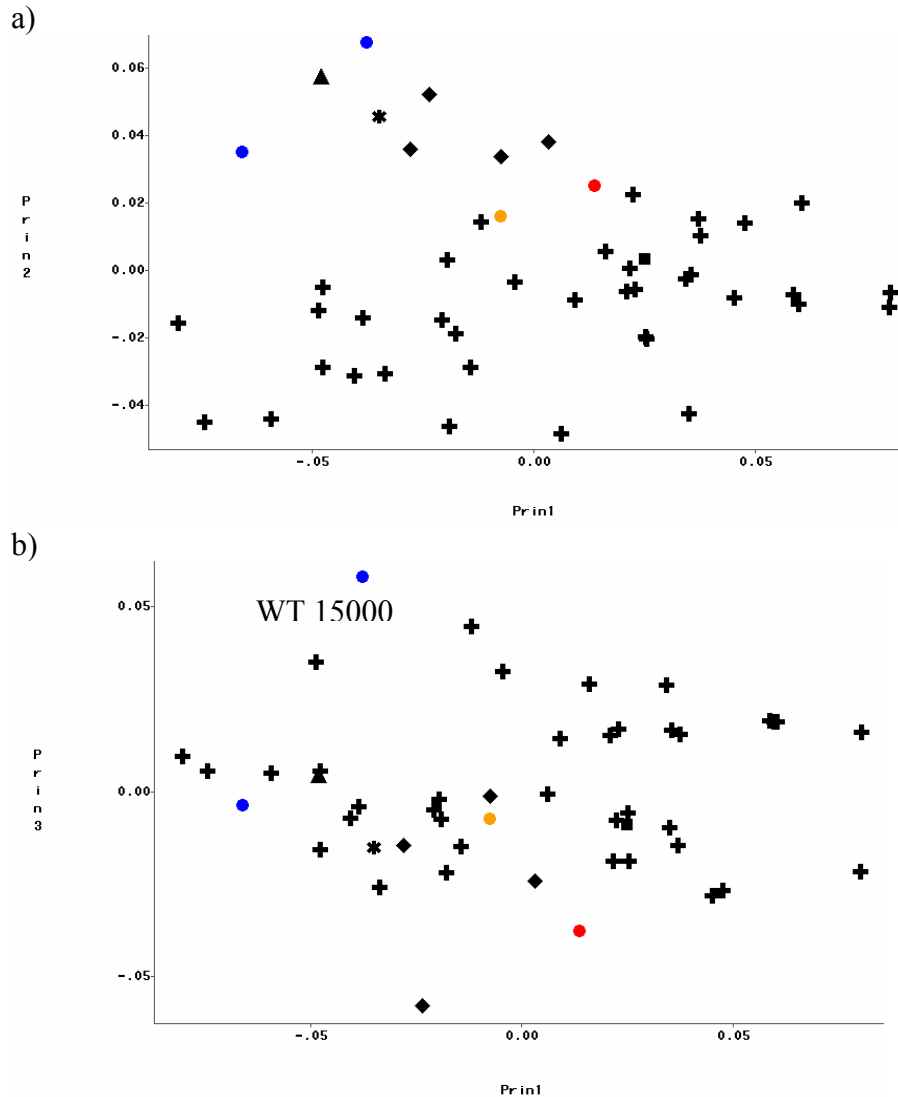
Figure 3.18: PCA of no-metopion/no-mid-parietal landmark set, fossils only including Petralona with the tympanomastoid landmark estimated. Petralona was the highest scoring mid-Pleistocene specimen on PC 2 but generally scored similarly to other mid-Pleistocene *Homo* fossils. See legend in Figure 3.8.



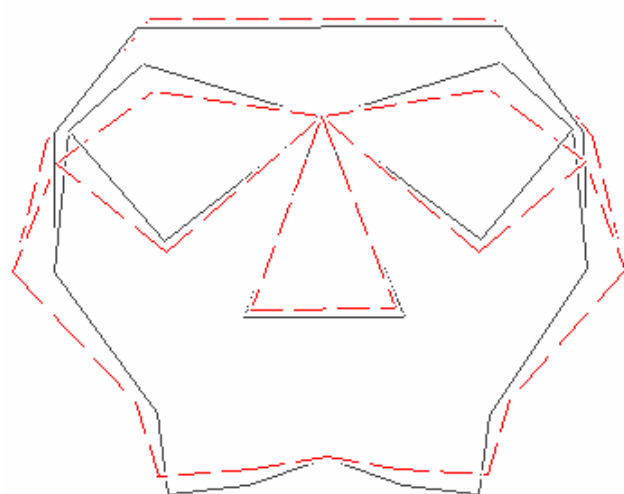
differences in $\ln(\text{centroid size})$ with *H. sapiens* having generally smaller faces than the fossil taxa. The exception was ER 1813, which had a small face but a more ‘archaic’ facial shape on this component.

On both PC 2 and 3, WT 15000 scored higher than all individuals, and much higher than the other fossil *Homo* specimens on PC 3 (Figure 3.19a, b). This may be due to the subadult status of WT 15000; the facial skeleton undergoes significant growth as a result of the development and eruption of the permanent dentition. For example, the hard palate continues to grow posteriorly through adulthood in humans (Scheuer and Black,

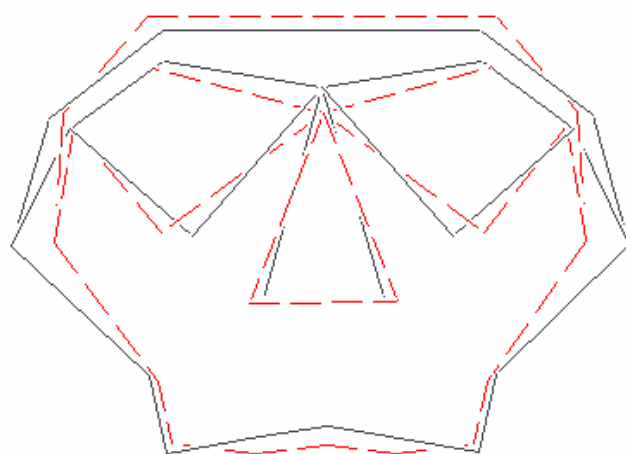
Figure 3.19: PCA of face landmark set. a) Plots of PC 1 vs. PC 2 and b) PC 1 vs. PC 3 are shown below. Fossil *Homo* generally score high on PC 2 while the African *H. erectus* fossils score lower on PC 1 than the Asian *H. erectus* specimens. On PC 3 WT 15000 has the highest score, which may be related to its subadult status (see text for discussion). The shape changes associated with this PC 1 (c) and PC 3 (d) are illustrated below in anterior and lateral views. See legend in Figure 3.8.



c)



d)



e)

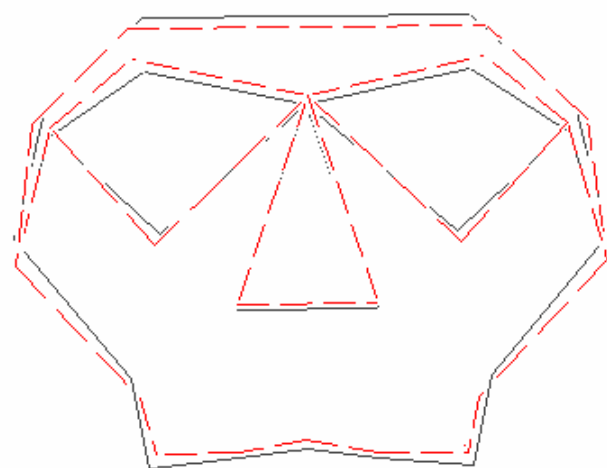
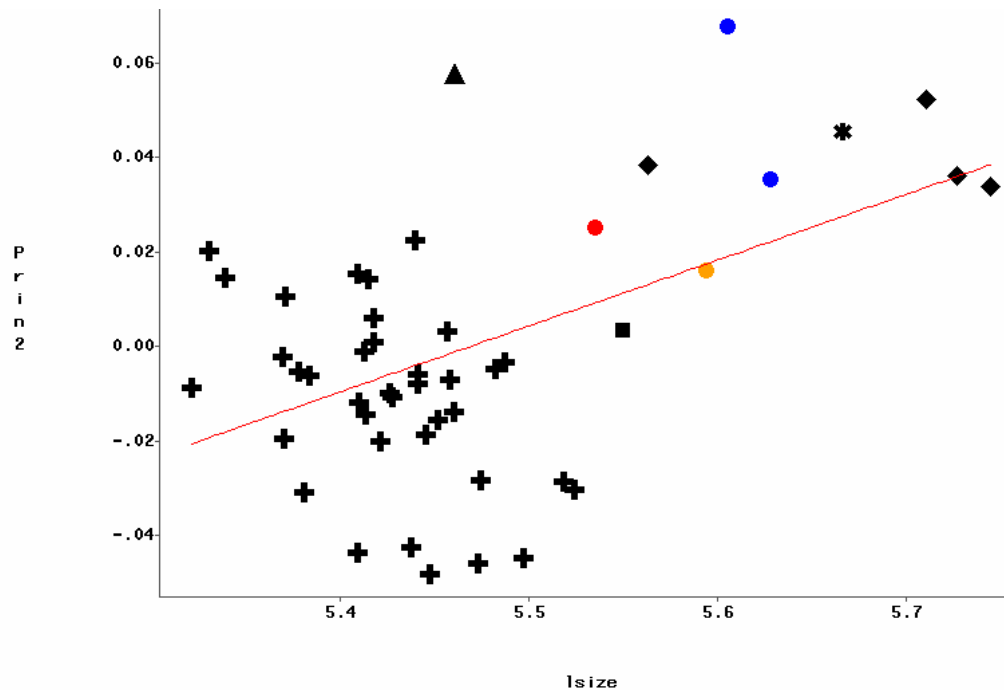


Figure 3.20: Regression of PC 2 scores from face landmark set, all-specimens PCA on $\ln(\text{centroid size})$ ($R^2=0.25$, $\alpha < 0.05$). The faces of modern humans are reduced in size relative to the fossil taxa (except ER 1813) and this size difference contributes to some of the shape differences between *H. sapiens* and other *Homo* species.



2000) and the morphology of the supraorbital torus continues to develop even after puberty in both humans and Neanderthals (Smith and Raynard, 1980; Ahern and Smith, 2004). Similar *in vivo* changes in the facial skeleton were therefore likely in *H. erectus* and may account for the extreme position of this individual along PCs 2 and 3.

Excluding WT 15000 from the analysis did not change the results greatly.

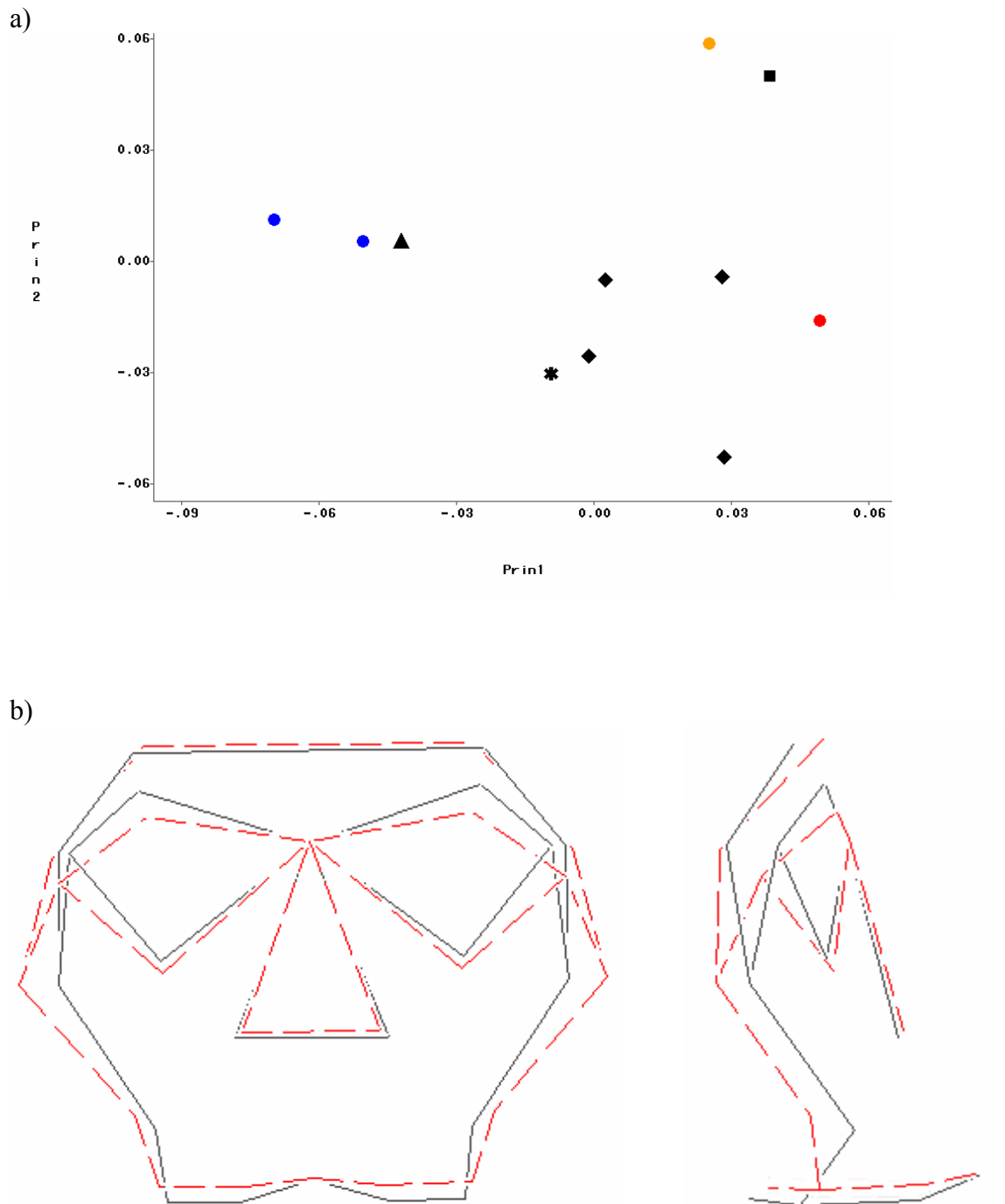
PCA face landmark set, fossils only: The *H. erectus* specimens do not group together to the exception of other fossil *Homo* as seen in the PCA plot in Figure 3.21. The two African specimens (ER 3733 and WT 15000) scored similarly to ER 1813 on the first two components and ER 3733 and 1813 also grouped together on PC 3. The two Asian

individuals, on the other hand, scored much higher on PC 1 along with mid-Pleistocene *Homo* and Jebel Qafzeh 6. As seen in Figure 3.21b, PC 1 reflected the narrower and shallower upper face as well as a thinner supraorbital torus at mid-orbit, wider nasal apertures and a more anterior origin of the zygomatic arch in higher scoring individuals. The higher scoring fossils on PC 2 (S17 and Jebel Qafzeh 6) had more superiorly positioned alveolare and alare, wider faces and taller orbits as illustrated in Figure 3.21c. It appears that intraspecific variation in facial morphology was greater than interspecific variation in the facial shape of fossil *Homo* taxa, at least as captured by this landmark set. Exclusion of WT 15000 from the PCA did not change results in a meaningful way.

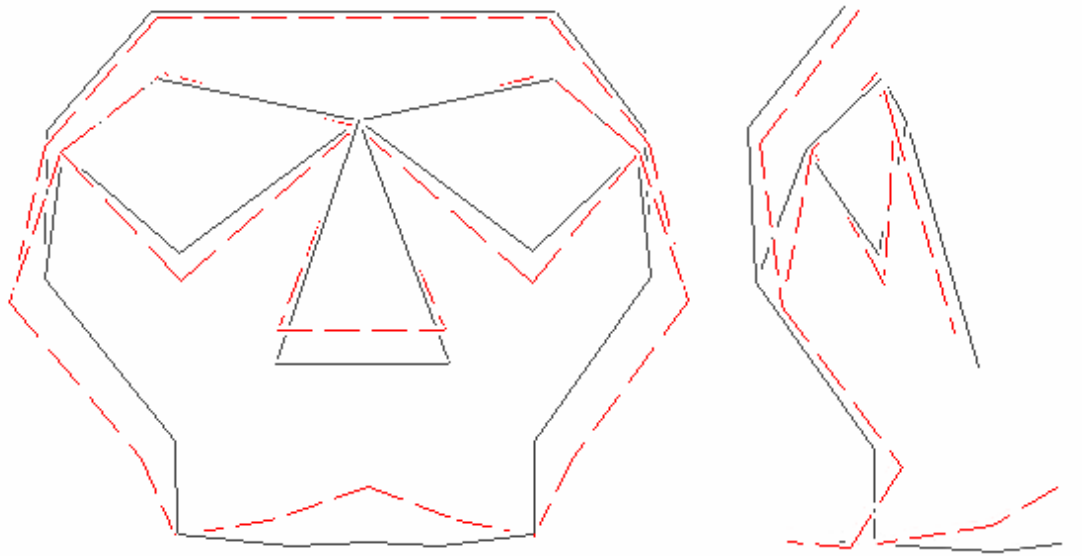
PCA frontal landmark set, all-specimens: The second cranial region that was examined across a large sample of *Homo* species was the frontal bone. The landmark set, which included a mix of midline and bilateral landmarks as well as semilandmarks from the MFP curve, was described in Table 3.3 and illustrated in Figure 3.4.

This region of the cranium provided good separation between *H. erectus* and all later *Homo* taxa (mid-Pleistocene *Homo*, Neanderthals and modern humans) but not early *Homo* (ER 1813 and 1470) which overlapped *H. erectus* (Figure 3.22a). The two different species of early *Homo*, *H. habilis* and *H. rudolfensis*, were treated as one group (early *Homo*) for significance testing. This approach was reasonable because ER 1813 and 1470 scored similarly on all components. However, while *H. erectus* was significantly different from mid-Pleistocene *Homo* and Neanderthals on PC 2 and from modern humans on both PCs 1 and 2, it did not differ significantly from early *Homo* (Table 3.5). These results were not altered by the alternative classifications of Ceprano

Figure 3.21: a) PCA of face landmark set, fossils only. *H. erectus* fossils do not group together in terms of their facial shape and are not significantly different from any of the other *Homo* taxa represented in this analysis. On PC 1, both the lowest and highest scoring individuals are *H. erectus* (WT 15000 and the Zhoukoudian reconstruction, respectively). Shape change along PC 1 (b) and PC 2 (c) are shown below. See legend in Figure 3.8.



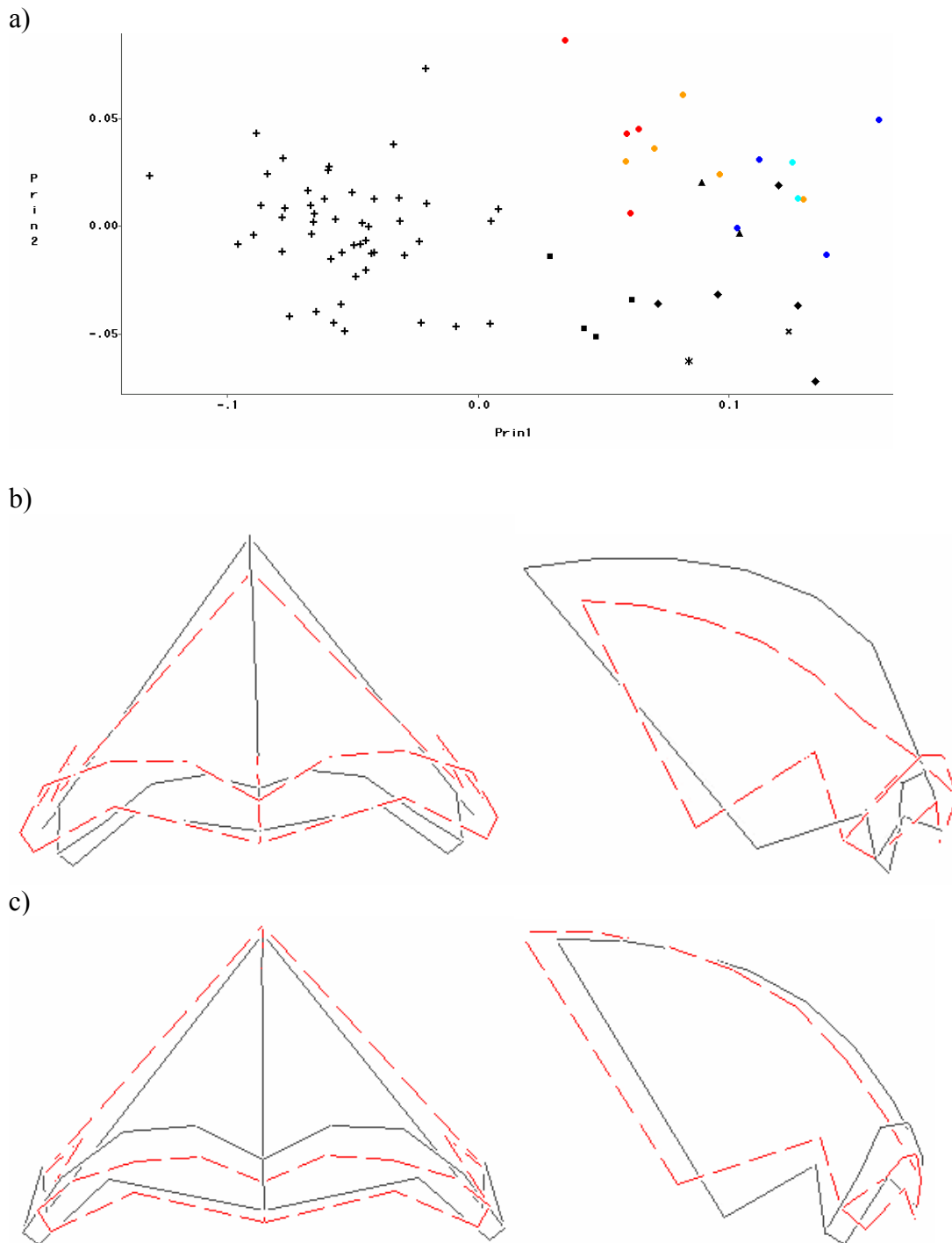
c)



as *H. erectus*, mid-Pleistocene *Homo* or as its own taxon. Overall size of the frontal bone did not affect the positions of individuals along either PC 1 or 2.

On PC 1, the recent human specimens scored lower than all of the fossil specimens, while both *H. erectus* and early *Homo* scored higher on PC 2 than mid-Pleistocene *Homo*, *H. neanderthalensis* and early modern humans. All three of the European Middle Pleistocene hominins (La Chapelle, Petralona and Ceprano) scored especially low on PC 2, although Ceprano overlapped some early *H. sapiens* specimens. The only exception was Bodo, which grouped with *H. erectus* rather than with mid-Pleistocene *Homo*. OL 45500 (Olorgesailie) scored highest of all-specimens on the first component. As illustrated in Figure 3.22b, the positive end of PC 1 was associated with a

Figure 3.22: a) PCA of frontal bone landmark set, all-specimens (PC 1 vs. PC 2 shown). While *H. erectus* overlaps the two early *Homo* fossils (ER 1813 and 1470), it does differ significantly from mid-Pleistocene *Homo*, Neanderthals and *H. sapiens* on PC 2 (and *H. sapiens* on PC 1 as well). Bodo is the mid-Pleistocene *Homo* specimen which overlaps *H. erectus* on PC 2. The 'X' is Ceprano which groups with mid-Pleistocene *Homo* specimens. The shape differences along PC 1 (b) and PC 2 (c) are shown below in anterior and lateral views. See legend in Figure 3.8.



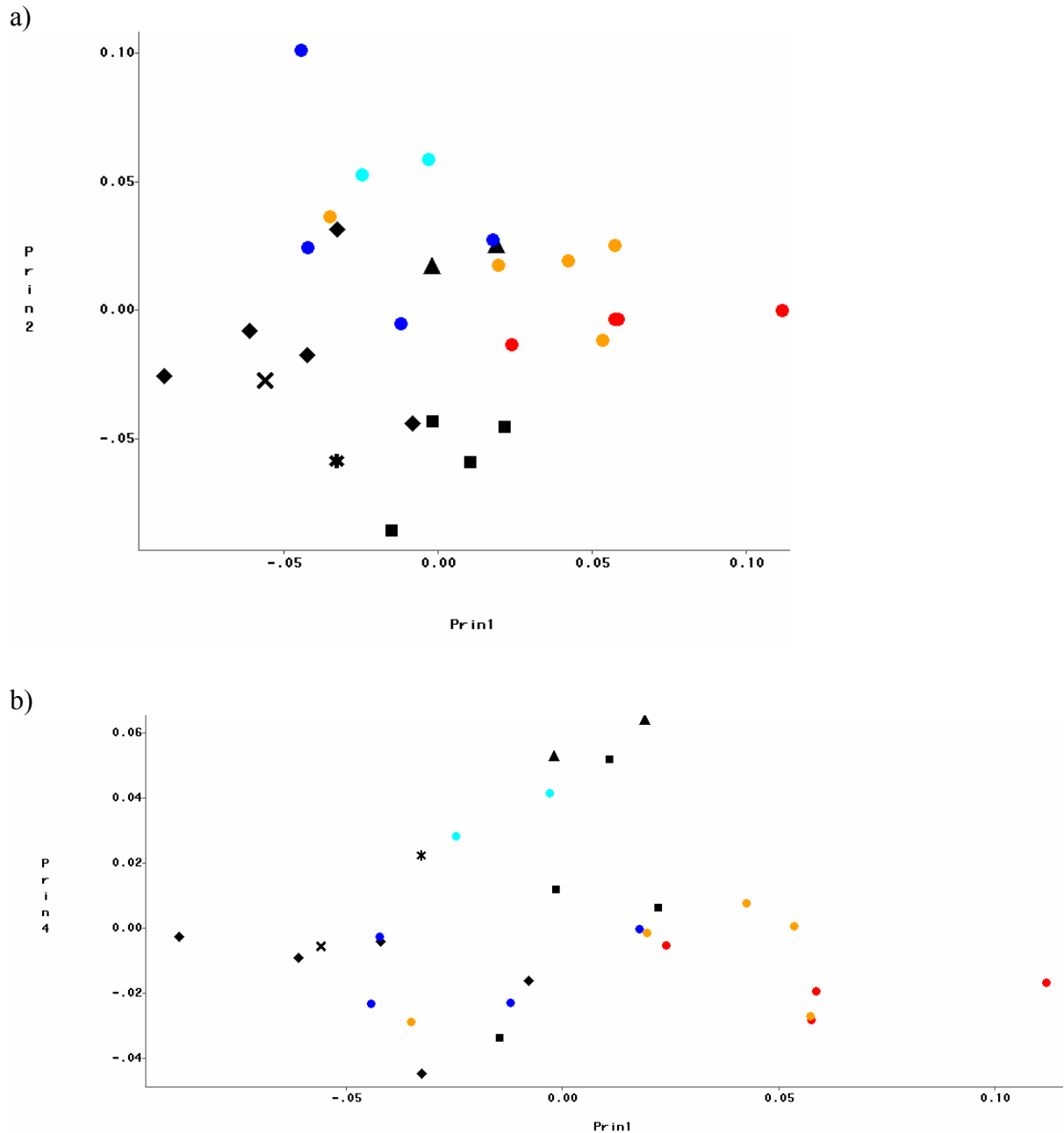
more sloping forehead and a relatively shorter frontal bone. High scoring individuals also had wider and thicker frontal tori which were more anteriorly projecting. Glabella overhung nasion to a greater degree and both frontotemporale and anterior pterion were more posteriorly positioned in lower scoring specimens. There was also a greater degree of constriction across frontotemporale relative to the supraorbital torus in higher scoring specimens. Figure 3.22c illustrates how PC 2 was mainly associated with differences in the shape of the supraorbital torus. At the positive end of PC 1 the torus was narrower, less arched over the orbits and thicker at the lateral ends. The supraorbital torus was positioned lower on the frontal bone and there was greater constriction across frontotemporale. In addition to the differences in the supraorbital region, there was also less expansion in the midline on the inferior half of the frontal squama and anterior pterion was more posteriorly positioned in higher scoring individuals. Excluding WT 15000 from the analysis did not change the results greatly.

PCA frontal landmark set, fossils only: When a PCA of the frontal landmarks without recent human specimens was performed, *H. erectus* was distinct from mid-Pleistocene *Homo*, early *H. sapiens* and early ‘*Homo*’ (which included both *H. habilis* and *H. rudolfensis*, as discussed above) on PCs 1, 2 and 4, respectively (Table 3.5). There was, however, overlap between mid-Pleistocene *Homo* and *H. erectus* on PC 2 as seen in Figure 3.23a. In particular, the higher scores of Kabwe and especially Bodo overlapped some *H. erectus* individuals. Arago XXI, on the other hand, grouped with the early modern humans rather than other mid-Pleistocene *Homo* individuals. However, this specimen has undergone a certain amount of plastic deformation, including a large crack

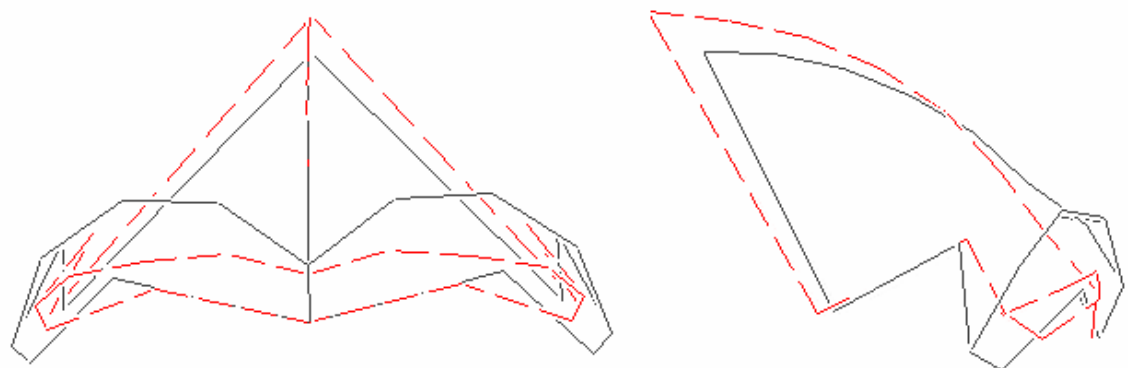
in the area of metopion which may have altered the shape of the midsagittal profile, causing it to appear more outwardly expanded. The single Neanderthal individual included in the analysis, La Chapelle, scored lower than all *H. erectus* specimens on PC 2, although this difference did not reach significance. OL 45500 and Daka scored lower than all other *H. erectus* fossils on the first component whereas the highest scoring *H. erectus* individuals were from Asia. S 17 scored lower than the other Asian specimens on PC 1. On PC 1, some mid-Pleistocene *Homo* fossils were more distinct from early *H. sapiens* than were African and Georgian *H. erectus* specimens, a result which differs from the neurocranial analyses.

Figure 3.23c illustrates that higher scoring fossils on PC 1 had a relatively longer frontal squama and a thinner, straighter supraorbital torus. The torus was also narrower, much less superiorly projecting with less torsion of the anterior surface posteriorly and a greater depression above glabella. On PC 2, the higher scoring specimens had a wider torus with an expanded glabellar region and thinner mid-torus (Figure 3.23d). The frontal squama was flatter medio-laterally and more receding in the mid-sagittal plane with a relatively shorter coronal border and greater constriction across the more superiorly positioned frontotemporale. These features were especially exaggerated in OL 45500, the partial cranium from Olorgesailie, which scored very high on PC 2.

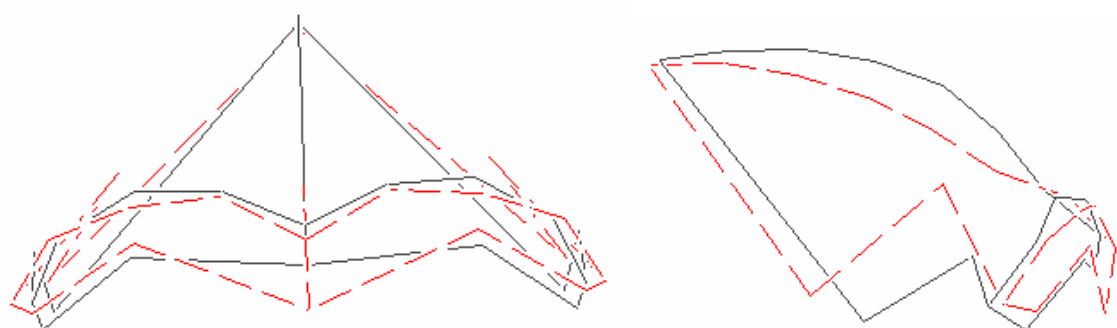
Figure 3.23: PCA of frontal bone landmark set, fossils only. a) PC 1 vs. PC 2 and b) PC 1 vs. PC 4 are illustrated below. The average score of *H. erectus* on PC 1 is significantly higher than that of mid-Pleistocene *Homo* on PC 1 and early *H. sapiens* on PC 2. The 'X' is Ceprano. The shape differences from the positive to the negative ends of PC 1 (c), PC 2 (d) and PC 4 (e) are shown below. See legend in Figure 3.8.



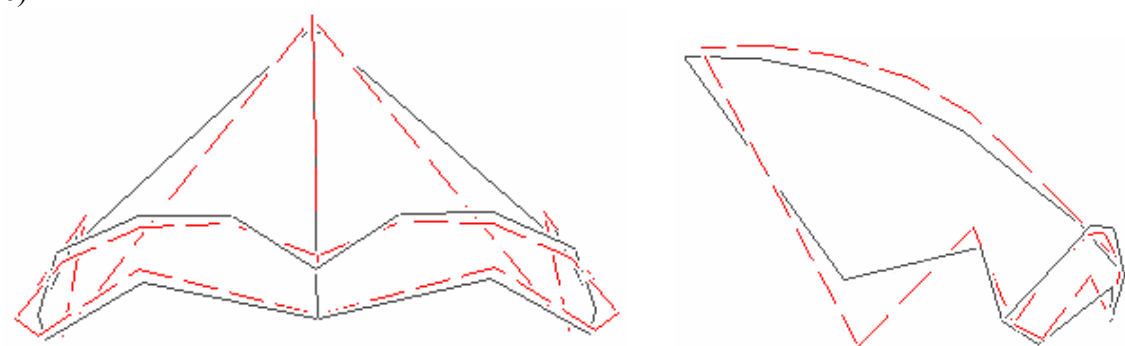
c)



d)



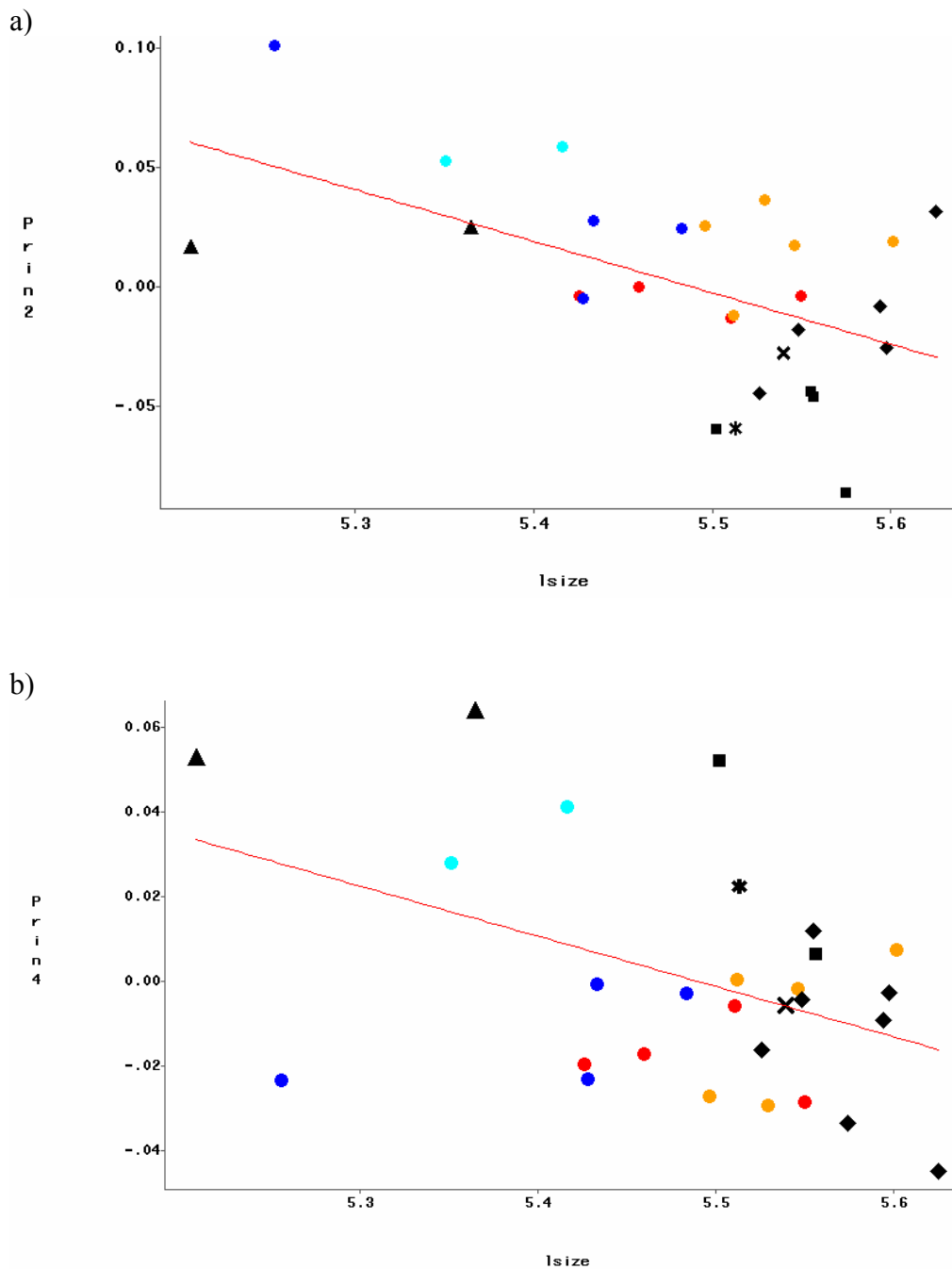
e)



As seen in Figure 3.23b, the high scores of the two early *Homo* fossils on PC 4 distinguished them from *H. erectus*, but Skhul 5 also scored quite high, so the shape changes associated with the positive end of PC 4 are not unique to early *Homo*. These shape features were a relatively shorter and more domed frontal squama (in the mid-sagittal plane), with less breadth across anterior pterion and a thinner, less projecting torus at mid-orbit (Figure 3.23e).

Size of the frontal bone as measured by these landmarks significantly influenced the positions of specimens along PCs 2 and 4. Shape differences between *H. erectus* and early *H. sapiens* do not appear to be related to scaling factors in the frontal bone. Despite being similar in size to several of the Asian *H. erectus* specimens, early *H. sapiens* scored much lower (and fell below the regression line) as seen in Figure 3.24a. As in many previous cases, the relationship between $\ln(\text{centroid size})$ and PC 4 scores was strongly influenced by the small size and extreme score of ER 1813 and was not significant when this specimen was excluded from the regression analysis (Figure 3.24b). However, ER 1470, although not nearly as small as ER 1813, also scored high. OL 45500 could also be viewed as an outlier in that it scored very low for its small size, but its score was similar to that of other *H. erectus* specimens. Taken together, these observations suggest that while size may have contributed to shape variation along PC 4, size differences do not account for the significant difference between early *Homo* and *H. erectus*.

Figure 3.24: Regression of PC 2 and PC 4 scores from frontal landmark set, fossils only PCA on $\ln(\text{centroid size})$. $\ln(\text{centroid size})$ accounts for 28% of variation in PC 2 scores (a) and 19% of variation in PC 4 scores ($\alpha < 0.05$) (b). See legend in Figure 3.8.



PCA temporal base landmark set, all-specimens: A region of the skull which was under-represented in the overall cranial analysis was the base. With the exception of a handful of specimens, very few well-preserved cranial bases are present in the *H. erectus* fossil

record. However, many individuals do preserve some portion of the cranial base, with the lateral temporal bone being particularly well-represented. Therefore, a third regional landmark set utilized 11 landmarks from the basal portion of the temporal bone as described in Table 3.3. These landmarks captured the general shape of the temporomandibular joint (TMJ), the tympanic tube, and the relative positions of the styloid foramen and temporosphenoid suture as seen in Figure 3.5.

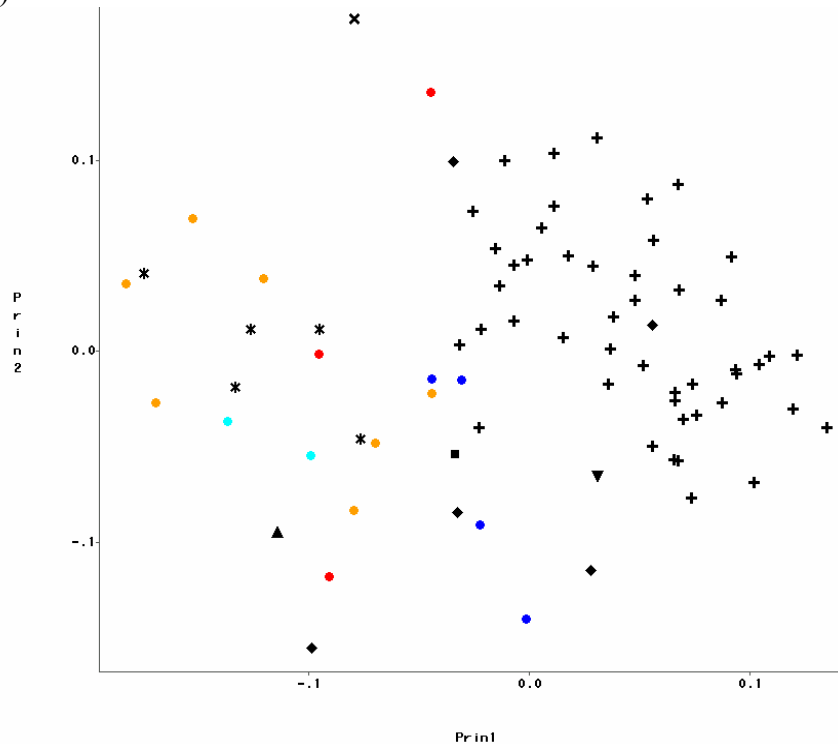
A large sample of fossil and extant *Homo* preserved this particular landmark set, including 16 *H. erectus* specimens. One of these *H. erectus* fossils was WT 15000, which was a young adult. Excluding WT 15000 did not affect the results in a meaningful way, so it was left in the analysis. While ER 1805 is often considered to be *H. habilis*, there is not complete agreement concerning its species status. Because ER 1805 did not fall close to OH 24 on the first several PCs, these specimens were not grouped together for significance testing. Although ER 3733 was initially included in this analysis, it was separated from all other individuals on PC 4 as a result of the very medial position of its lateral petrosal crest. This landmark was difficult to identify, possibly as a result of damage to the lateral tympanic plate as described by Rightmire (1990). Because this unusual morphology may have resulted from taphonomic processes, ER 3733 was excluded from the temporal base analyses.

The PCA plot in Figure 3.25a demonstrates that the first component served mainly to separate the modern human sample from the other *Homo* taxa, with the exception of mid-Pleistocene *Homo*. *H. erectus* also differed significantly from mid-Pleistocene *Homo* on PC 1. Interestingly, while Skhul 5 fell just at the edge of the modern human distribution on the first component, most African *H. erectus* crania were

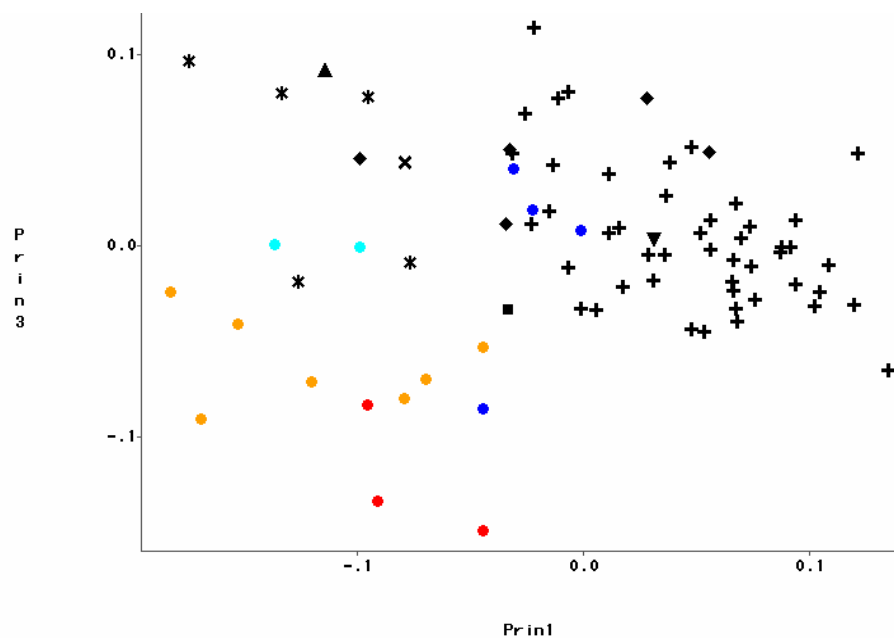
just within the modern human range on PC 1 (specifically, Daka, OH 9 and ER 3883) as were several mid-Pleistocene *Homo* specimens (Kabwe, Salé, ES 11693 [Eliye Springs] and LH 18). Dali clearly grouped with other fossil *Homo*, while Omo Kibish 2 was just within the bounds of the fossil *Homo* group. The fact that Salé scored higher than any of

Figure 3.25: PCA of temporal base landmark set, all-specimens. a) PC 1 vs. PC 2 and b) PC 1 vs. PC 3 are shown below. *H. erectus* differs from all later *Homo* taxa on PC 3 and from *H. sapiens* on PC 1 as well. ER 1805 (X) scores very high on PC 2 while Salé (upside down triangle) falls within the recent *H. sapiens* distribution on both PC 1 and 2. The shape differences from the negative to positive ends of PC 1 (c) and 3 (d) are shown below in inferior and lateral views. See legend in Figure 3.8.

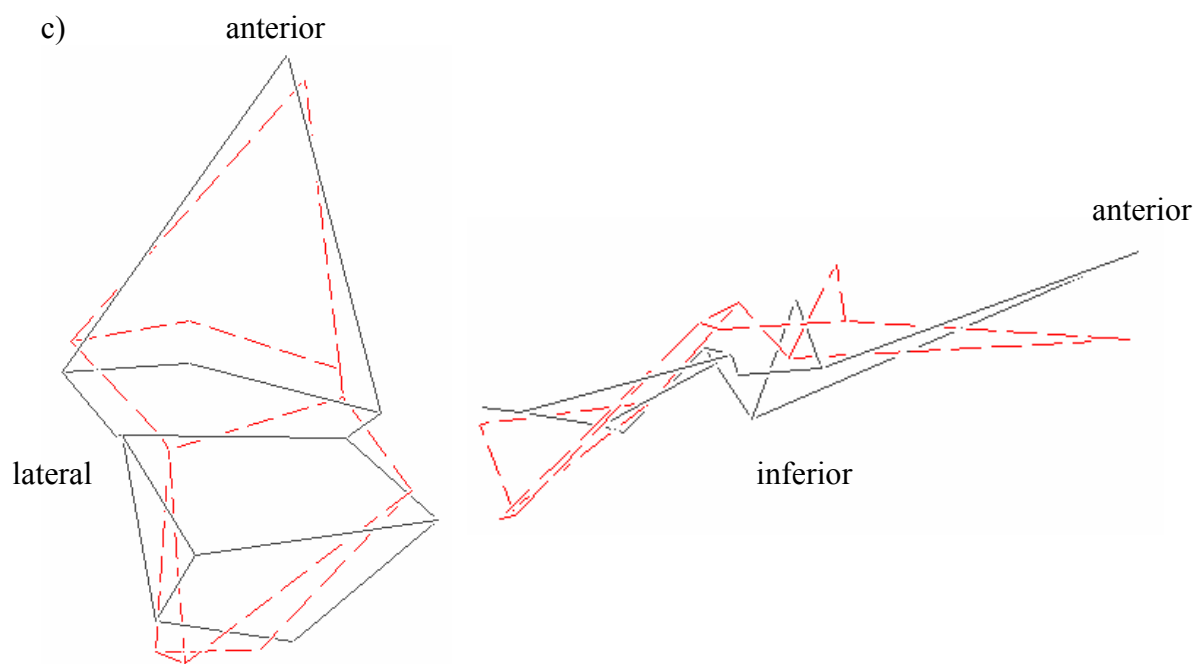
a)



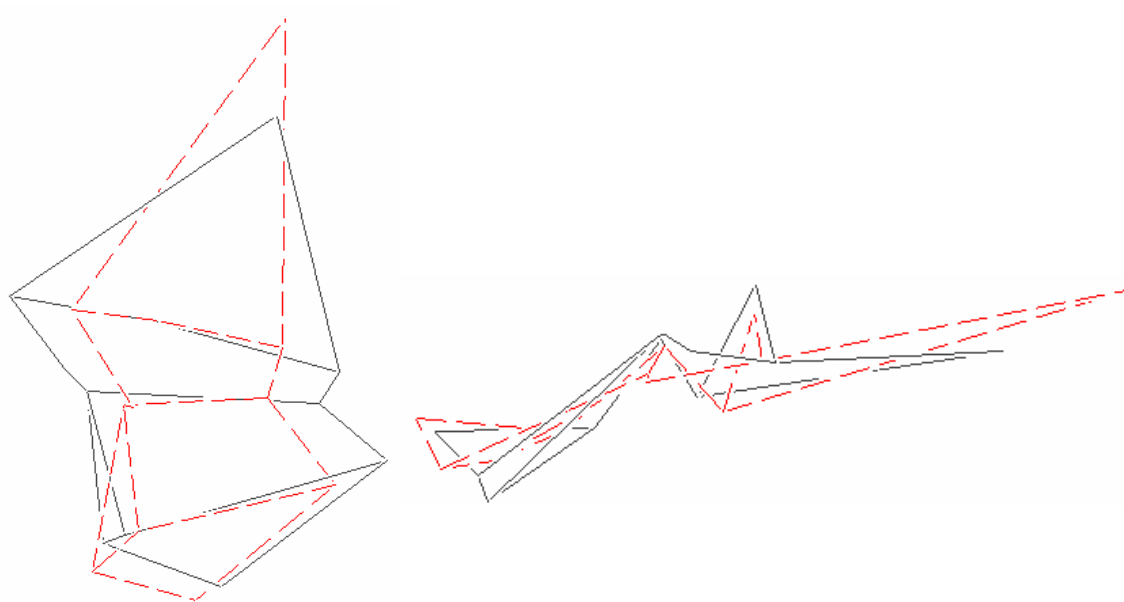
b)



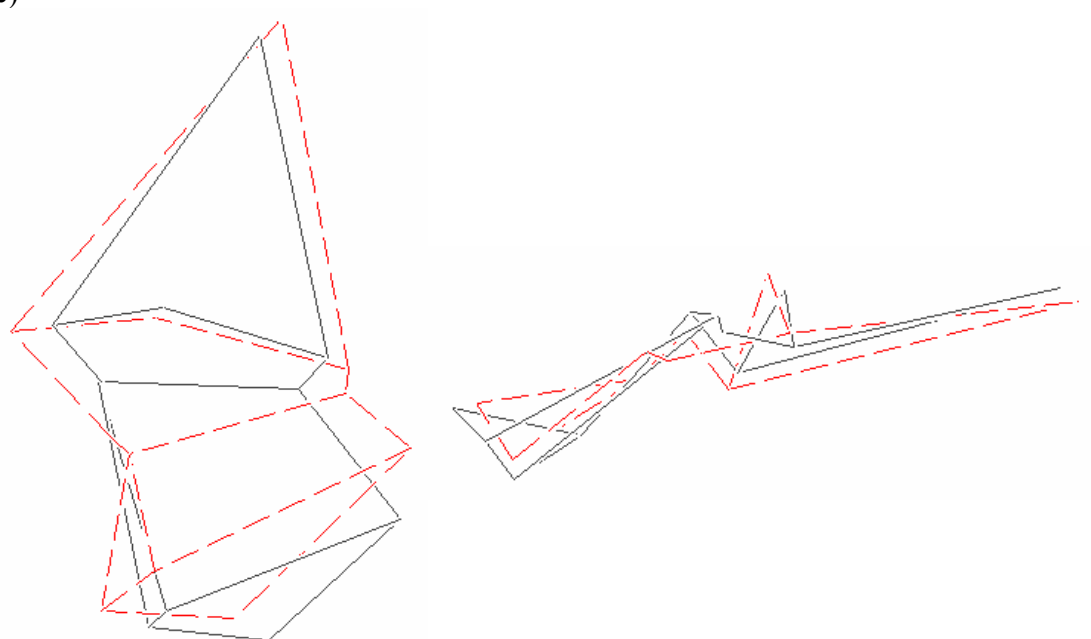
c)



d)



e)



the *H. erectus* fossils on PC 1, along with several other mid-Pleistocene specimens supports a non-*erectus* species assignment for this fossil.

There were numerous shape differences associated with PC 1 as seen in Figure 3.25c. At the negative end of PC 1, the TMJ was much wider overall and shorter laterally and centrally. The petrosal crest was relatively shorter and there was a larger gap between the petrosal crest and the mastoid process, resulting in a crest which was fairly perpendicular to the midline (in contrast to a postero-laterally oriented petrosal crest). In lower scoring individuals, the temporosphenoid suture, tympanomastoid junction and the lateral extent of the squamotympanic fissure were more superiorly positioned while the TMJ and petrosal crest are more inferiorly positioned so that the TMJ was inferior to the temporosphenoid suture rather than being on the same plane as the suture. Also, the lateral petrosal crest and tympanomastoid junction were much more superiorly positioned relative to the TMJ. This created a less flexed appearance laterally.

H. erectus differed significantly from all taxa (but not ER 1805) on PC 3, which was influenced in part by the very low scores of the Asian *H. erectus* (and WT 15000) in particular (Figure 3.25b). Of the mid-Pleistocene *Homo* specimens, Dali, LH 18 and Kabwe scored higher than all *H. erectus* while Omo Kibish 2 and Salé overlapped the higher scoring African and Georgian *H. erectus* specimens. La Ferrassie, La Chapelle and Saccopastore 1 also scored higher than all *H. erectus* individuals, although Gibraltar and Saccopastore 2 overlapped several of the African and Georgian *H. erectus* fossils. Both OH 24 and ER 1805 scored higher than *H. erectus*. The modern humans, including Skhul 5, spanned the middle and higher portions of PC 3. Ln(centroid size) of the basal temporal bone accounted for only a small percentage of variation in PC 1 and PC 3 scores

as seen in Table 3.5. Overall, the Asian *H. erectus* are more derived in their basal temporal bone shape relative to other *Homo* species.

Lower scoring individuals on PC 3 had a narrower TMJ and a very long anterior face of the tympanic tube (Figure 3.25e). The distance between the medial and lateral ends of the petrosal crest was shortened due to a more postero-lateral position of the medial end of the crest. The depth from the tip of the entoglenoid medially to the center of the TMJ also decreased from the positive to negative ends of this component.

ER 1805 scored significantly higher on PC 2 than did OH 24, *H. erectus* and mid-Pleistocene *Homo* (Figure 3.25b). Zkd 5 had the second highest score of all-specimens on PC 2. Higher scoring individuals were characterized by a relatively narrower TMJ and a very medially positioned postglenoid process as seen in Figure 3.25d. The petrosal crest was also quite narrow and its lateral extent was further from the mastoid process than in higher scoring individuals. There was a greater distance between the TMJ and the temporosphenoid suture and less vertical distance between the center and the lateral edge of the mandibular fossa.

The apparent narrowness of the temporal base structure in ER 1805 may have been exaggerated by both damage to the root of the zygomatic arch in the region of the lateral articular fossa and the unusual morphology of the postglenoid process. Despite this damage, Wood (1991) was able to measure the breadth of the mandibular fossa from the entoglenoid process to the lateral extent of the fossa, which he did note was quite narrow. This confirms that the lateral TMJ landmarks could be identified despite damage to the root. In ER 1805 the postglenoid process was a thin plate very closely applied to the anterior surface of the tympanic tube medial to the lateral border of the tube. This

morphology was unique to ER 1805 in this sample and would have affected the positions of both the postglenoid and lateral squamotympanic fissure landmarks, as the latter was generally taken at the medial junction of the postglenoid process and tympanic tube. Therefore, while the landmark configuration of ER 1805 likely reflected the true morphology of this fossil, it may not have captured the lateral extent of the posterior mandibular fossa (at the postglenoid process and lateral squamotympanic fissure) in the same way as other specimens in the analysis.

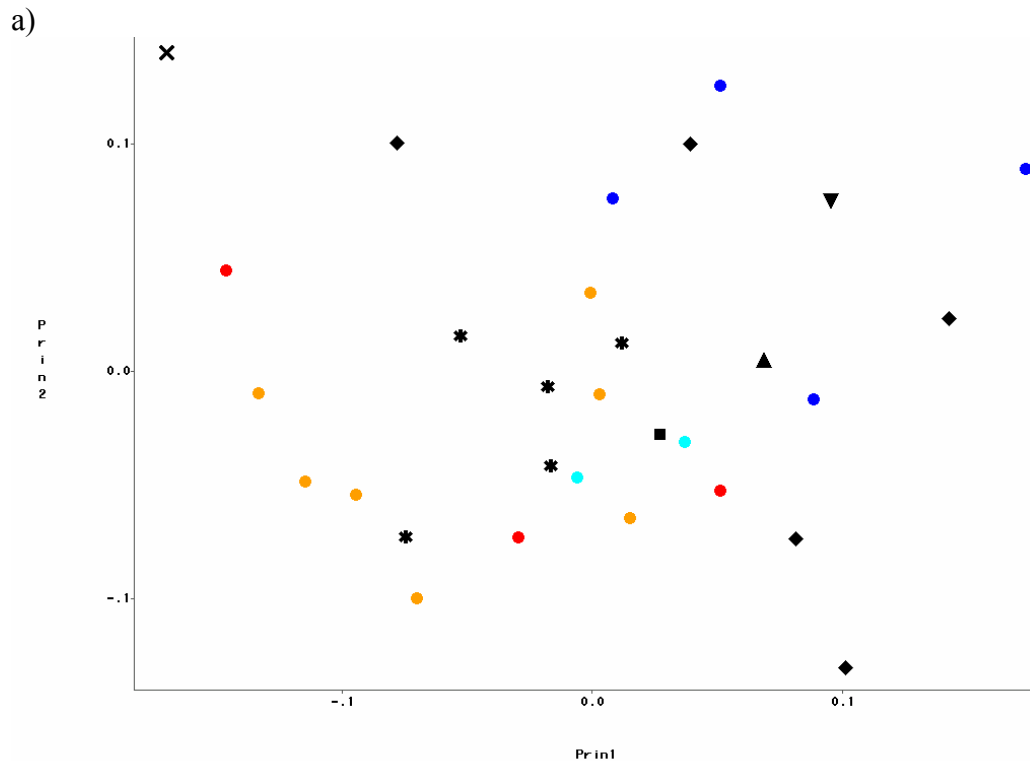
PCA temporal base landmark set, fossils only: As illustrated in Figures 26a and b, there was considerable overlap among fossil *Homo* taxa in their temporal base shape. The largest component of variation in this sample actually separated the African and Asian *H. erectus* subsamples, with the two Dmanisi fossils falling between the groups. Only WT 15000 overlapped the Asian distribution. Most mid-Pleistocene *Homo* (and Salé) looked more like the African fossils while Omo Kibish 2 and all of the Neanderthal specimens had either intermediate or low scores like the Asian specimens. OH 24 resembled the African *H. erectus* fossils while ER 1805 had the lowest score of all-specimens on the first component. On the second PC there was a division between the higher scoring early African *H. erectus* fossils, ER 1805, Omo Kibish 2, LH 18 and Salé and all other specimens.

The shape differences toward the positive end of PC 1, illustrated in Figure 3.26c, included a widening of the tmj (especially anteriorly) with there was less distance between the lateral end of the petrosal crest and the mastoid process (resulting in a more antero-medially angled petrosal crest). The angulation of the crest also resulted in the

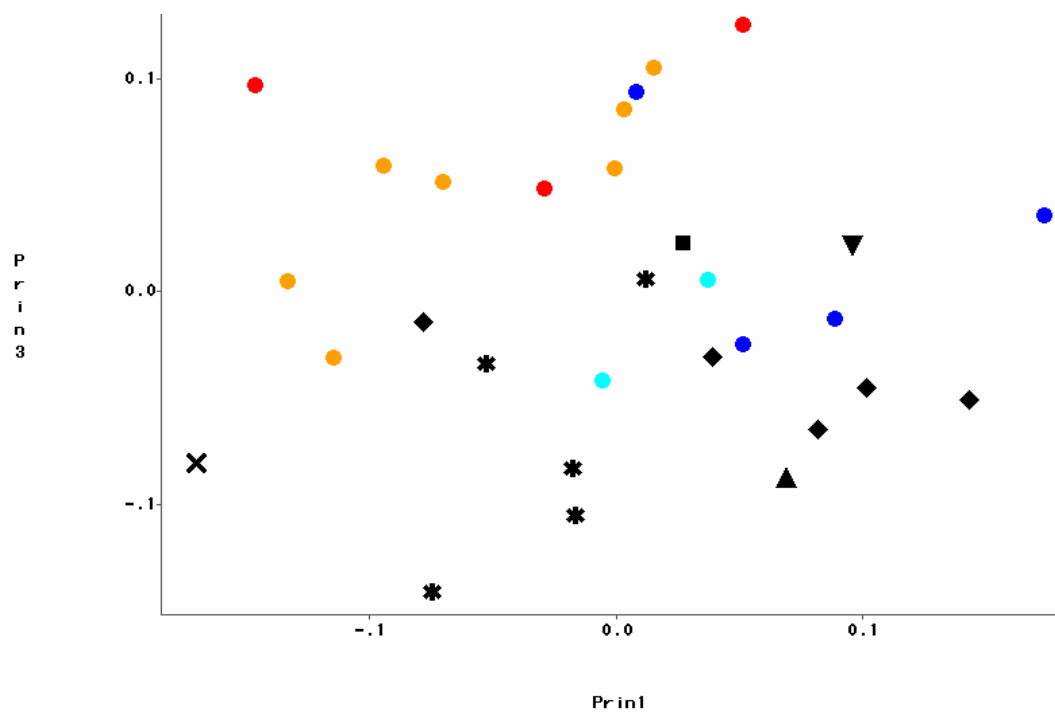
medial end being closer to the entoglenoid process posteriorly. Also, the temporosphenoid suture, tympanomastoid juncture and the lateral extent of the petrotympanic crest were more inferiorly located while the tmj and petrosal crest were more superiorly positioned, creating a flexed appearance laterally. Figure 3.26d demonstrates that the higher scoring fossils on PC 2 had a petrosal crest which was more infero-laterally angled whose lateral end was more medially positioned. The entoglenoid was inferiorly projecting, especially compared to the lateral articular fossa, and the squamotympanic fissure was narrow within the confines of the mandibular fossa. Salé has been considered to be either *H. erectus* or a more derived species of *Homo*. However, while this specimen did group with mid-Pleistocene *Homo* on PCs 1, 3 and 4, it was outside the range of this taxon on PCs 2 and 5. While Salé was within the range of *H. erectus* on the first 5 components, the numerous *H. erectus* fossils in this analysis frequently encompassed nearly the entire range of variation on any given component. Also, Salé scored higher than all other fossil specimens on PC 6 due to the medial position of the postglenoid process. Therefore, significance tests were run with Salé assigned to *H. erectus*, mid-Pleistocene *Homo* and its own group.

The only significant group difference was between *H. erectus* and Neanderthals on PC 3 where *H. erectus* score higher. Although not significant, early *Homo* specimens also scored lower than all *H. erectus* individuals on the third component. As seen in Figure 3.26e, the shape differences on PC 3 were mainly limited to the tympanic tube: higher scoring individuals had a narrower, more inferiorly projecting and more posteriorly positioned petrosal crest coupled with a deeper and more anteriorly positioned

Figure 3.26: PCA of temporal base landmark set, fossils only. a) PC 1 vs. PC 2 and b) PC 1 vs. PC 3 are shown below. ER 1805 (X) scores high on PC 2. Salé (upside down triangle) groups with African *H. erectus* and several mid-Pleistocene *Homo* specimens. There is a general division on PC 1 between the lower scoring Asian and higher scoring African *H. erectus* with the Dmanisi hominins exhibiting intermediate scores. On PC 2, the older African fossils score quite high. Despite some overlap, *H. erectus* and Neanderthals differ significantly in their PC 3 scores. The shape differences along PC 1 (c), PC 2 (d) and PC 3 (e) are shown below in inferior and lateral views. See legend in Figure 3.8.

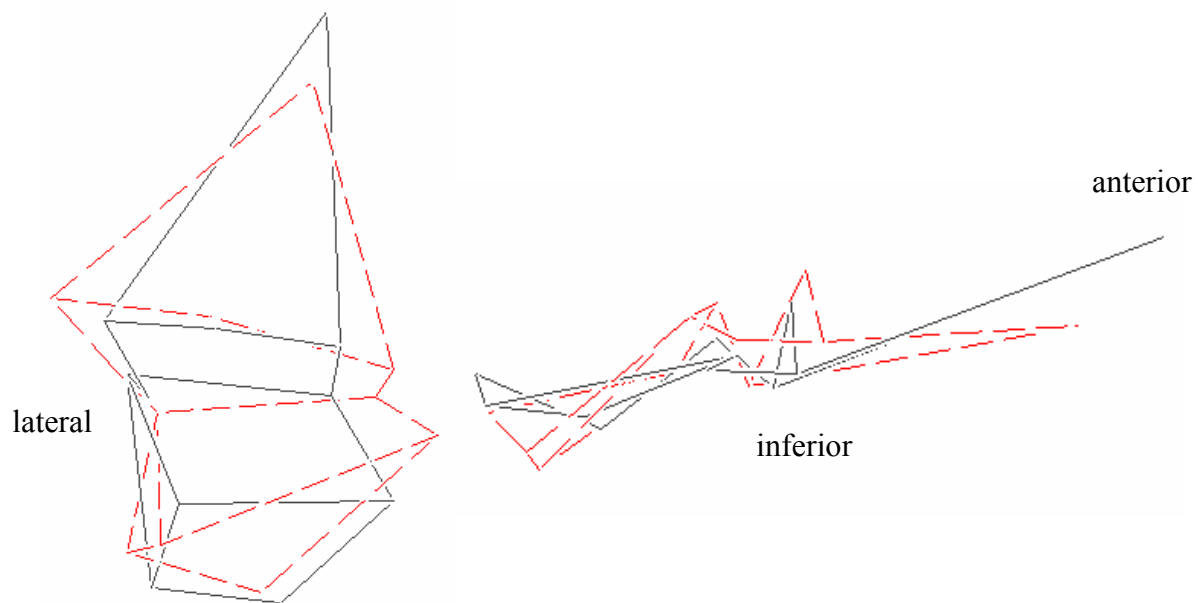


b)

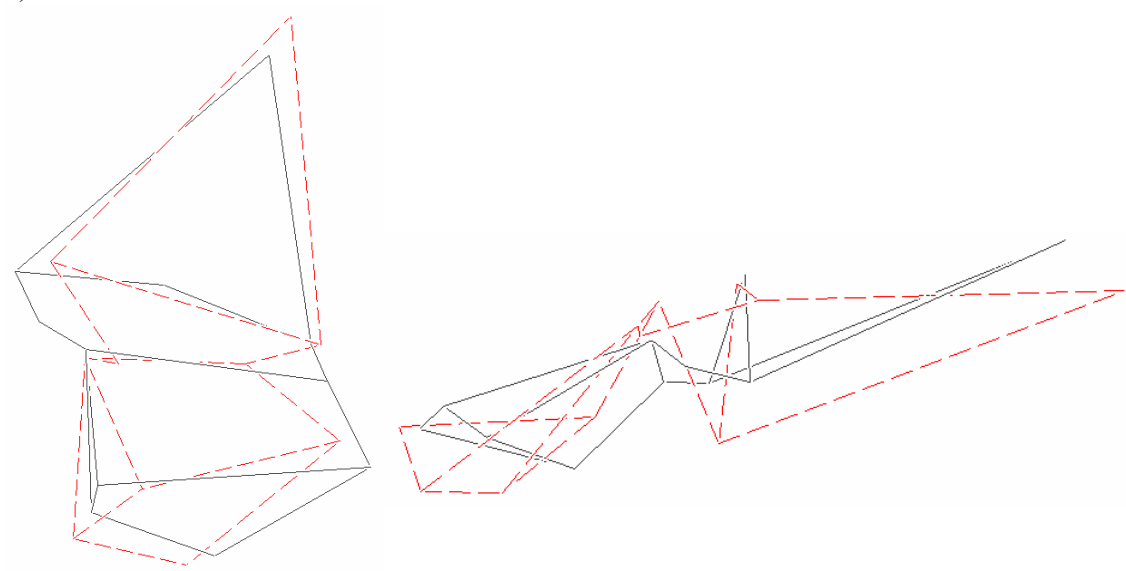


c)

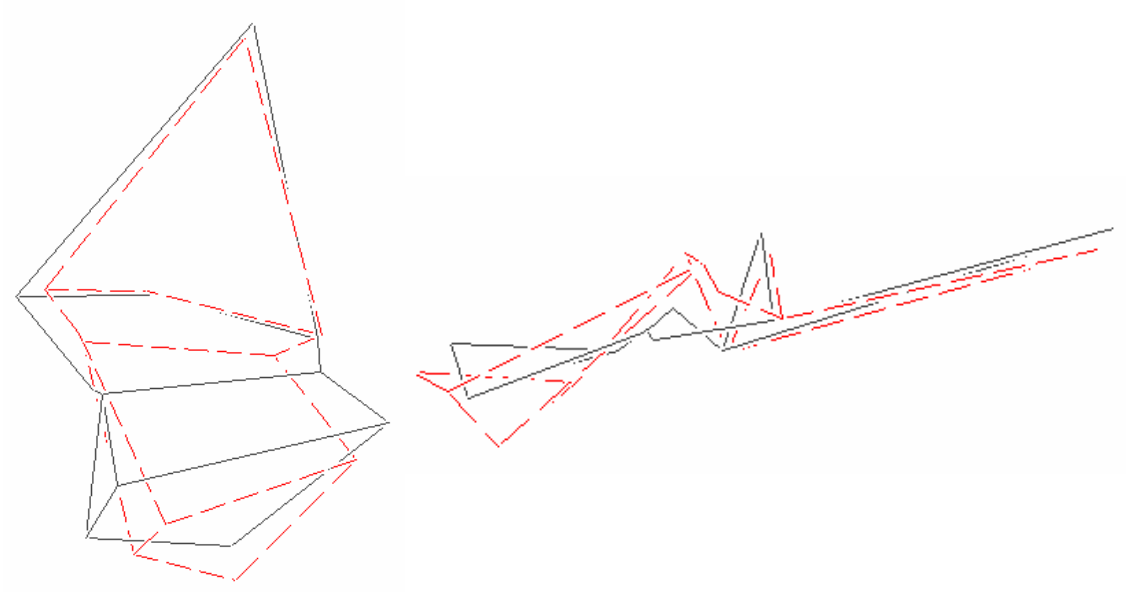
anterior



d)



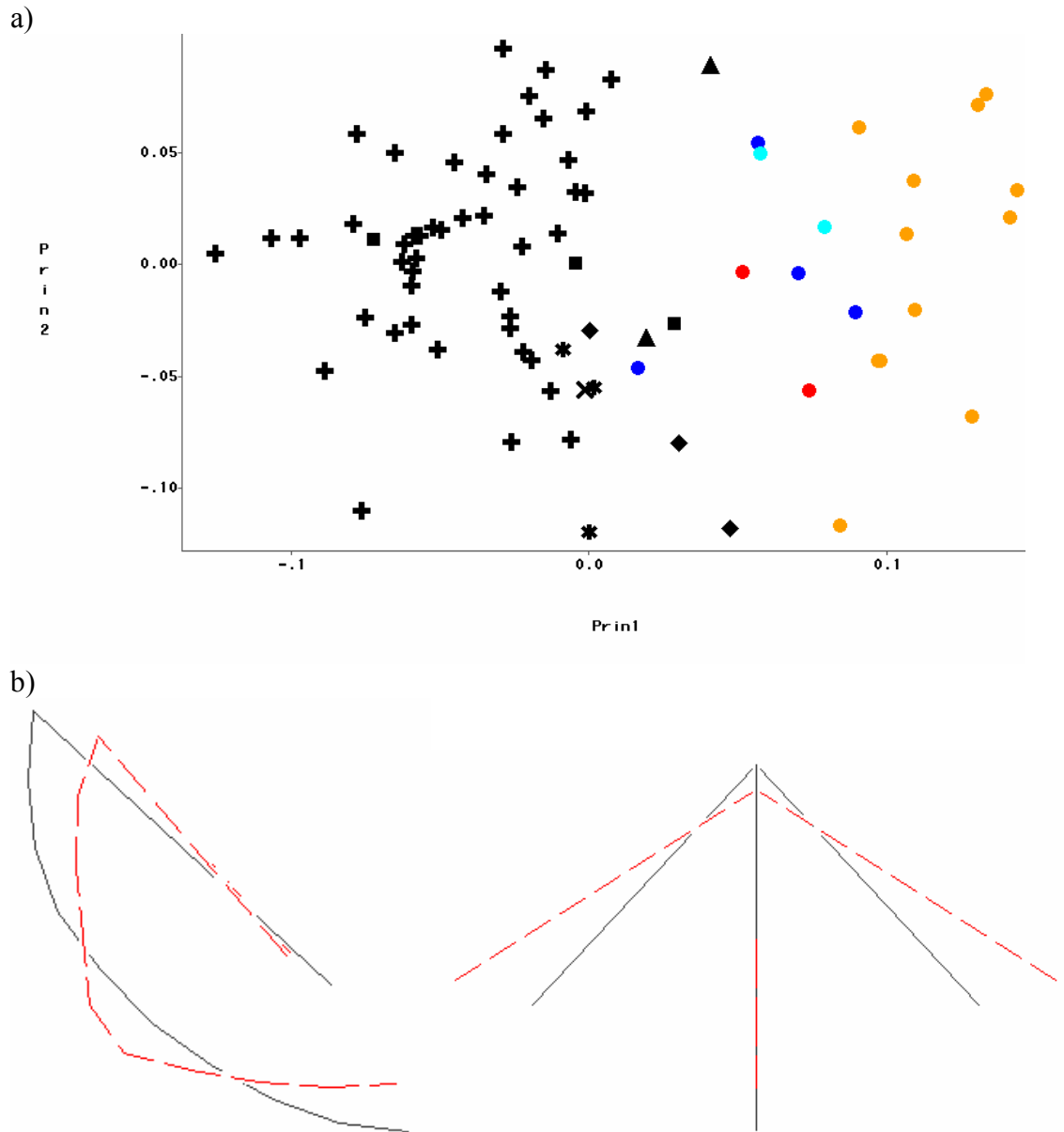
e)

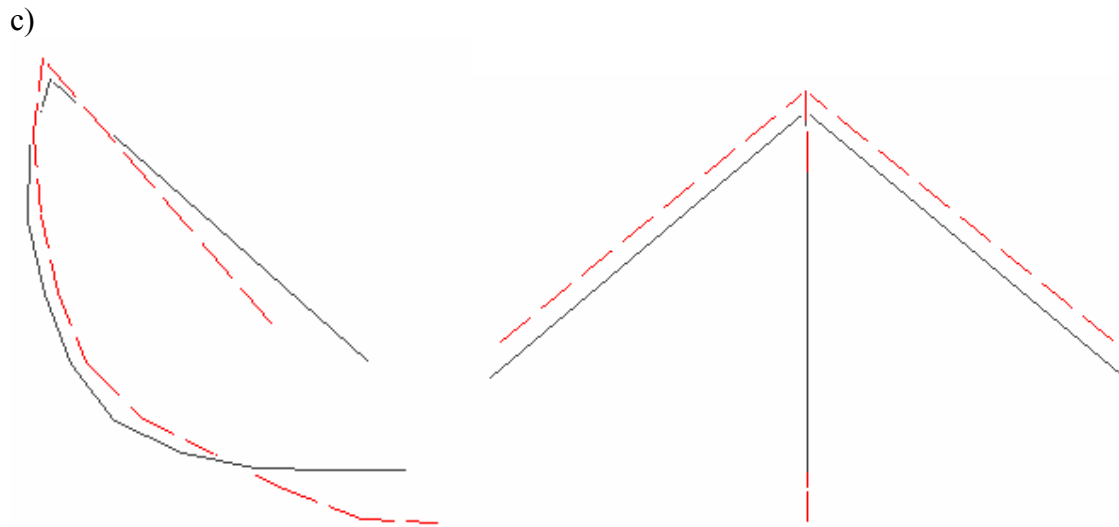


squamotympanic fissure (located at the anterior extent of the tympanic tube). This resulted in a long and steep anterior face of the tympanic tube in those individuals. When the subadult WT 15000 was excluded from the analysis the general pattern remains the same and *H. erectus* and *H. neanderthalensis* remained significantly different along this PC. When WT 15000 was excluded, a small portion (16%) of the variance in PC 3 scores was accounted for by $\ln(\text{centroid size})$.

PCA of occipital landmark set, all-specimens: The final regional analysis was of the occipital bone. This analysis mostly focused on the midline occipital profile from lambda to opisthion but also included asterion, as seen in Figure 3.6. *H. erectus* differed significantly from *H. sapiens*, *H. neanderthalensis* and mid-Pleistocene *Homo* on PC 1 (Table 3.5). There was very little overlap between *H. erectus* and *H. habilis* on PC 1, as seen in Figure 3.27a, although this difference did not reach significance. In contrast to other analyses, *H. erectus* occupies the high end of the first component in contrast to *H. sapiens* with both *H. habilis* and mid-Pleistocene *Homo* intermediate between the two. *H. neanderthalensis* overlaps modern humans on the first component but generally scored lower on PC 2. Figure 3.27b illustrates that higher scoring individuals on PC 1 had a more angled occipital squama with a more horizontal nuchal plane and a more vertical occipital plane (versus posteriorly angled). The occipital bone was also wider across asterion in these specimens. The shape associated with the negative end of PC 2 (Figure 3.27c) was a shorter squama in the midline, a more horizontal nuchal plane and a much longer lambdoid suture. Excluding the subadult WT 15000 does not affect the outcome significantly.

Figure 3.27: PCA of occipital bone landmark set, all-specimens. a) PC 1 vs. PC 2 is plotted below. *H. erectus* is significantly different from *H. sapiens*, *H. neanderthalensis* and mid-Pleistocene *Homo* on PC 1. ER 42700 is represented below by the X. Shape differences along PC 1 (b) and PC 2 (c) are shown below in lateral and posterior views. See legend in Figure 3.8.





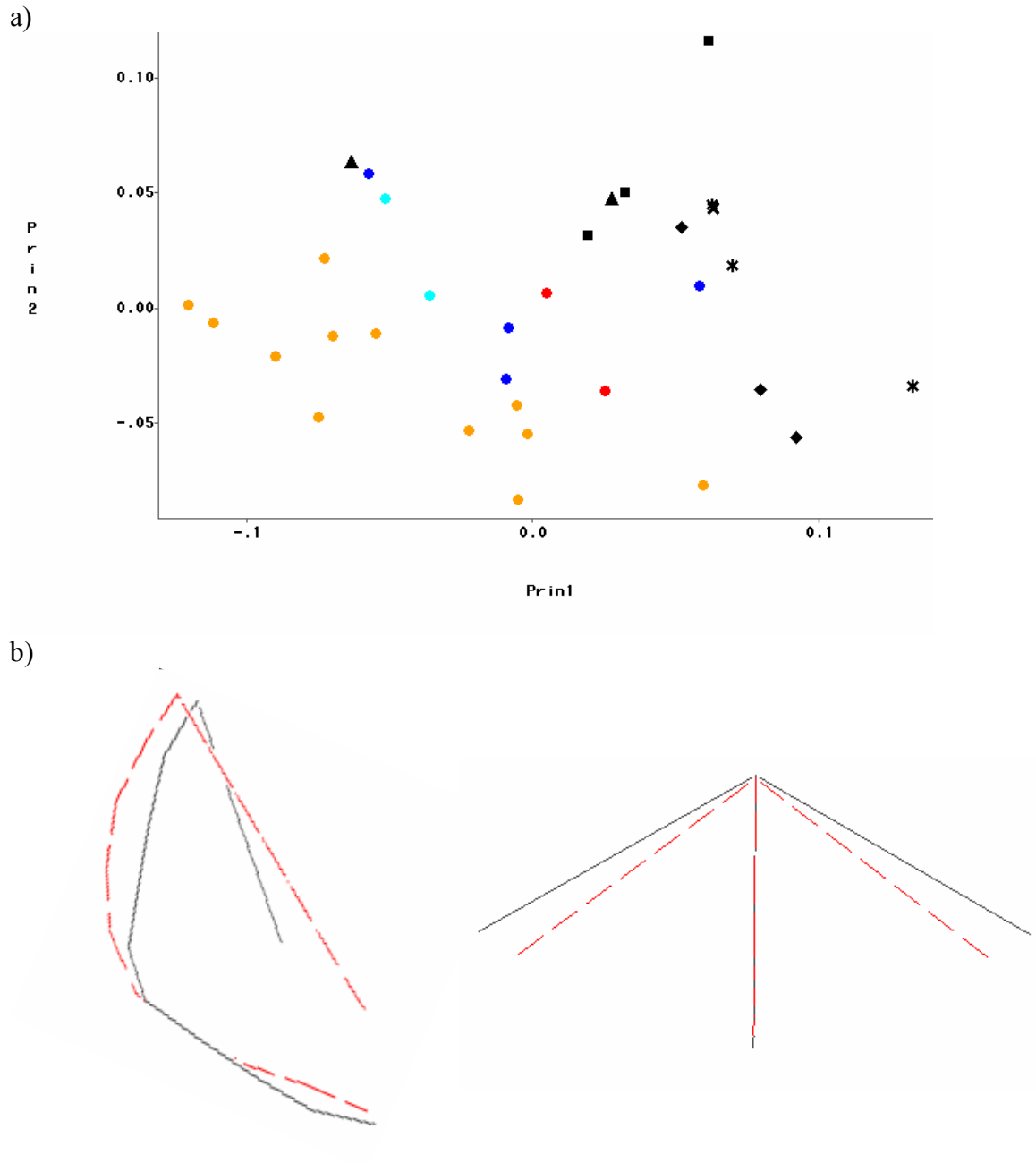
PCA of occipital landmark set, fossils only: *H. erectus* again differed from early modern humans, Neanderthals and mid-Pleistocene *Homo* on either PC 1 or 2 (Table 3.5).

Although ER 1813 scored higher than all *H. erectus* fossils on PC 2 (Figure 3.28a), and OH 24 only overlapped WT 15000 and D 3444, *H. erectus* and *H. habilis* were not significantly different. Daka and S 2 had particularly low scores on the first component.

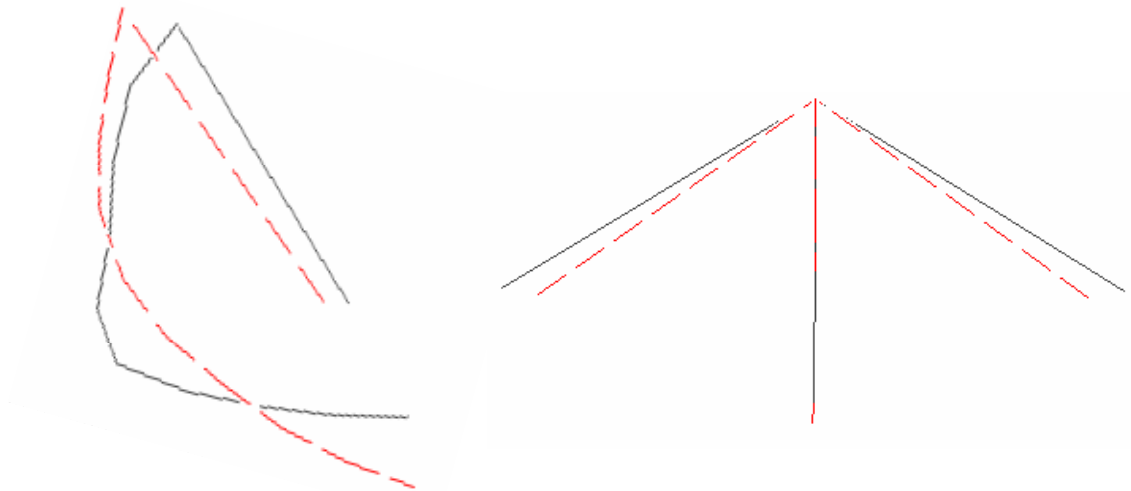
It should be noted that the occipital bone in the region of inion was reconstructed with plaster in OH 24 and this may not perfectly match the original morphology of this fossil.

Jebel Qafzeh 9 scored particularly high on PC 2. At the positive end of PC 1, illustrated in Figure 3.28b, specimens had longer occipital squamae that were more rounded and projecting posteriorly with a relatively superiorly positioned opisthion. The lambdoid suture was also long and asterion was more antero-medially located. Lower scoring

Figure 3.28: PCA of occipital bone landmark set, fossils only. a) PC 1 vs. PC 2 is shown below. *H. erectus* scored significantly lower on PC 1 than Neanderthals and mid-Pleistocene *Homo* and lower on PC 2 than early *H. sapiens*. ER 42700 is represented below by the X. Shape change on PC 1 (b) and PC 2 (c) are shown below. See legend in Figure 3.8.



c)

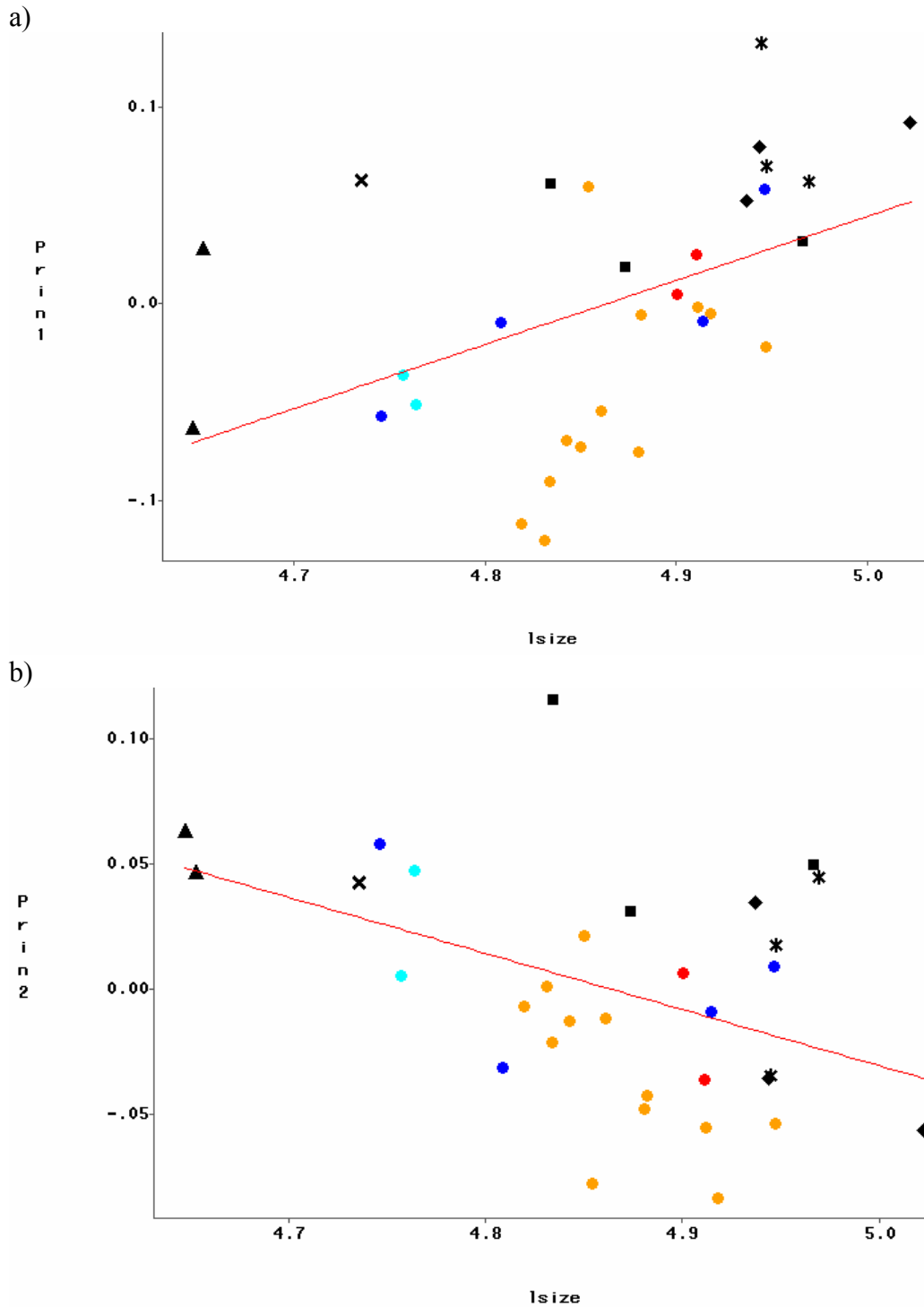


fossils on PC 2, including many of the Ngandong fossils, had a particularly vertical occipital plane, a superiorly angled nuchal plane and a distinct occipital torus with a supratatorial sulcus (Figure 3.28c).

$\ln(\text{centroid size})$ explained about a fifth of the variation in both PC 1 and PC 2 scores (Table 3.5) but did not account for differences between *H. erectus* and the other species. When PC 1 scores were regressed on $\ln(\text{centroid size})$, both Neanderthals and mid-Pleistocene *Homo* fell above the regression line (Figure 3.29a). When PC 2 scores were regressed on $\ln(\text{centroid size})$, modern humans fell above the line (Figure 3.29b). In both cases several of the Indonesian *H. erectus* fell well below this line. This PCA was not affected by the removal of WT 15000 from the analysis.

Comparisons of *H. erectus* to mean taxon shapes and to potential *H. erectus* fossils: In order clarify exactly how *H. erectus* differed from other *Homo* taxa in regard to overall

Figure 3.29: Regressions of PC 1 (a) and PC 2 (b) scores from occipital landmark set, fossils only PCA on $\ln(\text{centroid size})$. $\ln(\text{centroid size})$ accounted for about 20% of variation in both PC 1 and 2 scores. Allometric differences alone do not appear to account for the significant taxonomic differences observed on the first two components. See legend in Figure 3.8.

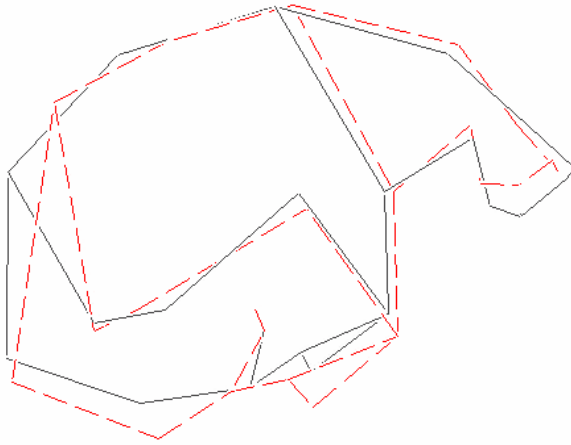


cranial shape, the mean configurations of *H. erectus* were compared to those of other taxa. Because the first component of every PCA that included recent *H. sapiens* specimens (i.e., ‘all-specimens’) significantly differentiated *H. sapiens* from *H. erectus*, and the shape change associated with PC 1 was described and illustrated for all analyses, further shape comparisons did not include recent *H. sapiens* but did utilize early anatomically modern *H. sapiens*, such as the Skhul and Jebel Qafzeh crania. The landmark sets used for these comparisons were the standard landmark set, the frontal bone and the occipital bone as these provided the best species discrimination. In order to avoid comparisons with only single fossils, less complete individuals were also included in the average configurations for the non-*erectus* samples in the neurocranial and frontal bone comparisons, as described in the ‘Methods’ section and summarized in Table 3.6. Only the most prominent shape differences are discussed below. Because more than one complete specimen was available for each species in the occipital bone comparison, no incomplete specimens were utilized.

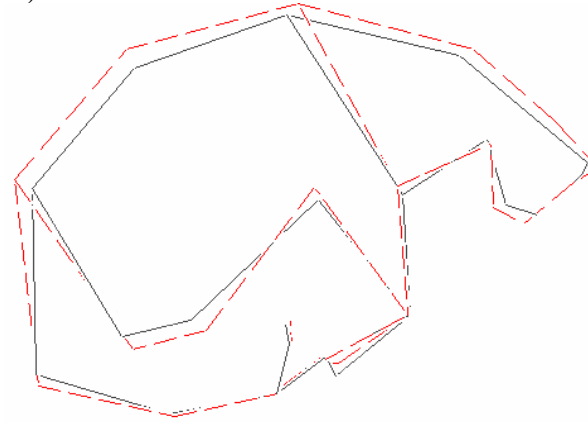
The cranial shape of *H. erectus* was consistently unique in having a very wide posterior vault relative to the mid-vault, a short lambdoid suture and a supraorbital torus which was straight both anteriorly and superiorly (Figure 3.30). The chord between the postglenoid and entoglenoid processes was more perpendicular to the midline in *H. erectus* whereas the entoglenoid process was more anteriorly positioned in the other species. However, mid-Pleistocene *Homo* did approach the *H. erectus* condition.

Figure 3.30: Comparison of mean *Homo erectus* landmark configuration to other *Homo* species means (standard landmark set). The black solid outline represents *H. erectus* while the red dashed outline represents the comparative group. Each comparison is shown in lateral and superior views. The comparative groups are: *H. habilis* (ER 1813) (a) and (e), mid-Pleistocene *Homo* (b) and (f), *H. neanderthalensis* (c) and (g) and early *H. sapiens* (d) and (h).

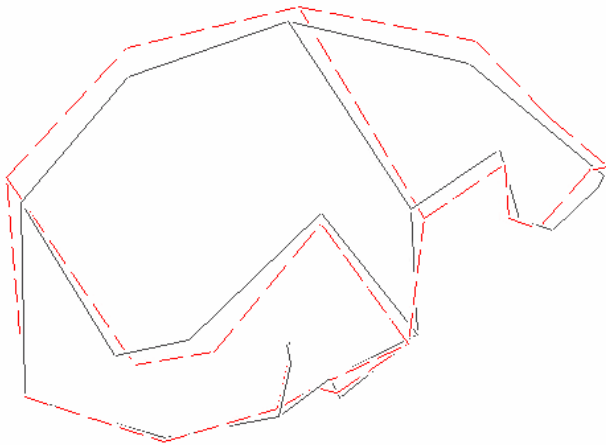
a)



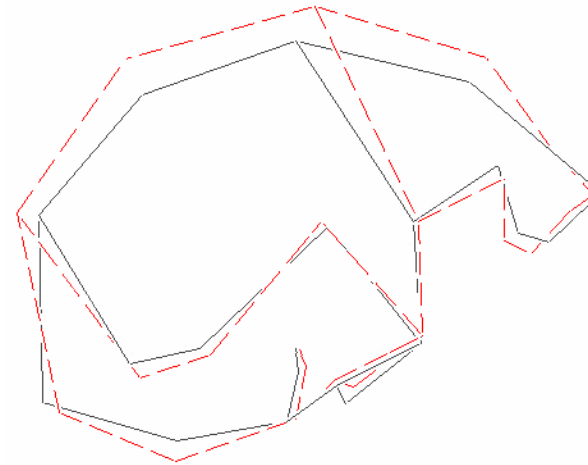
b)



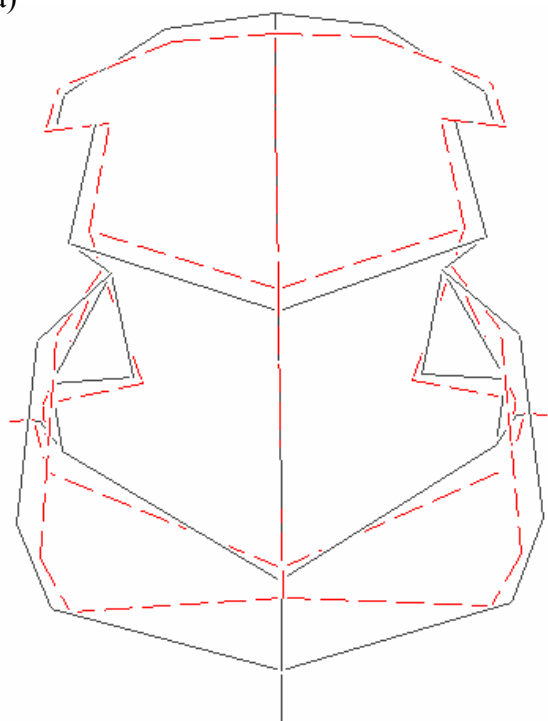
c)



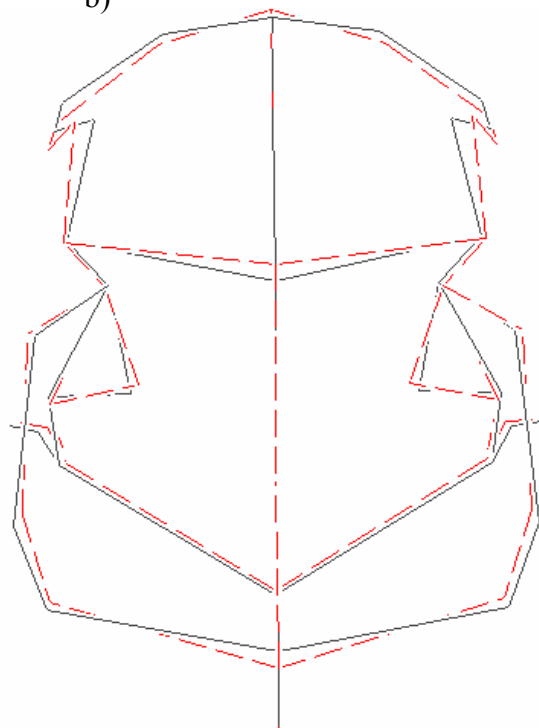
d)



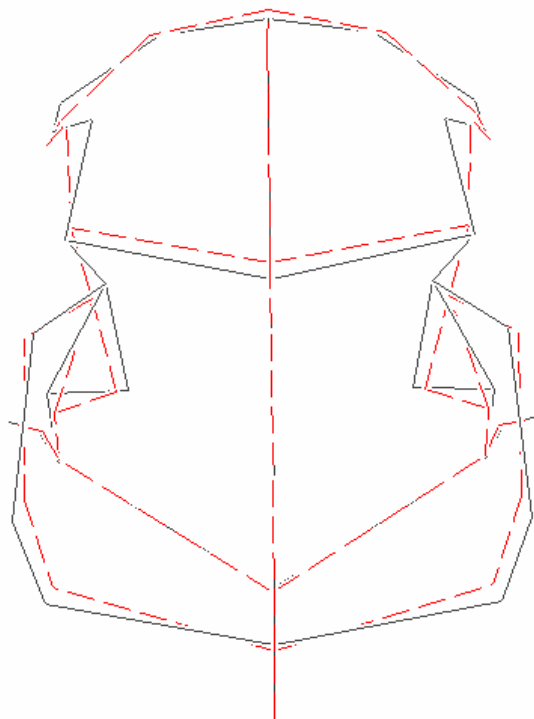
a)



b)



c)



d)

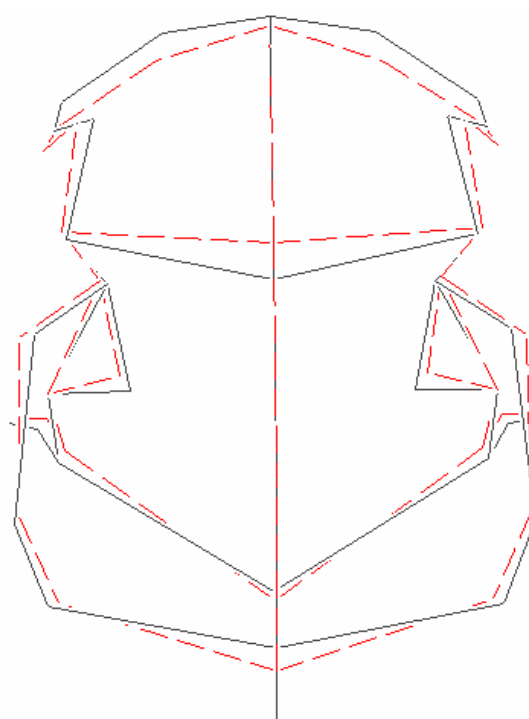


Table 3.6: Samples used to compare the mean species landmark configurations of *Homo erectus* and other fossil *Homo* species.

Analysis	Sample
Neurocranium (standard landmark set)	<u><i>H. erectus</i></u> : ER 3733, 3883, OH 9*, Daka, D 2280, 3444, S 2*, 17, Sm 1*, 3, Ng 6, 10*, 11, 12, Ngawi*, Zkd 3*, 5*, 11, 12 <u><i>H. habilis</i></u> : ER 1813 <u>mid-Pleistocene <i>Homo</i></u> : Kabwe, Dali, Omo Kibish 2*, Petralona* <u><i>H. neanderthalensis</i></u> : La Chapelle, La Ferrassie, Saccopastore 1* <u>Early <i>H. sapiens</i></u> : Skhul 5, Jebel Qafzeh 6*, Jebel Irhoud 1*
Frontal Bone	<u><i>H. erectus</i></u> : ER 3733, 3883, OL 45500, OH 9*, Daka, D 2280, 3444, 17, 3, Ng 6, 12, Ngawi, Zkd 3, 5, 11, 12 <u><i>H. habilis</i></u> : ER 1813 <u><i>H. heidelbergensis</i></u> : Arago 21, Dali, Bodo, Petralona, Ceprano, Kabwe <u><i>H. neanderthalensis</i></u> : La Chapelle, La Ferrassie* <u>Early <i>H. sapiens</i></u> : Skhul 5, Jebel Qafzeh 6, Jebel Irhoud 1, 2
Occipital Bone	<u><i>H. erectus</i></u> : ER 3733, 3883, WT 15000, Daka, D 2280, 3444, S 2, 4, 12, 17, Sm 1, 3, Ng 1, 6, 7, 11, 12, Ngawi, Zkd 11, 12 <u><i>H. habilis</i></u> : ER 1813 <u><i>H. neanderthalensis</i></u> : La Chapelle, La Ferrassie, Saccopastore 1 <u>mid-Pleistocene <i>Homo</i></u> : Dali, Petralona, ES 11693 <u>Early <i>H. sapiens</i></u> : Skhul 5, Jebel Qafzeh 6 and 9
ER 42700	<u><i>H. erectus</i></u> : ER 3733, 3883, OH 9*, Daka, D 2280, 3444, S 2*, 17, Sm 1*, 3, Ng 6, 10*, 11, 12, Zkd 3, 5, 11, 12 <u><i>H. habilis</i></u> : ER 1813 <u>mid-Pleistocene <i>Homo</i></u> : Kabwe, Dali, Omo Kibish 2*, Petralona*
Ceprano	<u><i>H. erectus</i></u> : ER 3733, 3883, OH 9*, Daka, D 2280, 3444, S 2*, 17, Sm 1*, 3, Ng 6, 10*, 11, 12, Zkd 3, 5, 11, 12 <u><i>H. neanderthalensis</i></u> : La Ferrassie, La Chapelle, Saccopastore 1* <u>mid-Pleistocene <i>Homo</i></u> : Kabwe, Dali, LH 18*, Ndutu*, Omo Kibish 2*, Petralona*

* - Indicates specimens included in the average configuration that were missing five or fewer unique landmarks (counting each bilateral landmark only once) in the neurocranial analyses (standard landmark set and Ceprano) or missing one unique landmark in the case of the frontal bone analysis.

H. erectus shared a low cranial profile, a comparable degree of postorbital constriction and a similar lambda-inion-opisthion angle with *H. habilis* but had a much more prominent supraorbital torus that was straight across anteriorly, whereas in *H. habilis* glabella was inferiorly positioned relative to the supraorbital notches. Perhaps the greatest differences between these two species were the much greater width at the anterior, posterior and mid- vault in *H. erectus*. *H. erectus* also had a less inferiorly projecting entoglenoid process, a relatively shorter nuchal plane and a relatively superiorly positioned anterior vault compared to *H. habilis*. The mid-temporal squama and asterion of *H. habilis* were lower while the parietal notch was higher compared to *H. erectus*. The final differences relate to the temporal base: the postglenoid process was more anteriorly positioned and the entoglenoid process was more laterally located.

H. erectus had slightly less superior expansion of the neurocranium relative to mid-Pleistocene *Homo* as well as a straighter supraorbital torus in superior view (in mid-Pleistocene *Homo*, Neanderthals and early modern humans, glabella was more anteriorly projecting than the mid-orbits). The mid-temporal squama was lower while the parietal notch and asterion were both located more superiorly in *H. erectus*. In superior view, *H. erectus* was slightly wider across asterion and the parietal notches, only slightly narrower across the temporal squama and exhibited greater constriction across frontotemporale relative to mid-Pleistocene *Homo*. The entoglenoid had slightly more inferior projection in *H. erectus* than in mid-Pleistocene *Homo*.

Compared to Neanderthals, the cranial profile of *H. erectus* was even lower and it was comparatively wider at posterior vault, narrower across the temporal squama and frontotemporale. Similar to the mid-Pleistocene *Homo* pattern, the position of asterion

and the parietal notch were lower in Neanderthals. In contrast to mid-Pleistocene *Homo*, however, Neanderthals had a slightly lower mid-temporal squama than *H. erectus*. The coronal suture of *H. erectus* was shorter than in Neanderthals and the supraorbital torus was straighter in superior view (as described above). In Neanderthals the postglenoid process was more posteriorly located and the entoglenoid process was more medially positioned.

The midline cranial profile of early modern *H. sapiens* was much higher than in *H. erectus*, and the frontal squama was more vertical anteriorly with a more marked supratotal sulcus. The reduced height at the back of the cranium was even more marked due to the more inferior position of opisthion in early *H. sapiens*. The entoglenoid process was more inferiorly projecting and posteriorly positioned in *H. erectus* than in early humans and the vault was wider posteriorly and narrower across the mid-temporal squama. The frontal squama was narrower in *H. erectus*, and the occipital bone was much more angled in the midline plane.

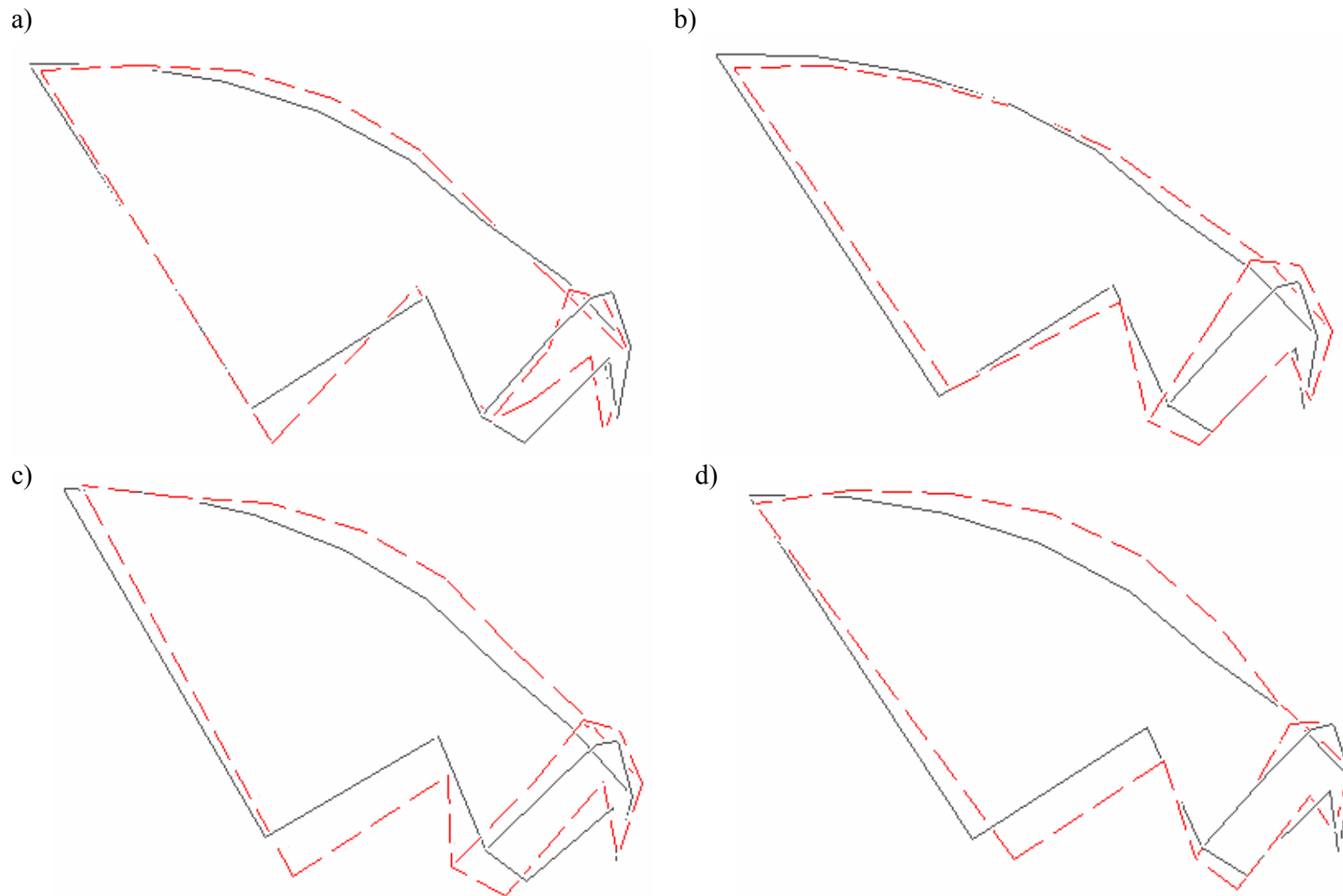
Average taxon configurations of the frontal landmark set were also compared in Figure 3.31. The Ceprano fossil was included in the mid-Pleistocene *Homo* sample because it groups with these specimens on most PCs. The shape of the supraorbital torus in *H. erectus* is unique, but differs from earlier and later species of *Homo* in different ways. Taken as a whole, *H. erectus* is most similar to mid-Pleistocene *Homo* in its frontal bone shape.

Compared to ER 1813 (*H. habilis*), *H. neanderthalensis* and early *H. sapiens*, the midline frontal profile of *H. erectus* is distinct in lacking a frontal tuberosity. The particularly flat frontal squama was also seen in mid-Pleistocene *Homo*, and there is a

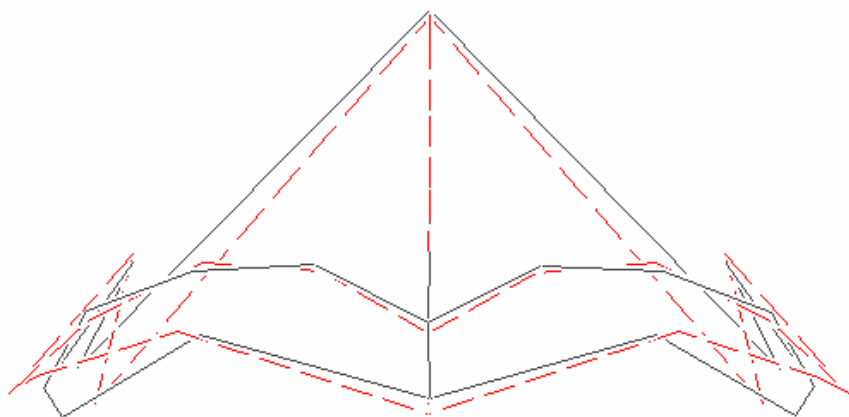
certain amount of geographic variation in this feature as the Zhoukoudian population has a more distinct tuberosity than other populations of *H. erectus* (Chapter 4). Anterior pterion is located more inferiorly in *H. habilis* and *H. neanderthalensis* and slightly inferiorly in early *H. sapiens* relative to *H. erectus*, but it is in a similar position in *H. erectus* and mid-Pleistocene *Homo*. Although difficult to see in the 2D representations in Figure 3.31, the position of anterior pterion, in combination with the flat midline profile in *H. erectus* and mid-Pleistocene *Homo*, indicates a very flat frontal squama in coronal section. The distance between the lateral extent of the supraorbital torus (i.e., frontomalar/temporale) and the minimum breadth across the temporal lines (i.e., frontotemporale), is greatest in *H. habilis*. *H. erectus* and mid-Pleistocene *Homo* also show fairly marked constriction behind the orbits relative to the Neanderthals and to early *H. sapiens*.

H. erectus does not display any torsion of the anterior (vermiculate) surface of the supraorbital torus at mid-orbit. The supraorbital torus of ER 1813 was thinner laterally and reached its highest point over mid-orbit whereas the torus of *H. erectus* was of comparable thickness across the orbit and reached its highest point more medially. The torus of mid-Pleistocene *Homo* was wider and both taller and more arched over mid-orbit compared to the straighter and thinner torus of *H. erectus*. *H. erectus* and Neanderthals had brow ridges of similar thickness, but they were more arched and postero-laterally angled in the latter. Viewed anteriorly, the shape of the tori were most similar in *H. erectus* and early *H. sapiens*, but it was not quite as anteriorly projecting at mid-orbit in early modern humans.

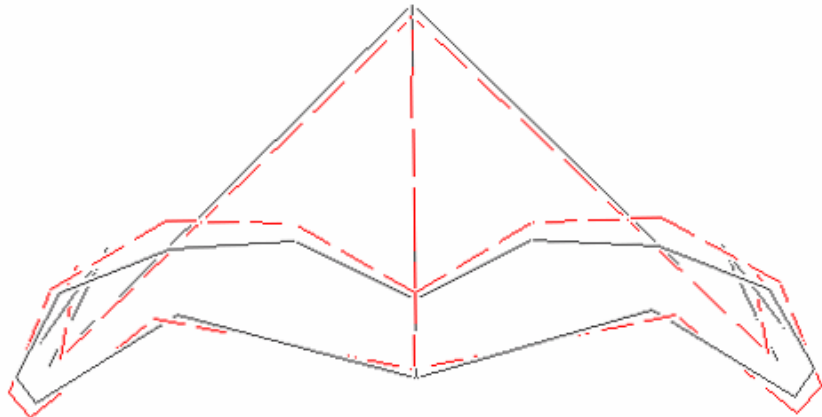
Figure 3.31: Comparison of mean configurations among *Homo erectus* and other *Homo* taxa: frontal landmark set. The black solid outline represents *H. erectus* while the red dashed outline represents the comparative group. The comparative groups are: *H. habilis* (a) and (e), mid-Pleistocene *Homo* (b) and (f), *H. neanderthalensis* (c) and (g) and early *H. sapiens* (d) and (h). The same configurations are shown in anterior view (above) and left lateral view (below).



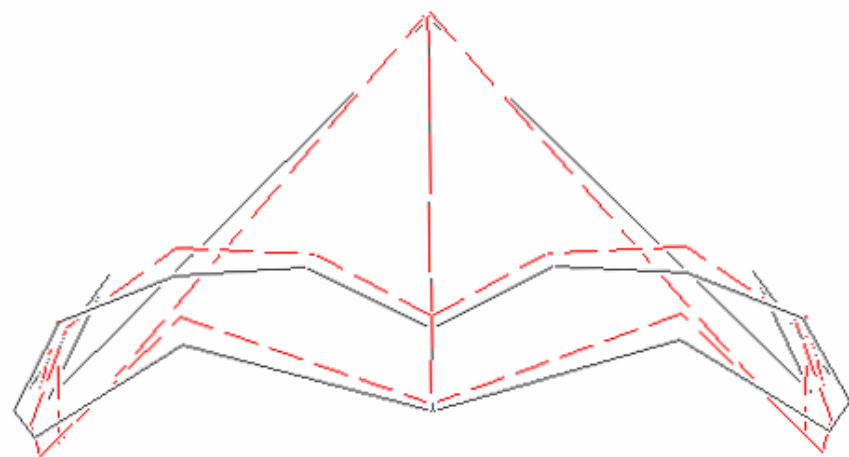
e)



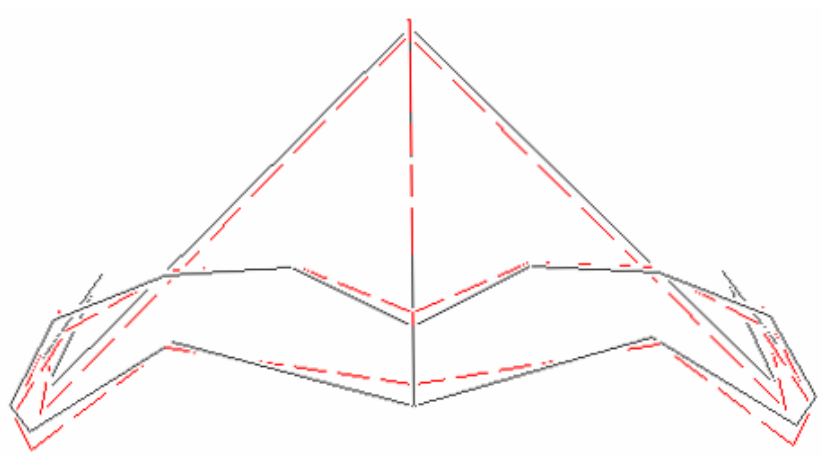
f)



g)



h)



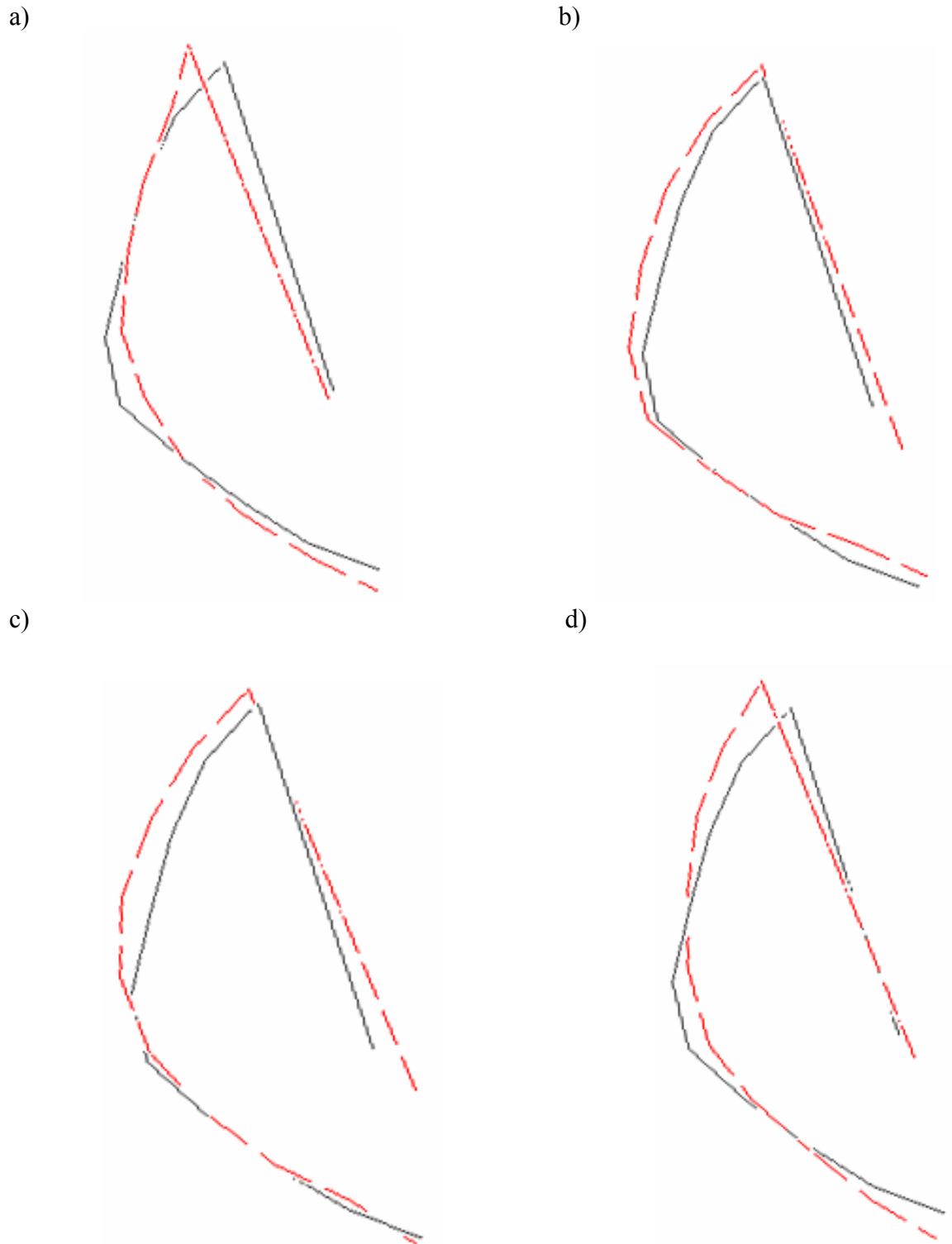
The final set of comparisons utilized the occipital landmark set (Figure 3.32). *H. erectus* was mainly distinguished from other taxa by a wide occipital bone at asterion. The more angled appearance of the mid-sagittal plane in *H. erectus* (compared to *H. habilis* and *H. sapiens*) was the result of the posteriorly projecting transverse occipital torus. The shape of the mid-Pleistocene *Homo* occipital bone was very similar to that of *H. erectus* but the former was slightly deeper antero-posteriorly (from asterion to opisthocranium). *H. neanderthalensis* differed in having a more superiorly positioned opisthocranium, possibly the result of the ‘bunning’ seen in Neanderthals. With the exception of *H. habilis*, the occipital plane of *H. erectus* was also less supero-posteriorly expanded. *H. habilis* and *H. sapiens* had a very similar occipital profile but *H. habilis* had a slightly wider occipital bone across asterion and a flatter occipital plane.

Although few consistently unique traits were identified by which *H. erectus* can be diagnosed, these comparisons can be used to formulate a “combination” definition for this species based on cranial shape (see “Discussion” section below).

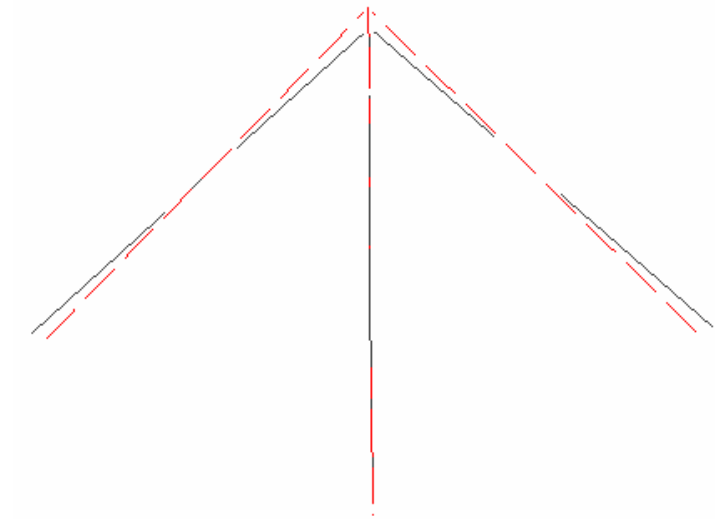
Homo erectus species composition

CDA and assignment to a taxonomic group: In addition to the PCAs, CDA was used to assign two specimens whose taxonomic status is unclear (ER 42700 and Ceprano) to *a priori* determined groups (taxa). CDA is a multi-group generalization of discriminant function analysis. The independent variables used to discriminate among groups in the CDAs were the scores on those PCs that accounted for 5% or more of the variance in the sample. The summary statistics for both analyses are provided in Table 3.7.

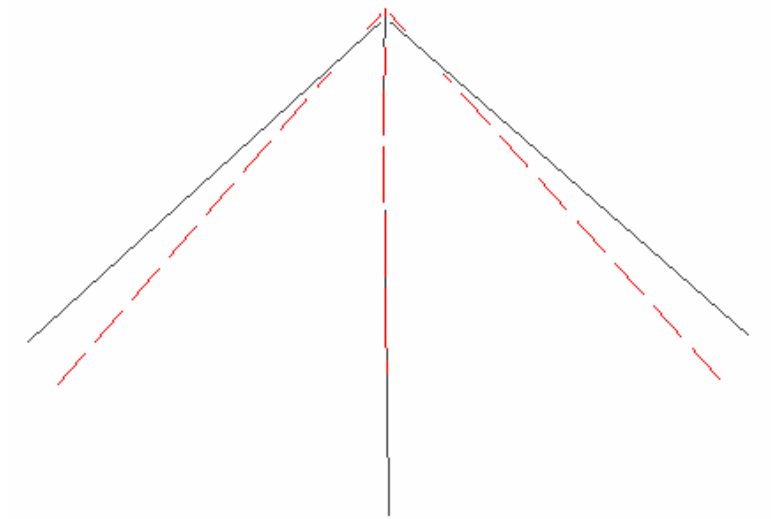
Figure 3.32: Comparison of mean occipital landmark set. The black outline is *Homo erectus*, which is compared to *H. habilis* (a) and (e), mid-Pleistocene *Homo* (b) and (f), *H. neanderthalensis* (c) and (g) and early *H. sapiens* (d) and (h). Both lateral and posterior views are shown below.



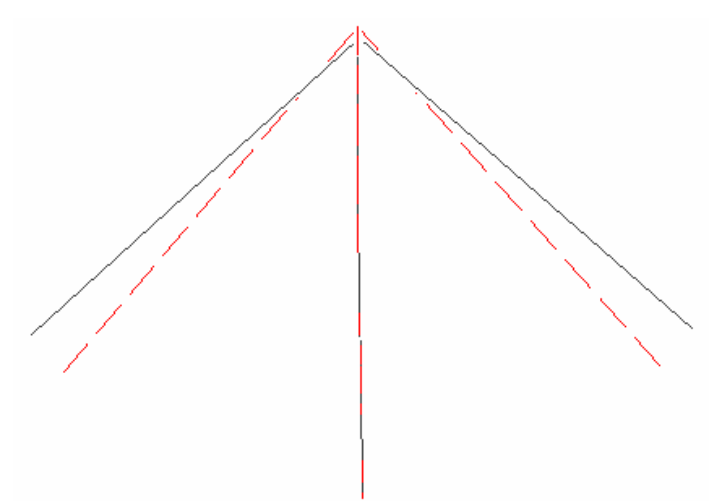
e)



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g)



h)

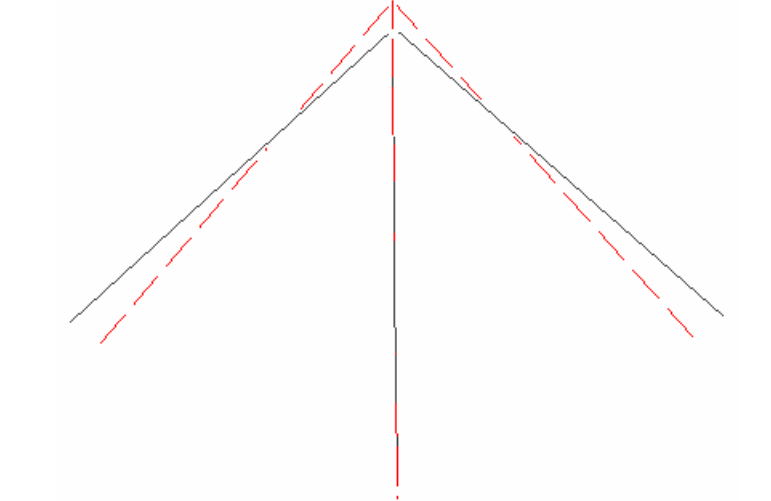


Table 3.7: ER 42700 canonical discriminant analysis. Summary statistics are provided from the canonical correlation, jackknife validation test, and *post hoc* classification of ER 42700 using the no-metopion landmark set.

Canonical correlation

Canonical Axis	% of total variance	Pr > F	<i>H. erectus</i> centroid	<i>H. he./H. n.</i> centroid	<i>H. sapiens</i> centroid	ER 42700 score
1	0.98	<0.0001	-6.20	-4.43	1.92	-1.95
2	0.02	0.0008	0.45	-1.71	0.03	0.31

Jackknife Validation

Specimen	Correct group	Group misclassified as
Skhul 5	<i>H. sapiens</i>	mid-Pleistocene <i>Homo</i> / <i>H. neanderthalensis</i>
Daka	<i>H. erectus</i>	mid-Pleistocene <i>Homo</i> / <i>H. neanderthalensis</i>

Posterior probabilities associated with classification of ER 42700

<i>H. erectus</i>	mid-Pleistocene <i>Homo</i> / <i>H. neanderthalensis</i>	<i>H. sapiens</i>
0.02	0.90	0.08

First, ER 42700 was examined using the hominin sample from the no-metopion landmark set, all-specimens analysis (Table 3.3). ER 1813 was excluded because it was the only representative of *H. habilis* in this sample and the jackknife validation procedure could not be performed with sample sizes of $n=1$. The first five PCs were utilized, which together accounted for 63% of the total variance. The jackknife procedure indicated that two of the 64 specimens were incorrectly classified: Daka and Skhul 5 were both classified as mid-Pleistocene *Homo* / Neanderthal (with posterior probabilities of 0.61 and 0.96, respectively). Therefore 97% of individuals were correctly classified.

Although ER 42700 was classified as an mid-Pleistocene *Homo* / *H. neanderthalensis* on the basis of overall cranial shape (Table 3.7), it is clear from the canonical plot in Figure 3.33 that ER 42700 did not really group any of the *a priori* groups and scored most like Skhul 5 (labeled in Figure 3.33) in this analysis.

The no-opisthion/no-mid-parietal landmark set was utilized to examine the affinities of Ceprano. Scores from the first six PCs were used, accounting for 67% of variance. A similar success rate was achieved as in the ER 42700 CDA; Skhul 5, Daka and Jebel Irhoud 1 were misclassified as mid-Pleistocene *Homo* / *H. neanderthalensis*. Ceprano was classified as an mid-Pleistocene *Homo* / *H. neanderthalensis* with a posterior probability of 1.0 (Table 3.8). The canonical plot (Figure 3.34) demonstrates that Ceprano fell close to the mid-Pleistocene *Homo* / *H. neanderthalensis* centroid on the first two canonical roots.

Figure 3.33: CDA of ER 42700. Both canonical axes were significant and ER 42700 (X) was classified into the mid-Pleistocene *Homo* / *H. neanderthalensis* group with a posterior probability of 0.9. However, it is clear that ER 42700 does not fall into any of the three *a priori* groups. The symbols correspond to those found in Figure 3.8, but because Skhul 5 was grouped with the recent humans for the CDA, it is labeled separately below.

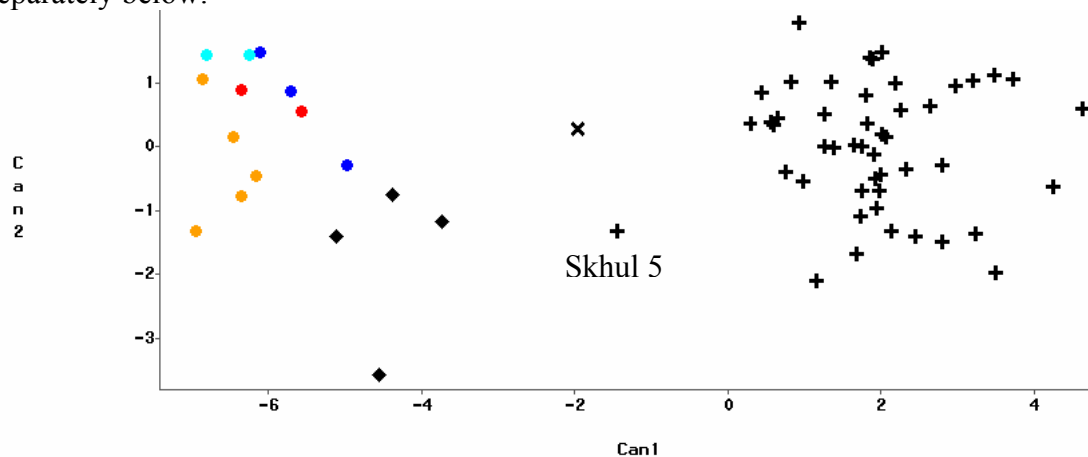


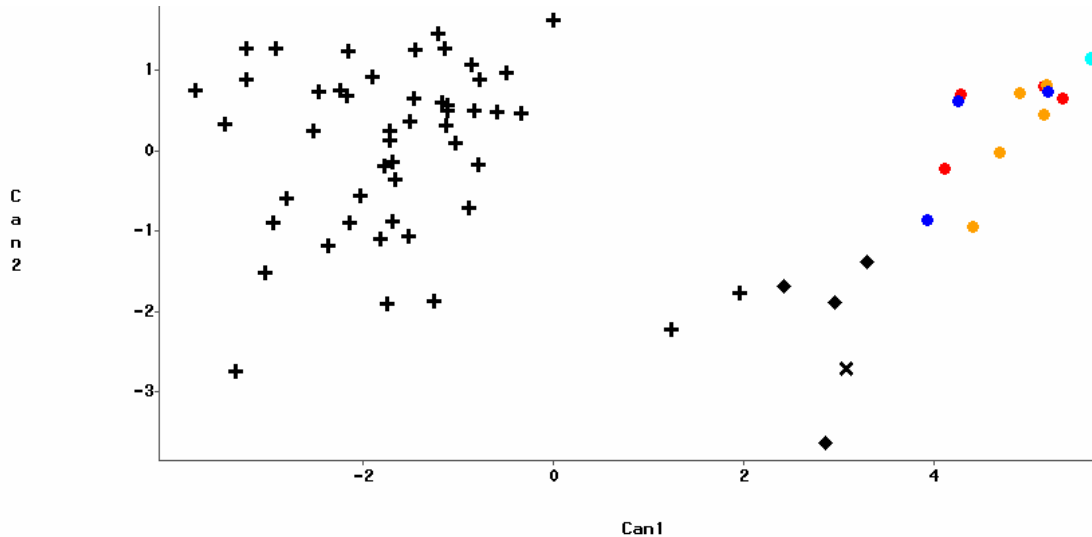
Table 3.8: Ceprano canonical discriminant analysis. Summary statistics are provided below from the canonical correlation, jackknife validation test, and *post hoc* classification of Ceprano using the no opisthion, midparietal landmark set.

<u>Canonical correlation</u>						
Canonical Axis	% of total variance	Pr > F	<i>H. erectus</i> centroid	<i>H. he./H. n.</i> centroid	<i>H. sapiens</i> centroid	Ceprano score
1	0.96	<0.0001	4.90	2.90	-1.63	3.09
2	0.04	0.0036	0.43	-2.15	0.05	-2.71

<u>Jackknife validation</u>		
Specimen	Correct group	Group misclassified as
Skhul 5	<i>H. sapiens</i>	mid-Pleistocene <i>Homo</i> / <i>H. neanderthalensis</i>
Daka	<i>H. erectus</i>	mid-Pleistocene <i>Homo</i> / <i>H. neanderthalensis</i>
Jebel Irhoud 1	<i>H. sapiens</i>	mid-Pleistocene <i>Homo</i> / <i>H. neanderthalensis</i>

<u>Posterior probabilities associated with classification of Ceprano</u>		
<i>H. erectus</i>	mid-Pleistocene <i>Homo</i> / <i>H. neanderthalensis</i>	<i>H. sapiens</i>
0.00	0.10	0.00

Figure 3.34: CDA of no-opisthion/no-mid-parietal landmark set. Both canonical axes were significant. Ceprano (X) was classified with the mid-Pleistocene *Homo* / *H. neanderthalensis* (diamonds) group with a posterior probability of 1.0. See legend in Figure 3.8.



Direct comparison of ER 42700 to other *Homo* species: The geological age of ER 42700 suggests that, of the species represented in this study, it was most likely a member of either early *Homo* or *H. erectus*. However, ER 42700 more closely resembled mid-Pleistocene *Homo* in terms of its cranial shape. Therefore, the no-metopion landmark set was used to compare ER 42700, the newly described subadult or young adult specimen from Ileret, to ER 1813 and the average *H. erectus* and mid-Pleistocene *Homo* landmark configurations (see Table 3.6 for samples).

In Figure 3.35 it is clear that some of the largest differences were the same regardless of which comparative taxon is used, particularly the great supero-posterior expansion at bregma, mid-parietal and lambda and the anterior position of the temporosphenoid suture seen in ER 42700. In addition, both inion and opisthion were positioned relatively higher in ER 42700. The expansion posteriorly resulted in a very wide occipital angle. As in *H. habilis*, the anterior cranial base of ER 42700 was more

inferiorly positioned and the supraorbital torus was more anteriorly projecting at glabella than at mid-orbit. Other aspects of shape were derived relative to *H. habilis* in a similar manner as later *Homo* species, including the elongated frontal squama, wide neurocranium, tall temporal squama, inferiorly positioned parietal notch and the infero-lateral angling of the supraorbital torus. The proportionally greater width of the posterior neurocranium relative to the temporal squama in ER 42700 specifically resembled *H. erectus*. The implications of these comparisons are incorporated into the Discussion.

Direct comparison of Ceprano to later *Homo* species: The Italian fossil calvarium from Ceprano was initially interpreted as the sole representative of *H. erectus* in Europe at ~700 – 800 ka (Ascenzi *et al.*, 1996, 2000; Clarke, 2000b). However, later comparative analyses highlighted the more modern configuration of the frontal bone anatomy, and this fossil may belong to a more derived species of *Homo* (Manzi *et al.*, 2001; Mallegni *et al.*, 2003). Ceprano differed consistently from *H. erectus*, mid-Pleistocene *Homo* and *H. neanderthalensis* in several characteristics of neurocranial shape (Figure 3.36): the smaller relative contribution of the parietal bone to the sagittal profile, the more lateral position of the temporal base structures relative to the vault walls, the more posterior position of inion and the more inferior location of the tympanomastoid junction. The position of the entoglenoid process forward of the postglenoid process resembled the Neanderthals but the entire TMJ was positioned more anteriorly. The great width of the posterior vault resembled *H. erectus* but the wide mid-vault at mid-temporal squama was more similar to that seen in mid-Pleistocene *Homo*, leading to a uniquely wide

Figure 3.35: Comparison of ER 42700 to other *Homo* taxa. ER 42700 (dashed red line) compared to *H. habilis* (a) and (d), *H. erectus* (b) and (e) and mid-Pleistocene *Homo* (c) and (f).

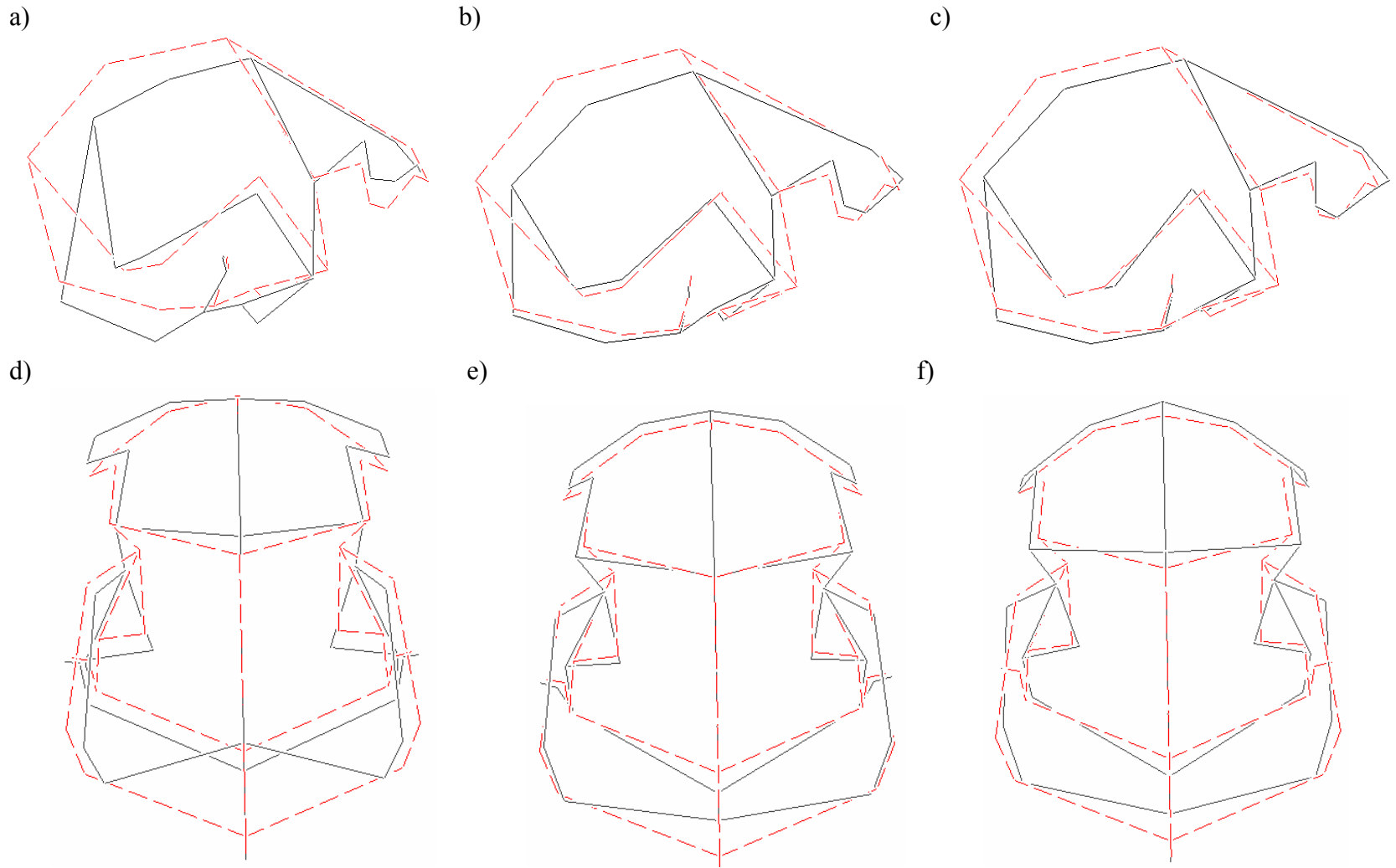
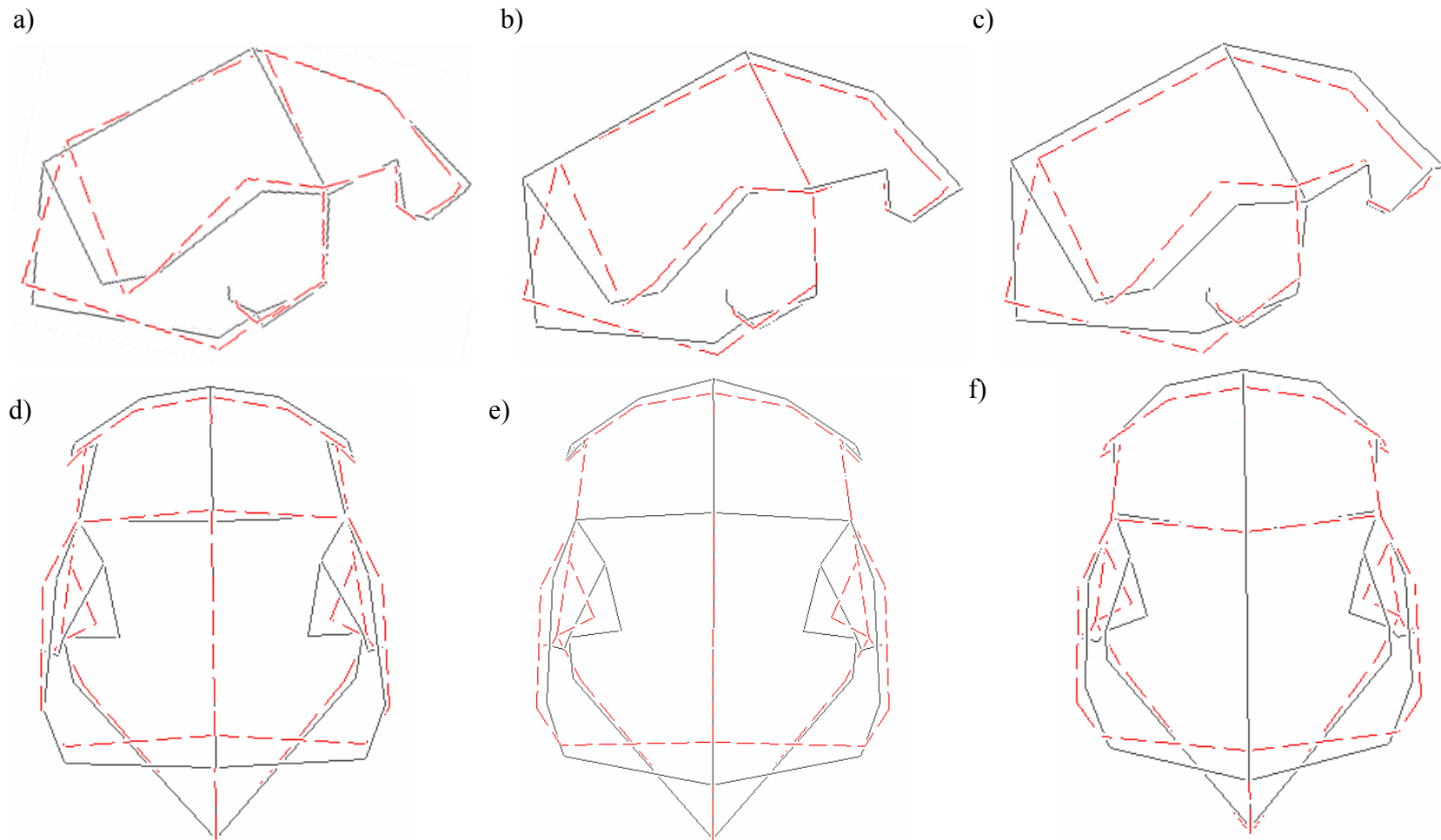


Figure 3.36: Comparison of Ceprano to other *Homo* taxa using the no-opisthion/no-mid-parietal landmark set. Ceprano (red dashed outline) was compared to the mean configurations of *H. erectus* (a) and (d), mid-Pleistocene *Homo* (b) and (e) and *H. neanderthalensis* (c) and (f). The same configurations are shown in left lateral view (above) and superior view (below).



neurocranium across both the mid- and anterior vault. The degree of constriction across frontotemporale was most like that of *H. heidelbergensis* but the supraorbital region was not quite as expanded, particularly in the midline (glabella and supraglabellar areas). The height at mid-temporal squama was also similar to *H. heidelbergensis* but the parietomastoid suture was more postero-inferiorly angled. The taxonomic affinities of the Ceprano cranium is discussed in the Discussion section below.

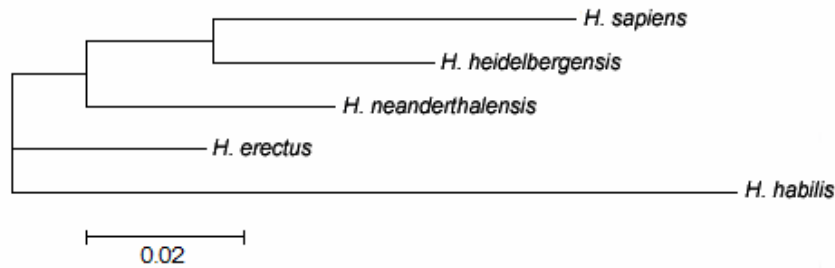
Phylogeny and cranial shape in Homo

Distance trees: Distance trees were generated from the standard; no opisthion, mid-parietal; and temporal base landmark sets using both the more and less speciose taxonomies, as described in “Methods.” When the less speciose taxonomy was applied, the trees failed to recover the *H. sapiens* – *H. neanderthalensis* sister group relationship, instead supporting a *H. heidelbergensis* – *H. sapiens* clade (Figure 3.37a and b). This was inconsistent with phylogenetic hypotheses which posit *H. heidelbergensis* as the last common ancestor of *H. neanderthalensis* and *H. sapiens*.

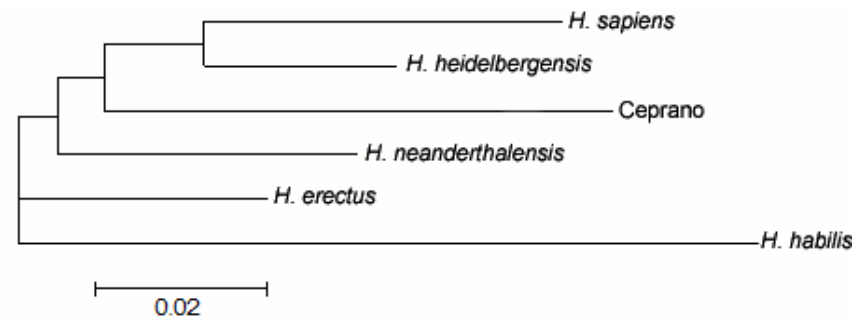
A weakness in the sample composition of *H. heidelbergensis* was the lack of any European representatives. As Petralona was missing only the tympanomastoid landmark, it was possible to estimate this landmark by using the average position for all fossil *Homo* (as described above). In order to test whether the inclusion of this specimen affects the outcome, Petralona was included in *H. heidelbergensis* and the trees were recreated using the no-opisthion/no-mid-parietal landmark set. The results were identical to the original

Figure 3.37: Distance trees of fossil *Homo* species using Procrustes distances using the less speciose taxonomy described in the text (Table 3.1). All tree building methods returned the same tree when the standard and no-opisthion/no-mid-parietal landmark sets were utilized [(a) and (b), respectively]. The weighted least squares tree differed from the others when the temporal base landmarks were used and both are shown below (c). Species means were used when more than one member of a species was available. The scale represents branch lengths.

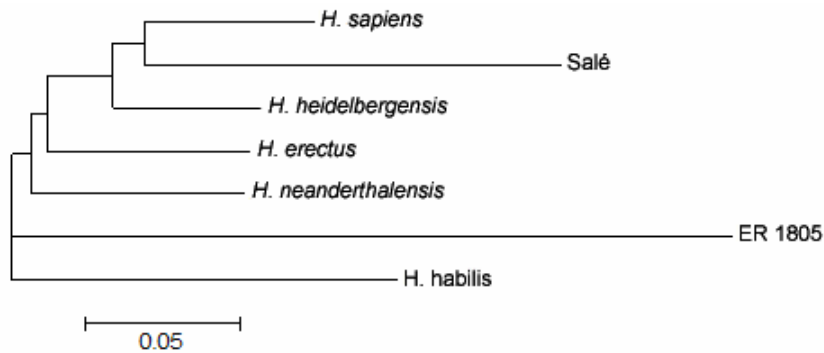
a)



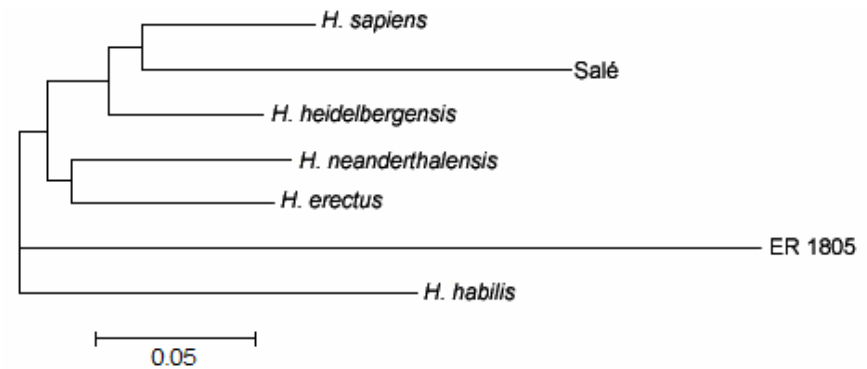
b)



c)



Weighted least square tree



results; the addition of a European *H. heidelbergensis* did not affect either the topology or the branch lengths of the distances trees generated by any of the tree building methods.

Greater success was achieved when the speciose taxonomy was applied (Figure 3.38a and b). Two of the landmark sets which captured overall cranial shape (the standard and the no opisthion, mid-parietal landmark sets) did recover trees consistent with the most speciose phylogeny proposed by Hublin (2001). While the trees generated by the WLS and ME methods for the no-opisthion/no-mid-parietal landmark sets were congruent with this phylogenetic hypothesis, the NJ and OLS trees were not.

In both cases the temporal base landmarks result in phylogenies which placed *H. neanderthalensis* as the sister group to *H. erectus* / *H. ergaster* and all other later species of *Homo* (Figures 3.37c and 3.38c). These analyses also highlighted the uniqueness of the *H. habilis* cranial shape and the distinctiveness of the ER 1805 temporal base shape.

Implications of different phylogenies for cranial evolution in *Homo*: Using two different hypotheses about the phylogeny of Plio-Pleistocene *Homo*, it was possible to track changes in cranial shape over speciation events and along particular lineages (e.g., the lineage which culminated in modern humans). The two trees were described above (the less speciose and more speciose trees, Rightmire, 1998b and Hublin, 2001, respectively) and illustrated in Figures 3.39 and 3.40. Comparisons were made between average configurations, when available, or individual specimens which were representative of each species (as described in Tables 3.1 and 3.4) using the no-opisthion/no-mid-parietal landmark set in order to include Ceprano (the sole representative of *H. mauritanicus* in the more speciose phylogeny). The individuals included in each species mean are listed

in Table 3.9 for each tree. Procrustes distances between each pair of mean species configurations were also presented at each node (see Figures 3.39 and 3.40), but these should be regarded cautiously as distances were generally greater in comparisons involving single specimens (e.g., ER 1813 and Ceprano) rather than averages of multiple individuals. Both ER 1813 with the lambda as originally recorded and as estimated by other early *Homo* fossils (details provided above) are shown.

Rather than list every aspect of shape change which occurred at each node, only the biggest changes will be noted here. Some of the most significant shifts in cranial shape occurred early on both trees. *H. erectus* s.s. and *H. ergaster* shared a very similar cranial shape with only very minor differences apparent between the two: *H. erectus* s.s. had a wider frontal bone and mid-vault, less inferiorly projecting entoglenoid process and more inferiorly positioned temporal squama and parietal notch than *H. ergaster*. As a result, the *H. habilis* – *H. ergaster* and *H. habilis* – *H. erectus* s.l. transitions on the two trees were very similar: there was a posterior expansion of the cranium, a lengthening of

Figure 3.38: Distance trees based on true Procrustes distances using the more speciose taxonomy described in the text (Table 3.4). Tree building methods generated identical trees for both the standard landmark set (a) and the temporal base landmark set (c). The neighbor joining and ordinary least squares trees differed from the weighted least squares and minimum evolution trees in the no-opisthion/no-mid-parietal landmark analysis [shown side by side in (b) below]. When more than one individual was available for a particular species then the group mean was utilized. The scale refers to branch lengths.

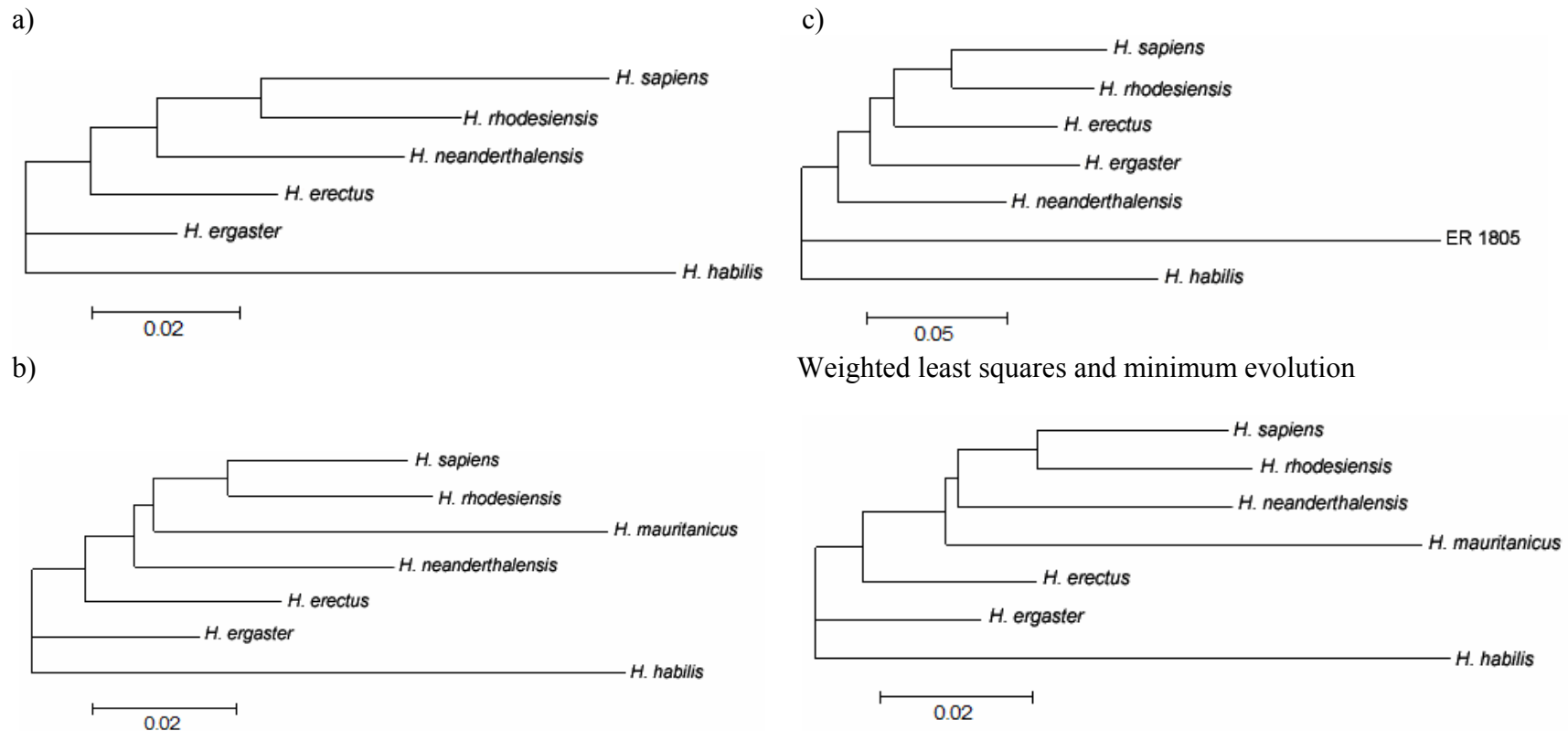


Table 3.9: Samples for species means compared at each node of the more and less speciose phylogenetic trees shown in Figures 3.39 and 3.40.

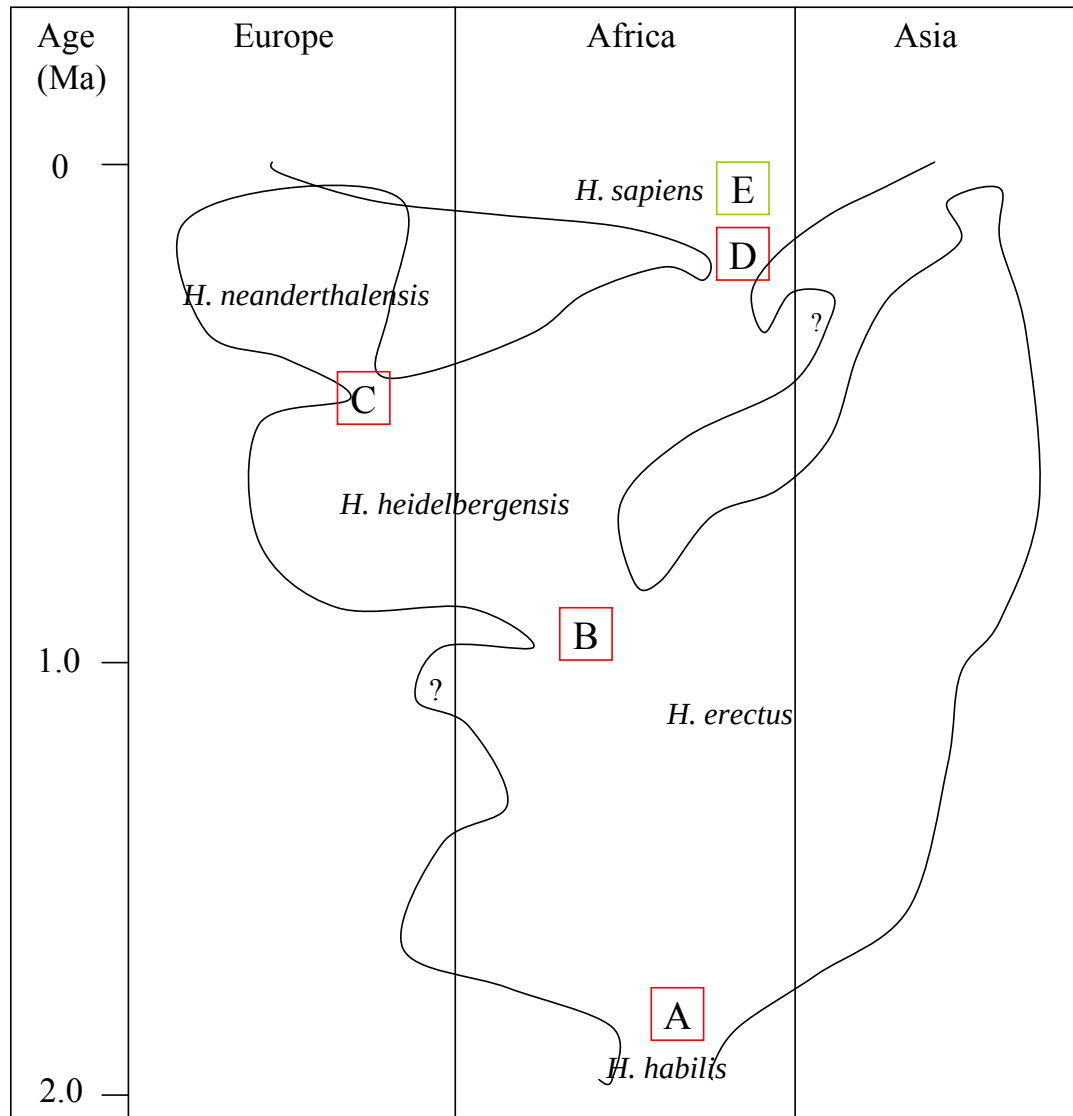
Analysis	Sample
Less speciose tree	<u><i>H. erectus</i></u> : ER 3733, 3883, D 2280, 3444, OH 9*, Daka, S 2*, 17, Sm 1*, 3, Ng 6, 10*, 11, 12, Ngawi*, Zkd 3, 5, 11, 12 <u><i>H. habilis</i></u> : ER 1813 <u><i>H. neanderthalensis</i></u> : La Ferassie, La Chapelle, Saccopastrore 1* <u><i>H. heidelbergensis</i></u> : Kabwe, Dali, LH 18*, Ndutu*, Omo 2*, Petralona*, Ceprano <u>Early <i>H. sapiens</i></u> : Skhul 5, Jebel Irhoud 1, 2*, Jebel Qafzeh 6*, 9* <u>Recent <i>H. sapiens</i></u> : 47 individuals
More speciose tree	<u><i>H. ergaster</i></u> : ER 3733, 3883, D 2280, 3444 <u><i>H. erectus</i></u> : OH 9*, Daka, S 2*, 17, Sm 1*, 3, Ng 6, 10*, 11, 12, Ngawi*, Zkd 3, 5, 11, 12 <u><i>H. habilis</i></u> : ER 1813 <u><i>H. mauritanicus</i></u> : Ceprano <u><i>H. neanderthalensis</i></u> : La Ferrassie, La Chapelle, Saccopastore 1*, Petralona* <u><i>H. rhodesiensis</i></u> : Kabwe, LH 18*, Ndutu*, Omo 2*, Dali <u>Early <i>H. sapiens</i></u> : Skhul 5, Jebel Irhoud 1, 2*, Jebel Qafzeh 6*, 9* <u>Recent <i>H. sapiens</i></u> : 47 individuals

* - Indicates specimens included in the average configuration that were missing five or fewer unique landmarks (counting each bilateral landmark only once).

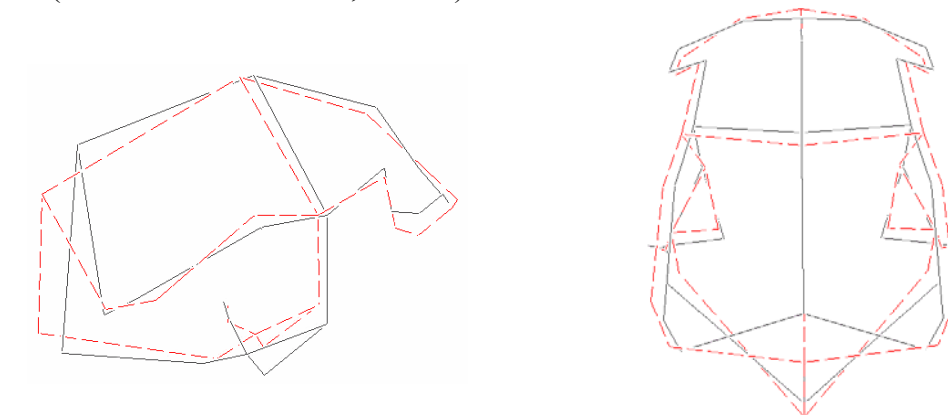
the frontal squama, a superior shift of the anterior cranial base and widening of the vault. The postglenoid process shifted anteriorly, the parietomastoid suture increased in length and there was an increase in the vertical height between the mid-temporal squama and the parietal notch. The supraorbital torus of *H. erectus s.l.* / *H. ergaster* was more expanded and straighter in anterior view whereas the supraorbital notches were more superiorly positioned than glabella in ER 1813.

This change in the height of the temporal squama was continued over the *H. erectus* – *H. heidelbergensis* transition (on the less speciose tree), along with a slight

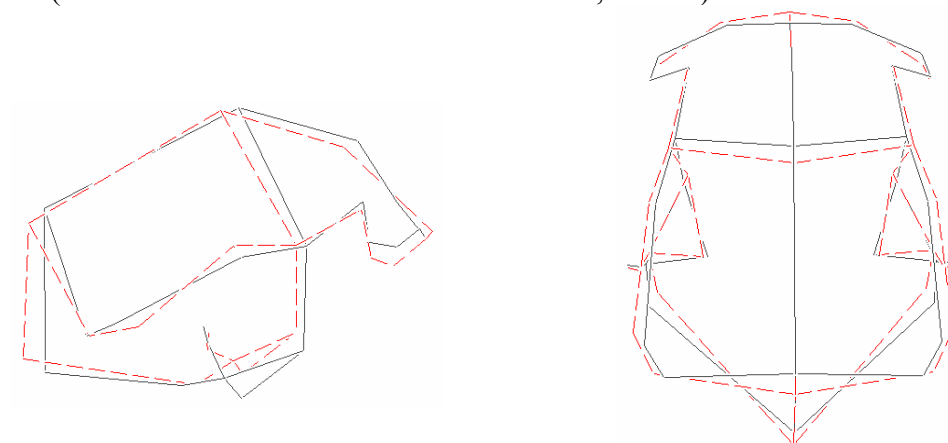
Figure 3.39: Cranial shape change at speciation events on less speciose phylogeny (shown with the no-opisthion/no-mid-parietal landmark set). The letters on the tree in red boxes correspond to speciation events illustrated below in lateral and superior views of the crania. In each case the black solid line represents the ancestor and the red dashed line is the descendant species. The *H. habilis* to *H. erectus* transition is also shown using both the original and the alternative lambda that was estimated for ER 1813 as described in the text. The transition E in the green box does not represent a speciation event but rather shows the changes from early to recent *H. sapiens*. Procrustes distances between the average configurations are provided in parentheses next to each comparison.



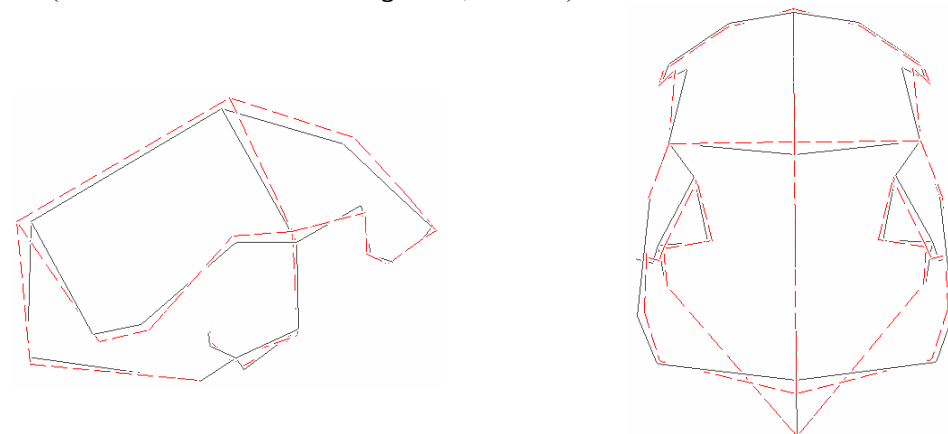
A (*H. habilis* – *H. erectus*, 0.1147)



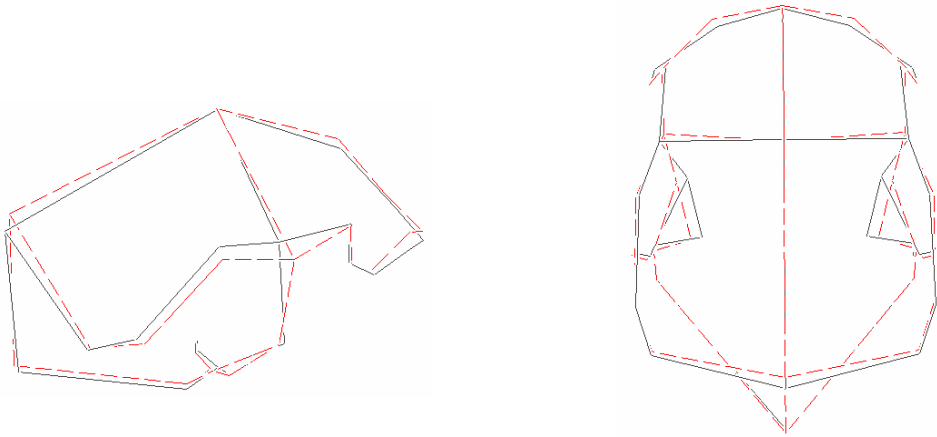
A (*H. habilis* alternative lambda – *H. erectus*, 0.0991)



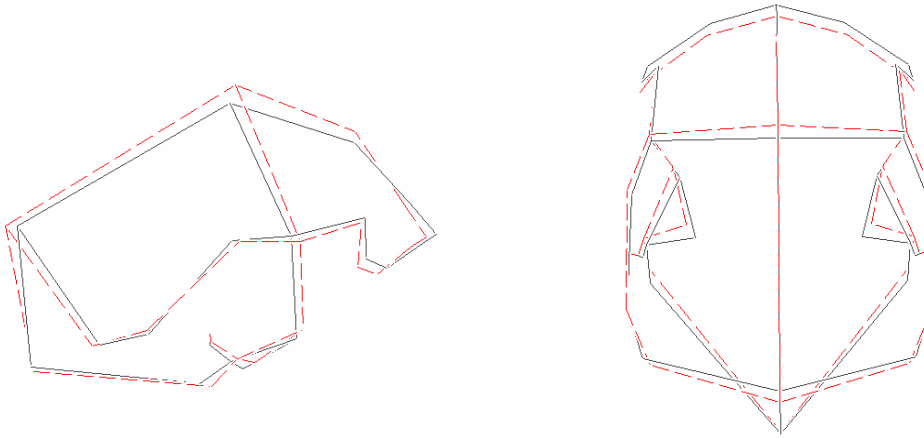
B (*H. erectus* – *H. heidelbergensis*, 0.0508)



C (*H. heidelbergensis* – *H. neanderthalensis*, 0.0630)



D (*H. heidelbergensis* – early *H. sapiens*, 0.0595)



E (early *H. sapiens* – late *H. sapiens*, 0.0589)

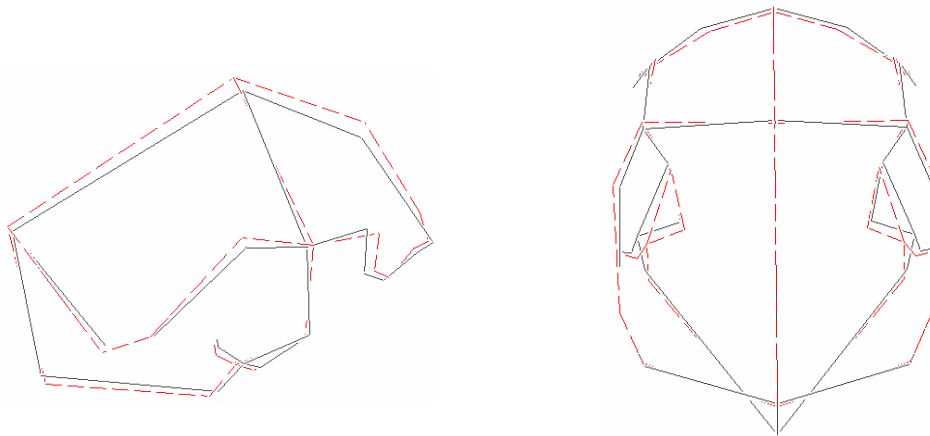
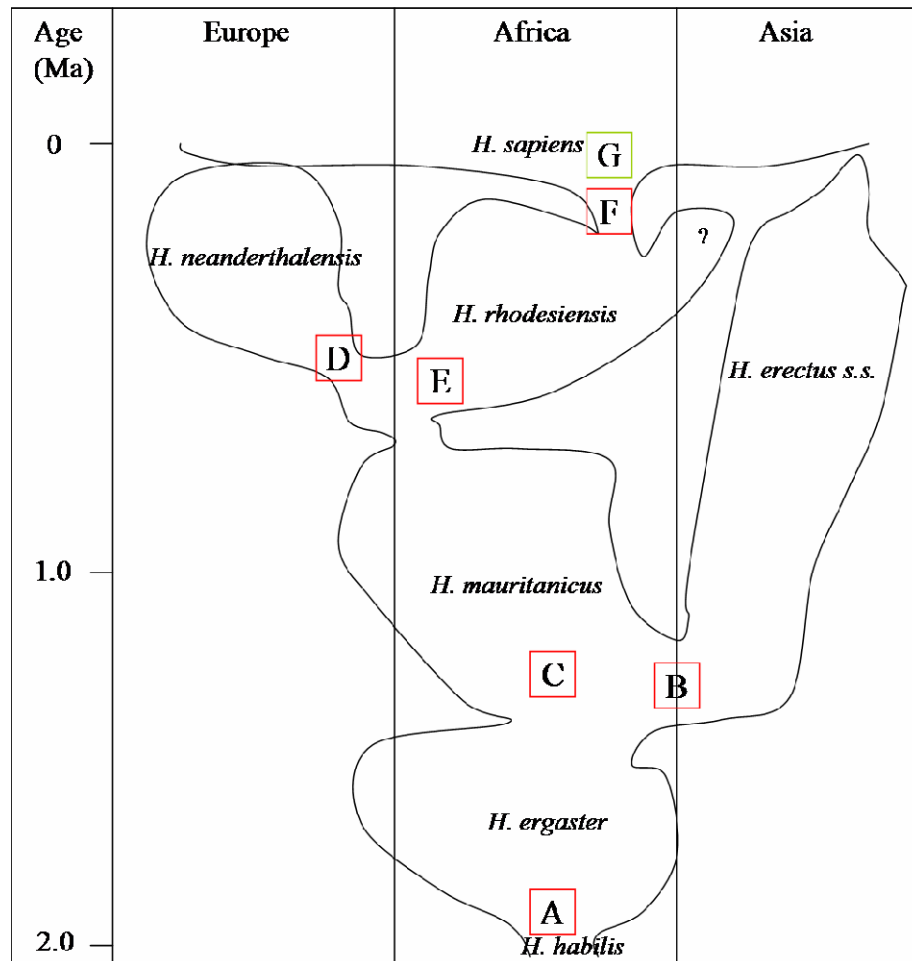
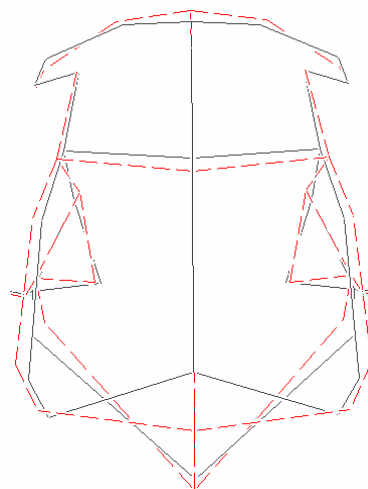
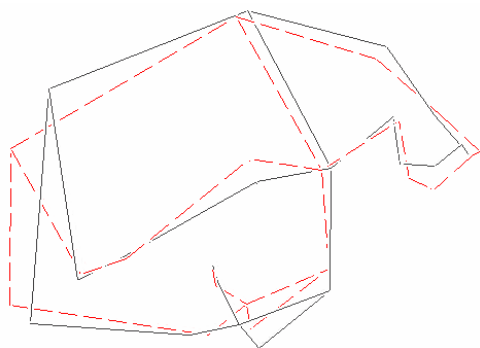


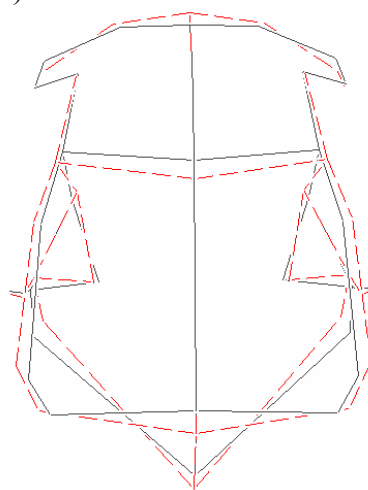
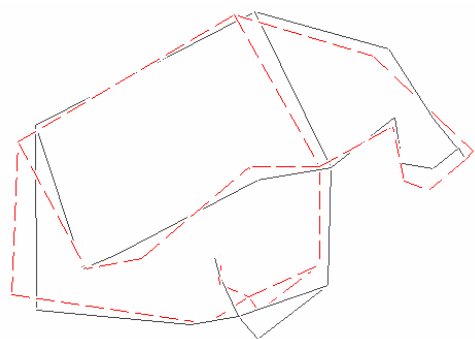
Figure 3.40: Cranial shape change at speciation events on the more speciose phylogeny (shown with the no-opisthion/no-mid-parietal landmark set). The letters in red boxes on the tree correspond to speciation events illustrated in the lateral and superior views of the crania. In each case the black solid line represents the ancestor and the red dashed line is the descendant species. The *H. habilis* to *H. ergaster* transition is also shown using the alternative lambda estimated for ER 1813 as described in the text. The transition G in the green box does not represent a speciation event but rather shows the changes from early to recent *H. sapiens*. Procrustes distances between the average configurations are provided in parentheses next to each comparison.



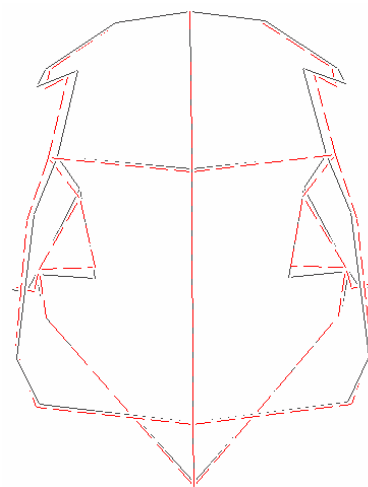
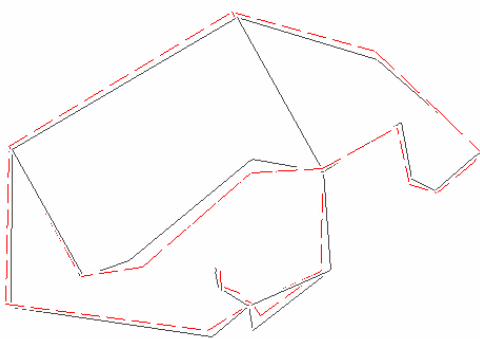
A (*H. habilis* – *H. ergaster*, 0.1033)



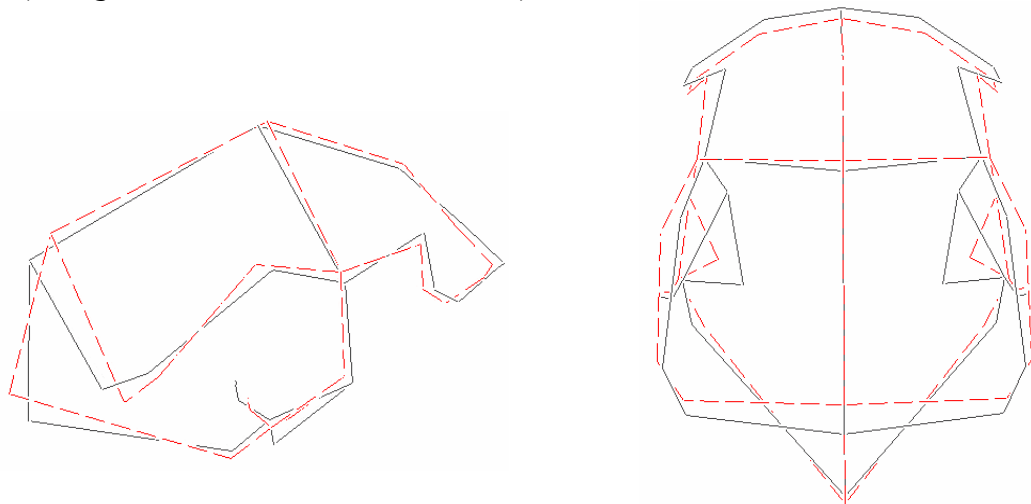
A (*H. habilis* alternative lambda – *H. ergaster*, 0.0846)



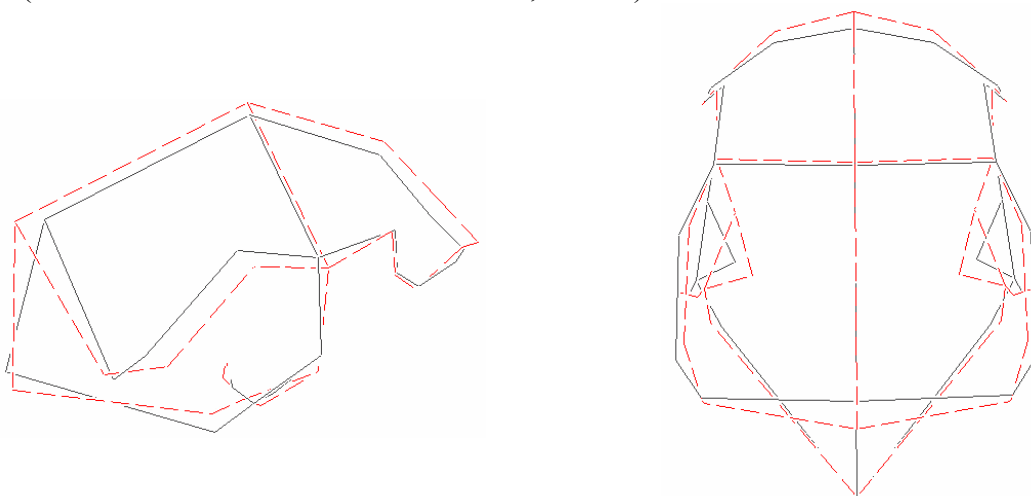
B (*H. ergaster* – *H. erectus*, 0.0455)



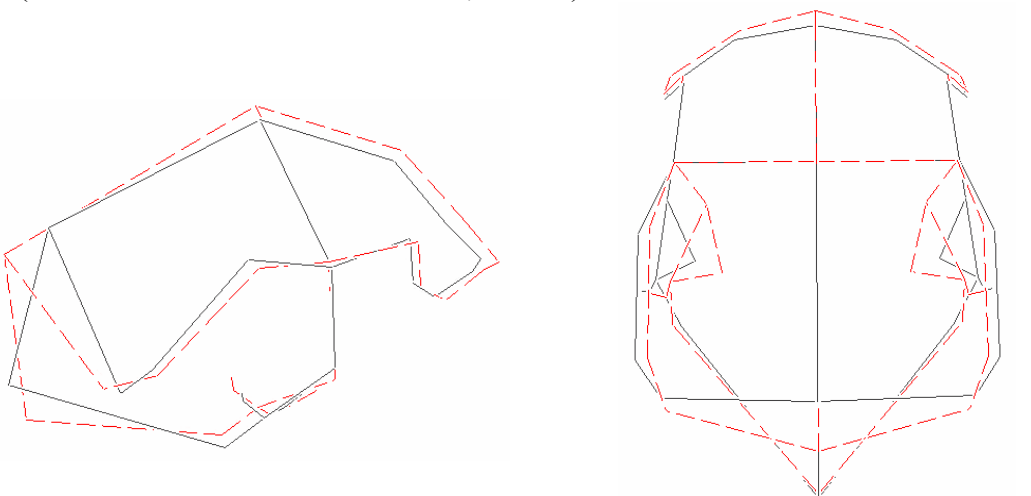
C (*H. ergaster* – *H. mauritanicus*, 0.1075)



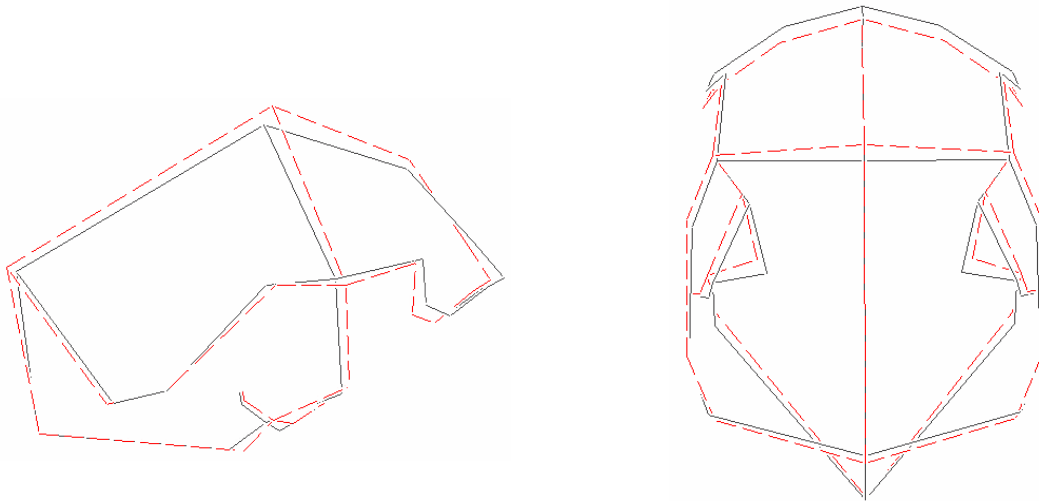
D (*H. mauritanicus* – *H. neanderthalensis*, 0.0953)



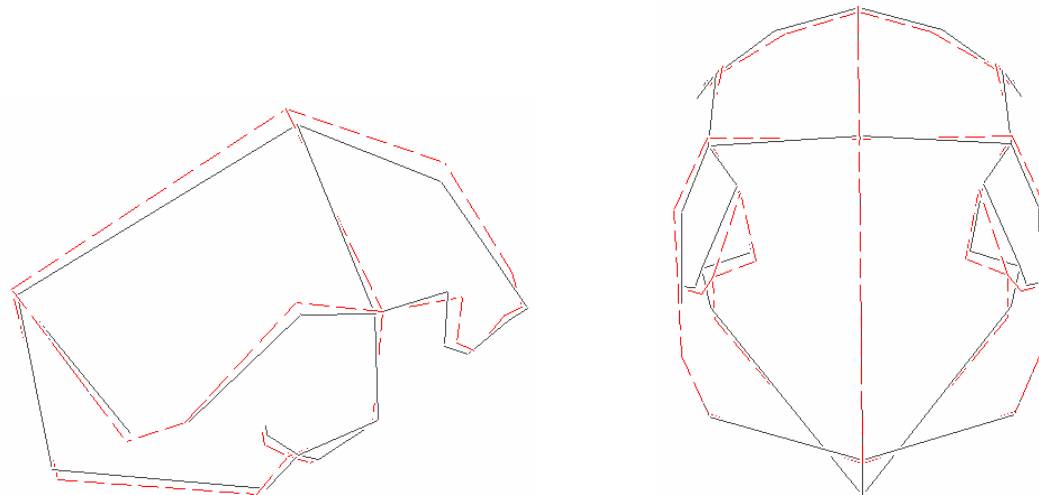
E (*H. mauritanicus* – *H. rhodesiensis*, 0.1095)



F (*H. rhodesiensis* – early *H. sapiens*, 0.0623)



G (early *H. sapiens* – late *H. sapiens*, 0.0589)



increase in vault height along the mid-sagittal plane superiorly. The constriction across frontotemporale decreased in *H. heidelbergensis* and the posterior cranium narrowed slightly from *H. erectus* to *H. heidelbergensis*.

H. sapiens was characterized mainly by a lengthening of the parietal bones in the sagittal plane, an increase in the steepness and height of the frontal squama, and a decrease in the supraorbital torus projection. There was relatively greater width across the mid-temporal squamae and the postglenoid and entoglenoid processes and the temporosphenoid suture also shifted anteriorly and slightly laterally in early *H. sapiens*.

Recent humans had even higher vaults at bregma with further expansion at metopion compared to early modern humans and the temporal squama increased in height. The entoglenoid and postglenoid processes were more posteriorly positioned and the postglenoid process was more medially located in recent *H. sapiens*.

Compared to *H. heidelbergensis*, the Neanderthals showed a decrease in the relative height of the temporal squama, an increase in the relative projection of the supraorbital torus over the orbits and a longer coronal suture. In terms of the temporal base, the entoglenoid process and temporosphenoid suture were more laterally located and the postglenoid process was more posteriorly positioned. As in ER 1813, glabella was more inferiorly positioned relative to the supraorbital notches in the *H. neanderthalensis*.

The most apparent changes along the more speciose tree not seen on the less speciose tree involved *H. mauritanicus* (i.e., Ceprano). This specimen was unique in several aspects of its anatomy and the speciations involving *H. mauritanicus* were generally associated with very high Procrustes distances. In particular, the parietal bone contributed relatively less to the sagittal profile and there was less projection of the supraorbital torus. In addition, Ceprano was wide across the posterior cranium and the temporal squamae (which is in a more superior position) with a very laterally positioned tmj relative to both potential ancestors and descendants.

Contribution of Homo erectus to modern human ancestry

PCA of Australians-only and Australasian landmark sets, all-specimens: These PCAs addressed whether Wadjak 1, KS 17 and WLH-50 were more similar to late Indonesian fossil *Homo*, early modern humans from African and the Middle East or to modern humans from elsewhere in the world. Two analyses were run, one which included more landmarks but excluded Wajak 1, and a second which included Wajak 1 but dropped several landmarks. Details about the samples and landmarks were discussed in “Methods” and summarized in Table 3.10.

The positions of the taxa along PC 1 were similar in both analyses: modern humans were significantly different from all other taxa but not from Wajak 1, KS 17 and WLH-50 (which were treated as their own group for the MANOVA) as summarized in Table 3.11. Although KS 17 fell toward the center of the recent human distribution, both Wadjak 1 and WLH-50 were on the edge of the recent human sample but also overlapped early *H. sapiens* as seen in Figures 3.41a and 3.42a. The shape differences along PC 1 were related to the greater globularity of the sagittal profile, narrower posterior cranium and reduction of the supraorbital torus in recent human (Figure 3.41b and 3.42b). The Indonesian hominins all scored low on PC 4 in the Australasian landmark set (Figure 42a) but the three humans from Indonesia and Australia did not group with them on this component. While they also scored low in the Australians only analysis (Figure 3.41a), they overlapped several other specimens on this component, including D 3444, Jebel Qafzeh 6 and several recent humans in addition to KS 17 and Wadjak 1. The shape differences on PC 4, visualized in Figures 3.41c and 3.42c, included greater expansion

Table 3.10: Composition of landmark sets and samples used to test the multiregional model of modern human origins in Southeast Asia / Australia.

Analysis	Landmarks ¹	# Landmarks	Sample ²	# Specimens
Australians-only set, all-specimens	IN, OPC, LA, MP, BR, ME, PTS, GL, FMO, MTI, MTS, FT, AS	18	<u>H. erectus</u> : ER 3733, 3883, Daka, D 2280, 3444, S 17, Sm 3, Ng 6, 10, 11, 12, Ngawi 1, Zkd 3, 5, 11 and 12 <u>Early Homo</u> : ER 1813 and 1470 <u>H. neanderthalensis</u> : La Chapelle and La Ferrassie <u>mid-Pleistocene Homo</u> : Petralona and Dali <u>Early H. sapiens</u> : Jebel Irhoud 1, Skhul 5 and Jebel Qafzeh 6 <u>Early Australians</u> : Kow Swamp 17 and WLH-50. <u>Recent H. sapiens</u> : 47	74
Australians-only set, CDA sample	Same as above	18	Same as above - <i>H. erectus</i> except from Ngandong, <i>H. heidelbergensis</i> , <i>H. neanderthalensis</i>	56
Australasian set, all-specimens	Same as above - GL, ME, AS	14	Same as Australians only set, all-specimens + <u>H. erectus</u> : Sm 1 <u>Unknown</u> : ER 42700 <u>Early Indonesian</u> : Wadjak 1	77
Australasian set, CDA sample	Same as above	14	Same as above - <i>H. erectus</i> except from Ngandong, <i>H. heidelbergensis</i> , <i>H. neanderthalensis</i>	57

1, A minus sign (-) indicates that this landmark was excluded

2, A plus sign (+) indicates that this specimen added and a minus sign (-) indicates that this specimen was excluded.

Table 3.11: PCA results for Australian and Australasian analyses. MANOVA was used to test for significant group differences on the first four principal components and significant group differences were then determined for each component using a Bonferroni correction. In regards to the pairwise contrast, for the Australians only and the Australasians analysis the early modern human sample from Australasia is in **bold**, while LB1 (*H. floresiensis*) is in **bold** in the Liang Bua analyses.

Analysis	% of Variance on	Regression on size R ² value ($\alpha < 0.05$)				MANOVA Wilks' Lambda	Pairwise Group differences (Bonferroni correction at $\alpha < 0.05$) ¹			
	PC1–PC4	1	2	3	4	P value	1	2	3	4
Australians only, all specimens	0.75	-	-	.10	.08	< 0.0001	Au ¹ - H.e., H.he. & E.H. H.s.- H.e., E.H. H.he. & H.n.	-	-	-
Australasians, all specimens	0.78	-	-	-	.15	< 0.0001	EAs/Au ¹ - H.e., H.he. & E.H. H.s.- H.e., E.H., H.he. & H.n. H.e.- ER 42700	-	-	E.H.- H.e. & H.s.
Liang Bua set, all specimens	0.66	-	.15	-	-	< 0.0001	H.s. – H.e., H.he., H.n., H.h. & H.f. ER 42700- H.f. , H.e. & H.h. ²	H.h.- H.e., H.s., H.he., H.n. & ER 42700 H.s.- H.e.	-	-
Liang Bua set, in size-shape space	0.78	.97	-	-	-	< 0.0001	H.f. - H.e., H.he., H.n. & H.s. H.e.- H.s., H.h. & ER 42700 H.he.- H.s., H.h., ER 42700 H.n.- H.h, H.s. & ER 42700 H.s.- ER 42700 ³	H.f. - all but H.h. H.s.- all H.h.- all but H.f. H.e.- H.he.	-	-

1, Au is the group of early modern humans from Australia (Kow Swamp 17 and WLH-50) and EAs/Au also includes the southeast Asian specimen Wadjak 1.

2, H.f. = *H. floresiensis* (Liang Bua 1); In the Liang Bua analysis the results are reported with ER 42700 treated as its own group for significance testing. When ER 42700 is grouped with H.e., then H.s. still differs from all other groups on PC 1 as do H.he. and H.h. On PC 2 H.h. differs significantly from H.s., H.e. and H.he., and H.s. differs from H.e.

3, The results are reported here for ER 42700 as its own group. When ER 42700 is classified as *H. erectus*, the H.n.-H.s. contrast on PC 1 is no longer significant.

of the supraorbital torus, a more anteriorly positioned inion and slightly less expansion at mid-parietal.

CDA of Australians-only and Australasian landmark sets, all-specimens: The results were very similar for both the Australians only and Australasian CDAs, as can be seen in the canonical plots in Figure 3.41d and 3.42d. Therefore, only the results of the Australasian CDA are discussed further. Scores from the first six PCs (accounting for 85% of the total variance) were used as independent variables in the CDA. The first two canonical roots were significant in each analysis, and the first component separated the early *H. sapiens*, recent *H. sapiens* and Ngandong groups (Figure 3.42d). WLH-50 was classified as an early *H. sapiens* (posterior probability, 1.0) while KS 17 was classified as a recent *H. sapiens* (posterior probability, 0.98). Wadjak 1 was classified as an early *H. sapiens* (posterior probability, 0.65). It was clear that the greatest separation occurred between the Ngandong fossils and early / recent *H. sapiens* along the first canonical root in both analyses. The cross-validation procedure correctly classified all members except one into their original groups (a single *H. sapiens* specimen was classified as an early *H. sapiens*) (Table 3.12).

Figure 3.41: PCA and CDA results from Australians only landmark set. a) PC 1 versus PC 4 is shown below. The upside down purple triangles are Kow Swamp 17 and WLH-50. These two specimens as a group differed significantly from mid-Pleistocene *Homo*, *H. erectus* and early *Homo* on PC 1. Shape differences along PCs 1 (b) and 4 (c) were illustrated in lateral view. d) In the CDA, Kow Swamp 17 grouped with the recent humans at the negative end of the first canonical axis whereas WLH-50 grouped with the early modern humans. Both canonical axes were significant. See legend in Figure 3.8.

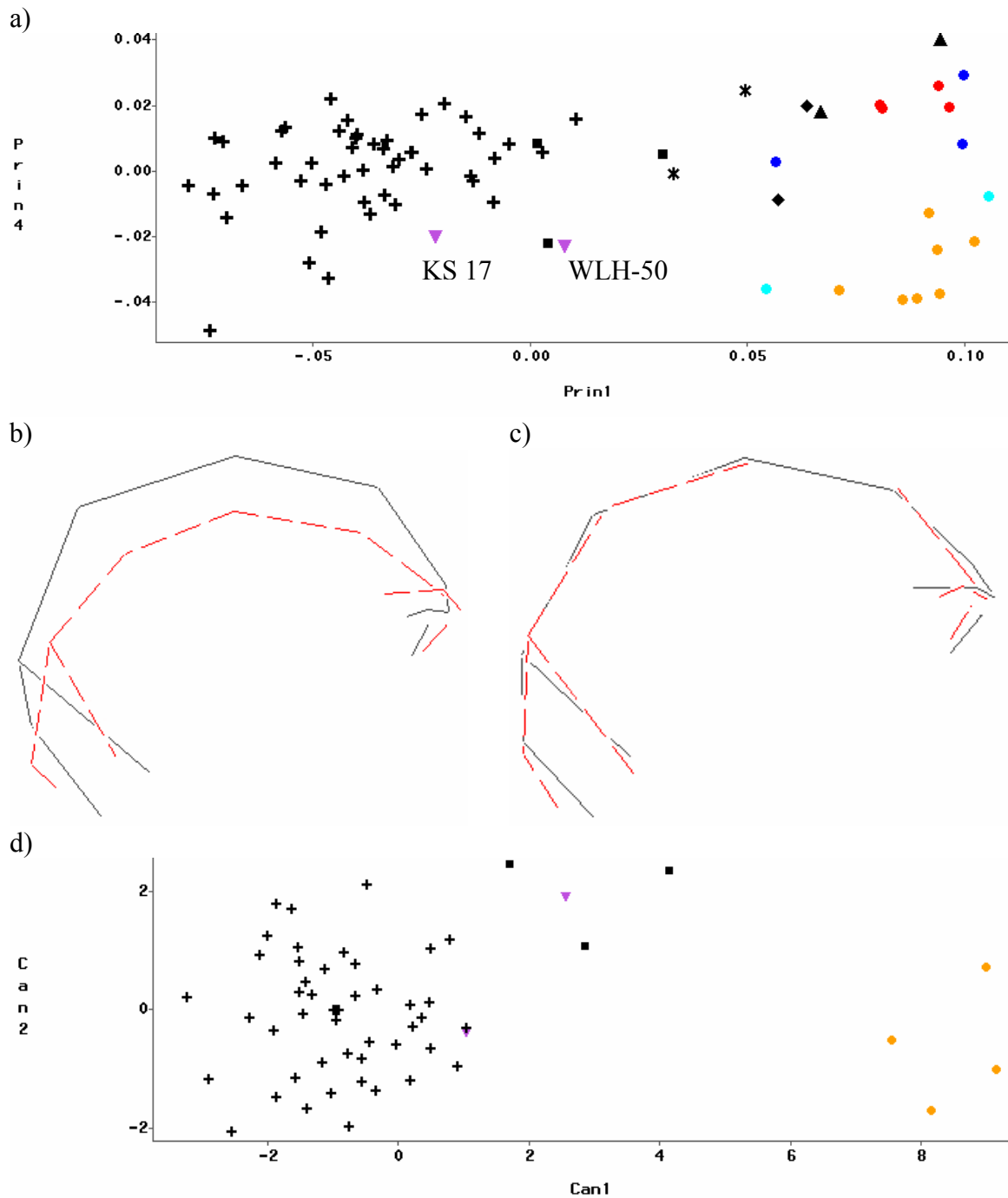


Table 3.12: Australasian canonical discriminant analysis. Summary statistics are provided below from the canonical correlation, jackknife validation test, and *post hoc* classification of KS 17, WLH-50 and Wajak 1 using the Australasian landmark set.

Canonical correlation

Can. Axis	% total variance	Pr > F	Centroid			Score		
			Ngandong	Early <i>H. sapiens</i>	Recent <i>H. sapiens</i>	KS 17	WLH-50	Wajak 1
1	0.96	<0.0001	-8.57	-2.86	0.91	-0.28	-2.04	1.94
2	0.04	0.0448	-0.59	0.91	-0.08	0.26	-0.78	1.61

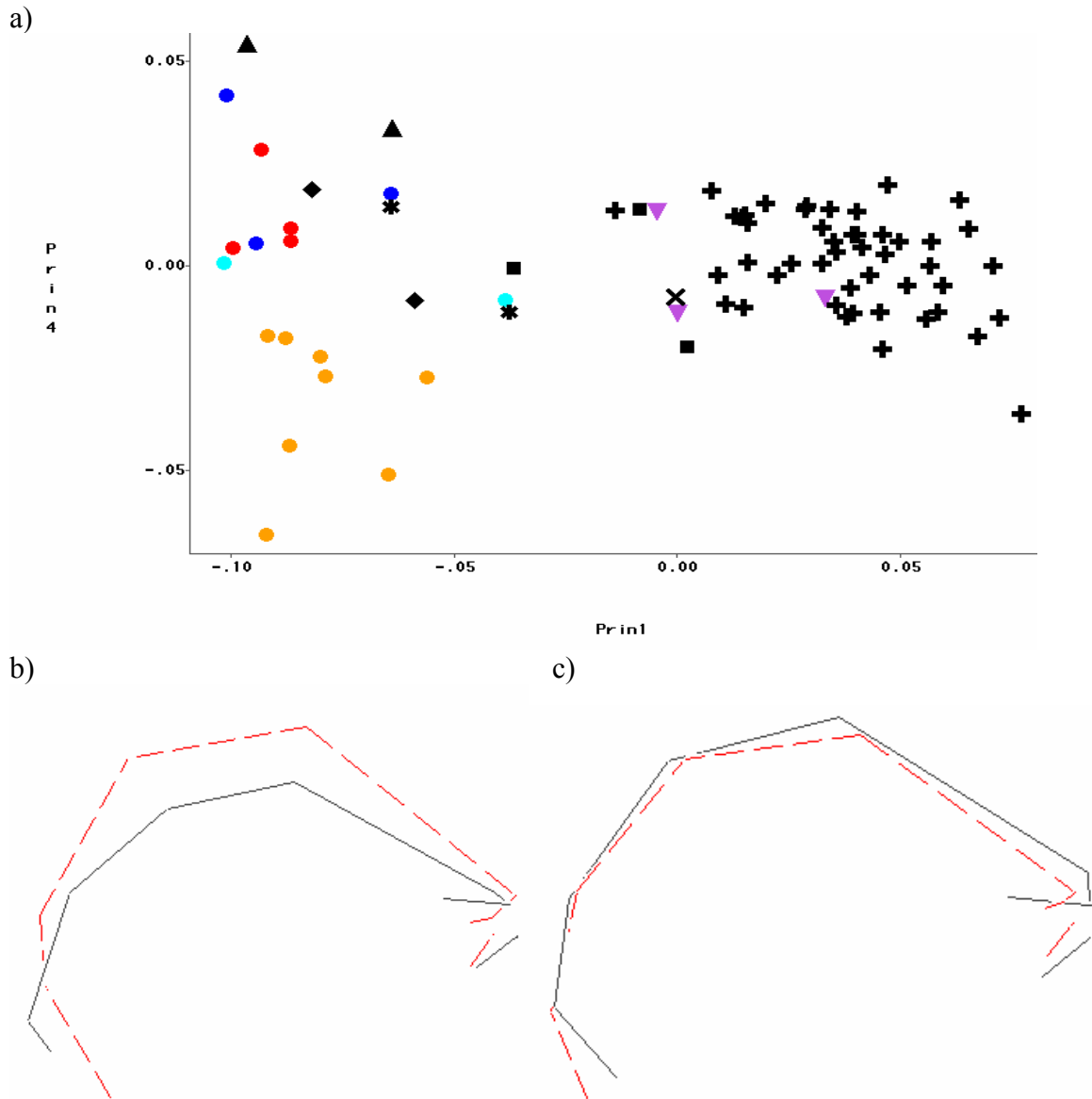
Cross validation

Specimen	Correct group	Group misclassified as
Teita 13	Recent <i>H. sapiens</i>	Early <i>H. sapiens</i>

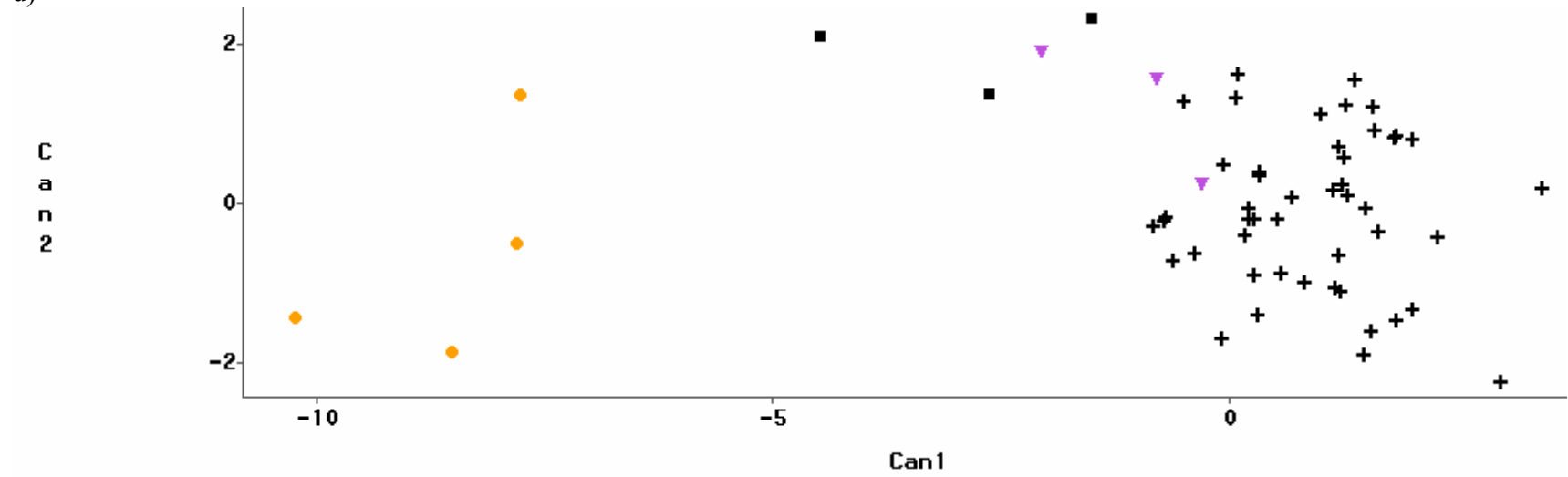
Posterior probabilities associated with classification

Specimen	Ngandong	Early <i>H. sapiens</i>	Recent <i>H. sapiens</i>
KS 16	0.00	0.02	0.98
WLH-50	0.00	1.00	0.00
Wajak 1	0.00	0.65	0.35

Figure 3.42: PCA and CDA results from Australasian landmark set. a) PC 1 versus PC 4 is plotted below. The black 'X' is ER 42700. The upside down purple triangles are (from left to right) WLH-50, Wadjak 1 and Kow Swamp 17. These three specimens as a group differ significantly from mid-Pleistocene *Homo*, *H. erectus* and early *Homo* on PC 1. Shape differences along PC 1 (b) and PC 4 (c) are shown below in lateral view. d) Both WLH-50 and Wadjak 1 were classified with early *H. sapiens* while Kow Swamp 17 was classified as a recent human in the CDA. Both canonical axes were significant. See legend in Figure 3.8.



d)



Position of Homo floresiensis

PCA Liang Bua landmark set, all-specimens: The landmark set used to examine the affinities of the LB1 fossil was similar to the standard landmark set but was lacking several landmarks as summarized in Table 3.13. As seen in Figure 3.43, the LB1 specimen clearly grouped with *H. erectus* on PC 1, falling with some of the earlier representatives of this species (ER 3733 and D 2280) rather than the geographically closer Indonesian *H. erectus*. On PC 2, it scored slightly higher than the *H. erectus* individuals, in the direction of ER 1813, but also overlapped some recent *H. sapiens*. On no component did this specimen separate out uniquely, nor did it form a separate group with *H. sapiens*.

PCA in size-shape space (Liang Bua landmark set, all-specimens): As described in the introduction, a PCA in size-shape space was also performed using this dataset (Figure 3.44a). There was a very tight relationship between PC 1 scores and $\ln(\text{centroid size})$ ($R^2 = 0.97$, $\alpha < 0.05$) as this measure was much more variable than any single shape coordinate. This first component captured differences both in $\ln(\text{centroid size})$ and in the shape variation associated with size that was consistent across taxa. LB1 had the lowest score on PC 1 because of its very small size. The PC 1 score of LB1 was within the *H. erectus* range when $\ln(\text{centroid size})$ was used to predict the PC 1 score at the size of LB1. The score of LB1 on PC 1 was not within the ranges of *H. sapiens* or mid-Pleistocene *Homo*.

The shape changes from the negative to positive ends of PC 1 (corresponding to an increase in size) were less expansion at mid-parietal, bregma and lambda (which also shifted anteriorly) (Figure 3.44b). There was also more anterior projection at the

Figure 3.43: PCA of Liang Bua landmark set, all-specimens. a) PC 1 versus PC 2 is plotted below. LB 1 (the brown upside down triangle) overlapped with *H. erectus* fossils on PC 1 and with the edge of the modern human distribution on PC 2. The 'X' is ER 42700. The shape change along PCs 1 (b) and 2 (c) are shown in lateral view. See legend in Figure 3.8.

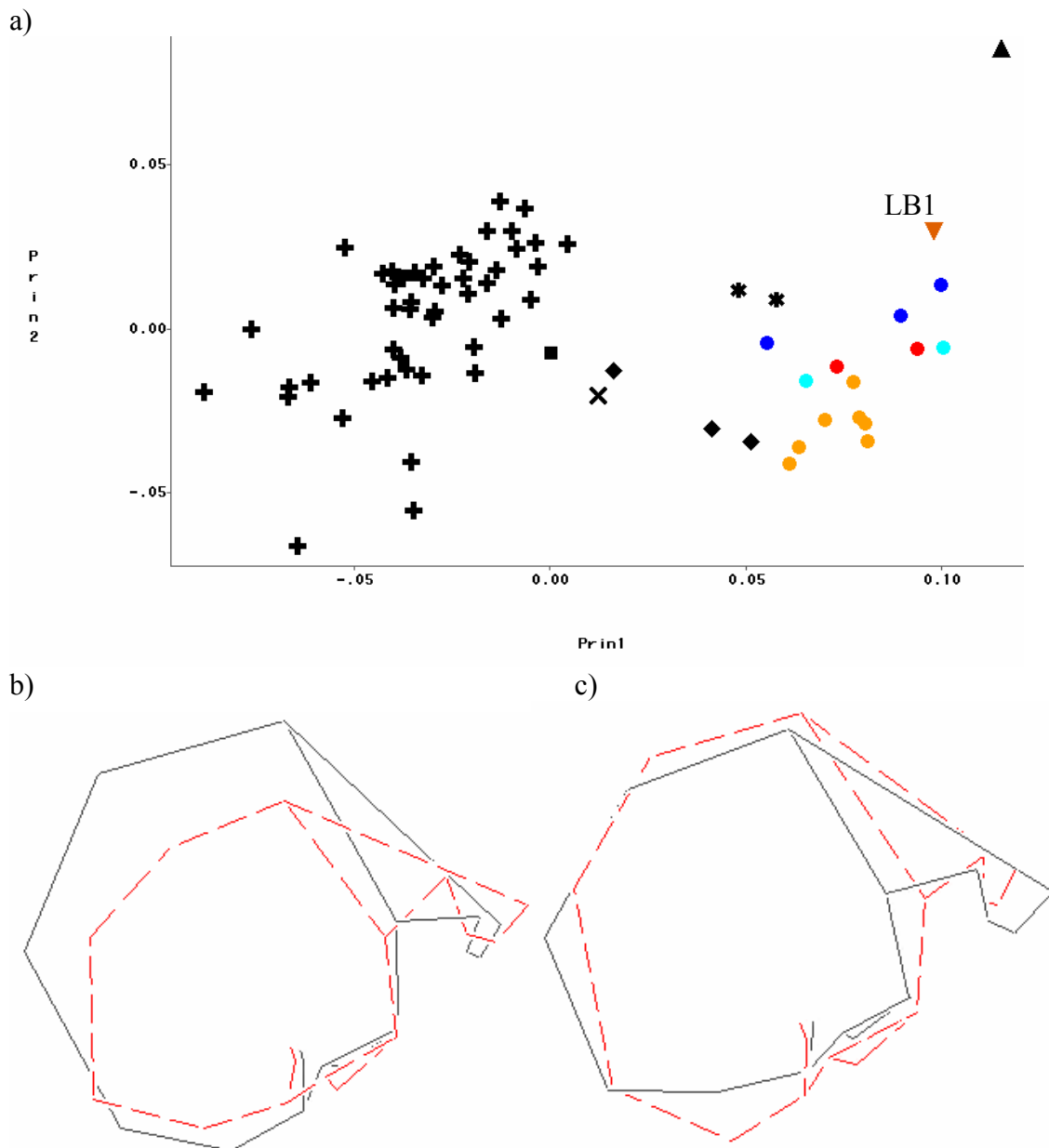


Table 3.13: Composition of landmark sets and samples used to examine the affinities and scaling relationships of Liang Bua 1.

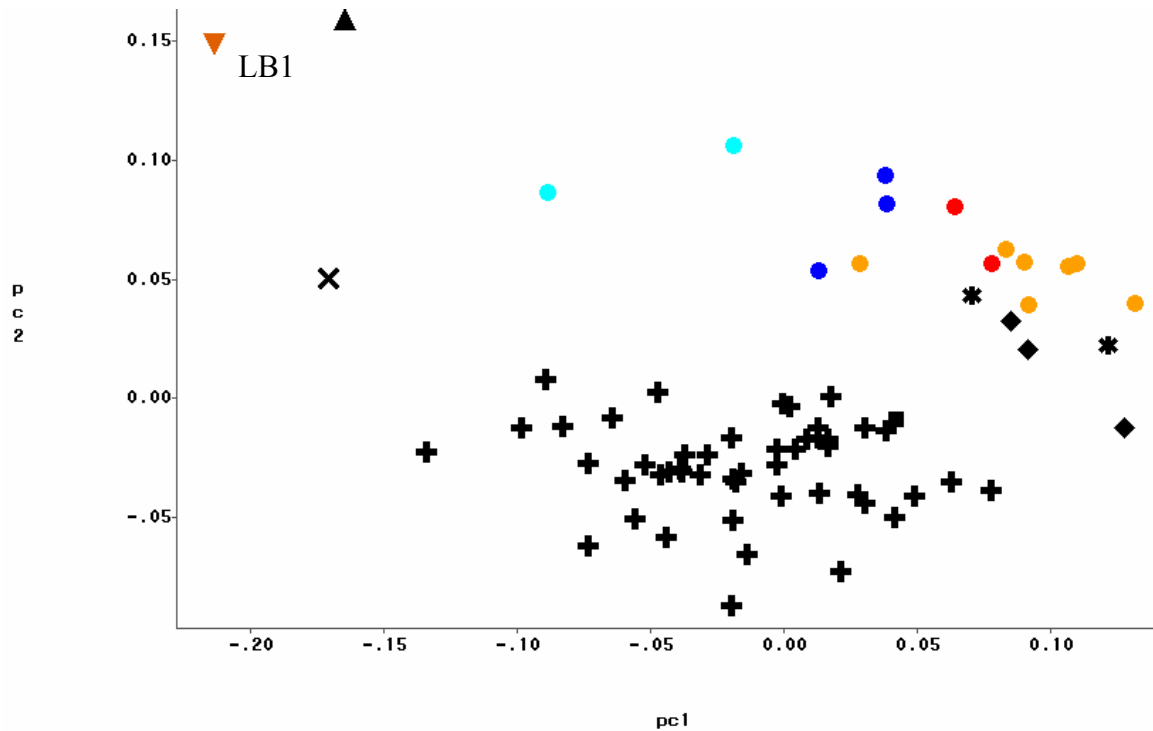
Analysis	Landmarks ¹	# Landmarks	Sample ²	# Specimens
Liang Bua set, all-specimens	IN, LA, MP, BR, SON, FMT, FMO, PO, AU, FT, AP, OP, TM, PG, EG, TS	27	<u>H. erectus</u> : ER 3733, 3883, Daka, D 2280, 3444, S 17, Sm 1, 3, Ng 6, 10, 11, 12, Zkd 11 and 12 <u>H. habilis</u> : ER 1813 <u>H. neanderthalensis</u> : La Chapelle and La Ferrassie <u>mid-Pleistocene Homo</u> : Kabwe, Dali and Omo Kibish 2 <u>Early H. sapiens</u> : Skhul 5 <u>Recent H. sapiens</u> : 48 ⁴ <u>H. floresiensis</u> : Liang Bua 1 <u>Unknown</u> : ER 42700	71

1, A minus sign (-) indicates that this landmark was excluded

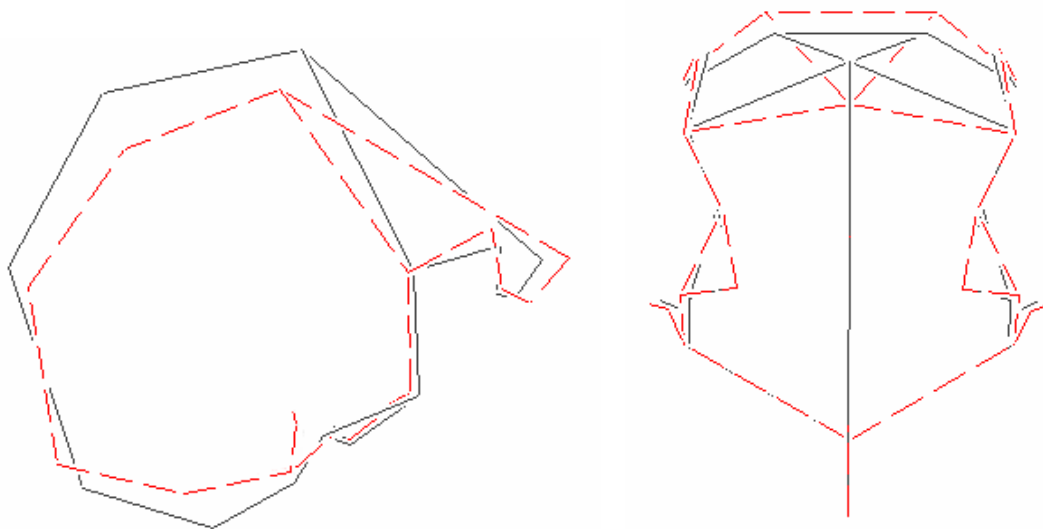
2, A plus sign (+) indicates that this specimen added and a minus sign (-) indicates that this specimen was excluded.

Figure 3.44: a) PCA in size-shape space of Liang Bua landmark set, all-specimens. The first component is highly correlated with centroid size ($R^2 = 0.97$, $\alpha < 0.05$). LB 1, the upside down brown triangle, scores very low on PC 1 due to its small size. It is within the range predicted by the regression of PC 1 and PC 2 scores on $\ln(\text{centroid size})$ for the *H. erectus* sample but not for the *H. sapiens* or mid-Pleistocene *Homo* samples. The shape changes associated with the positive (black solid line) and negative (red dashed line) ends of PC 1 (b) and 2 (c). See legend in Figure 8.

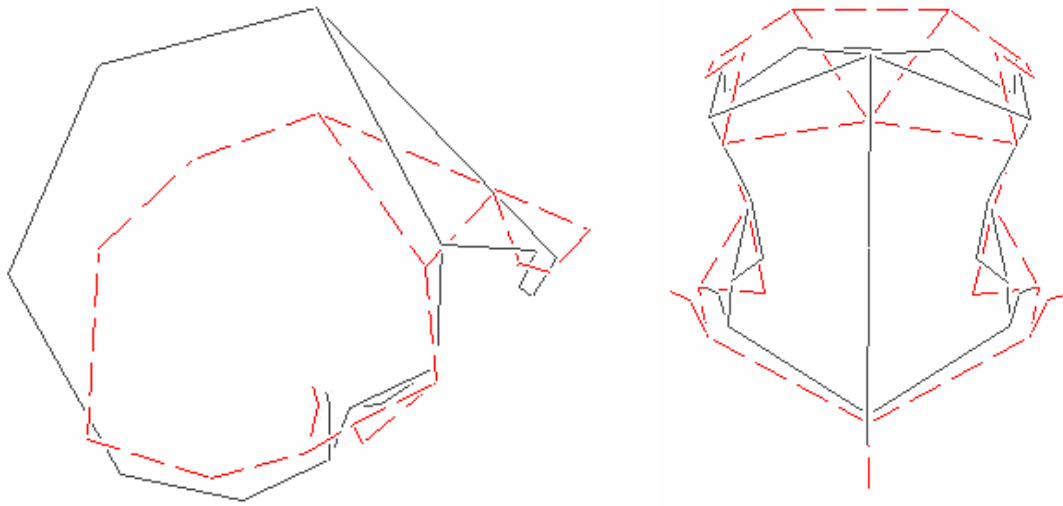
a)



b)



c)



supraorbital notches and greater width across the temporal bone in larger specimens.

Opisthion was less inferiorly projecting and inion was more posteriorly located in higher scoring individuals.

The relationship between PC 2 and $\ln(\text{centroid size})$ was not significant for the sample as a whole, but was significant within *H. erectus* ($R^2 = 0.51$, $\alpha < 0.05$), and it approached significance for the three mid-Pleistocene *Homo* specimens ($R^2 = 0.99$, $\alpha = 0.06$); in both cases the relationship was negative. Therefore, the second PC encompassed both species differences and some intra-species allometry. LB1 fell within the 95% confidence intervals for the regression of PC 2 scores on $\ln(\text{centroid size})$ for *H. erectus* whereas ER 1813 and 42700 did not. The magnitude of shape differences was greater on PC 2 than on PC 1 because it was variation in size that was mainly driving PC 1 but variation in shape which was responsible for PC 2. As seen in Figure 44c, higher scoring specimens had a longer, flatter mid-sagittal profile with a more angled occipital bone and a longer frontal bone. Frontotemporale was positioned more postero-

superiorly, the supraorbital torus was more anteriorly projecting and the entoglenoid process was less inferiorly projecting. There was also much greater breadth across the temporal bones and greater constriction across frontotemporale in higher scoring fossils.

Discussion

Homo erectus species definition and composition

It is clear from the above results that quantitative methods focused on 3D neurocranial shape can successfully distinguish *H. erectus* from other *Homo* species, including those with whom it likely shares either a sister-group or ancestor – descendant relationship such as mid-Pleistocene *Homo* and *H. habilis*. However, it does not differ from all taxa in the same way, and the identification of shape “autapomorphies” was difficult. Although the face and temporal base shape of *H. erectus* were very similar to those of other *Homo* species, the shape of the overall cranium, the frontal bone and the occipital bone discriminated between *H. erectus* and other species. In fact, *H. erectus* maintained a very consistent pattern of neurocranial shape across a wide geographic, temporal and size range. *H. erectus* consistently had a low cranial vault in the mid-sagittal profile, a long frontal squama with a prominent supraorbital torus that was relatively straight anteriorly and superiorly and an inferiorly projecting entoglenoid process. The frontal squama was receding in the midline, flattened in the coronal plane and exhibited marked constriction behind the orbits, while the supraorbital torus was less arched over the orbits and had a particularly vertical anterior surface (no posterior torsion

of the anterior surface). The occipital bone was both wide and angled in the mid-sagittal plane, although there was variation in the posterior profile.

The identification of these aspects of cranial shape is in agreement with past broad-based descriptions of *H. erectus* cranial morphology (e.g., Le Gros Clark, 1964; Howell, 1978; Howells, 1980; Rightmire, 1990). Although *H. erectus* shared most aspects of its cranial shape with other species of *Homo*, this set of characters together form the foundation of a combination definition (a unique combination of plesiomorphic, synapomorphic and autapomorphic traits; Wood, 1984). This study also identified a single autapomorphic shape character in *H. erectus*, the very great breadth across the posterior neurocranium. These characters are unlikely to represent independent traits, and many likely reflect the result of developmental and functional integration in the hominin skull. The aspects of cranial shape which differentiate *H. erectus* from other *Homo* species are intended to supplement existing character-based definitions of *H. erectus*.

Overall cranial shape consistently differentiated *H. erectus* from mid-Pleistocene *Homo*, *H. sapiens* and *H. habilis*. The *H. erectus* – Neanderthal contrast reached significance only in the most complete representation of overall cranial shape (standard landmark set), because these species differ primarily in the greater height at the posterior cranium and expansion of the frontal bone seen in Neanderthals. These aspects of shape were not captured when metopion, opisthion and the mid-parietal landmarks were excluded in subsequent analyses of cranial shape. Neanderthals did differ significantly in their occipital and temporal base shape, and the sole Neanderthal fossil in the frontal bone analysis (La Chapelle) was well separated from *H. erectus*. These findings indicate

that Neanderthals shared a long, low cranial vault and wide cranial base with *H. erectus* but these two species differed in more detailed aspects of cranial morphology.

The Dmanisi hominins, which have generally been considered to be *H. erectus* or *H. ergaster* did indeed group with other *H. erectus* fossils and were well within the range of cranial shape for this species. Daka was often on the edge of the distribution of modern humans, usually in the direction of later *Homo* taxa. In fact, although this specimen had the closest affinities with *H. erectus* in the PC plots, it was sometimes misclassified as a mid-Pleistocene *Homo* in the CDAs. The fragmentary specimen from Olororgesailie (OL 45500) could only be included in the frontal bone analysis, where it fell outside the *H. erectus* distribution. However, many aspects of the OL 45500 frontal bone shape were consistent with the other African *H. erectus* specimens (Chapter 4). Daka and OL 45500 are the youngest African *H. erectus* specimens (~1.0 and ~0.9 Ma, respectively), but whereas Daka is more similar to later *Homo* taxa, OL 45500 appears to express the African *H. erectus* pattern to the extreme. Despite the hints of more modern morphology in Daka, particularly the greater height of the posterior cranium, longer occipital plane, narrower posterior and mid-vault and tall, arched supraorbital torus, Daka fits the *H. erectus* cranial *Bauplan* most closely and does not group with members of any other *Homo* species. The Olororgesailie specimen is somewhat separated from the other *H. erectus* fossils but clearly exhibits the African *H. erectus* frontal bone shape. At this time it seems that the fossil specimens from Dmanisi, Daka and Olororgesailie can best be accommodated within *H. erectus*.

Initial descriptions have emphasized the affinity of the subadult or young adult specimen from Ileret with *H. erectus*. One way in which this specimen was said to

resemble *H. erectus* was in its “overall vault shape” (Leakey *et al.*, 2003, p. 136). However, this specimen consistently failed to group with *H. erectus* fossils in both the PCA and CDA. ER 42700 differed from *H. erectus* fossils in having greater expansion at bregma, the mid-parietal and particularly lambda, resulting in a more forward angled occipital plane. Although metopion was not calculated for this specimen because of damage to the frontal bone posteriorly, this specimen was clearly more domed (antero-posteriorly) than other *H. erectus* specimens and it is expected that it would have shown greater expansion in this region. Although its small size overlaps the range of early *Homo* (Spoor *et al.*, 2005), its cranial shape most closely resembles mid-Pleistocene *Homo* specimens, particularly Kabwe, when the entire neurocranial shape is considered. ER 42700 neither resembled other small *H. erectus* fossils, such as those from Dmanisi, nor did this specimen resemble a scaled down version of *H. erectus* when the size and shape were analyzed simultaneously in the size-shape PCA. Although ER 42700 may be a subadult individual, other subadult specimens such as WT 15000 and D 2700 do not exhibit the unusual morphology seen in this fossil. In addition, the spheno-occipital synchondrosis was nearly fused, and it seems highly unlikely that further growth and development would yield a more *erectus*-like cranial shape. While this specimen should probably not be included in *H. erectus*, it is unclear to what species it should be assigned or whether it represents further species diversity in the early Pleistocene.

The Ceprano calvarium was initially described as a European *H. erectus* specimen (Ascenzi *et al.*, 1996), and has continued to be included in this species by some workers (Ascenzi *et al.*, 2000; Clarke, 2000a,b; Rightmire, 2004) while it has also been assigned to *H. antecessor* (Manzi *et al.*, 2001), *H. mauritanicus* (Hublin, 2001) and *H. cepranensis*

(Mallegni *et al.*, 2003). The results of this study were in broad agreement with those of Manzi *et al.* (2001) in finding that Ceprano was intermediate in some ways between *H. erectus* and mid-Pleistocene *Homo*, although it appeared to have closer affinities with the later *Homo* taxa than with *H. erectus* in the CDA. While Ceprano shared a low cranial profile with *H. erectus*, it expressed features like a wider mid-vault and a higher temporal squama in common with mid-Pleistocene *Homo*. A PCA of 2D landmarks from the mid-sagittal profile positioned Ceprano within the *H. erectus* distribution (Bruner and Manzi, 2006), but the utilization of both midline and bilateral landmarks in this study highlighted the more intermediate position of Ceprano between *H. erectus* and mid-Pleistocene *Homo*. Similar results were obtained in the frontal bone analysis here as in Bruner and Manzi (2006); the frontal bone morphology of Ceprano was most similar to mid-Pleistocene *Homo* and *H. neanderthalensis* individuals and distinct from *H. erectus*. While not unambiguous, the results taken as a whole do not support the inclusion of Ceprano in *H. erectus*. To what species it should be assigned to remains unclear as none of the three proposed species (*H. cepranensis*, *H. mauritanicus* and *H. antecessor*) contain sufficient comparative material to make this determination.

The only analysis which included Salé, a north African fossil which has also been assigned to both *H. erectus* and later species of *Homo* (e.g., Jaeger, 1975; Bräuer, 1984; Hublin, 1985, 2001; Rightmire, 1990, 2004), was the temporal bone analysis. Unfortunately, this analysis did not provide good separation between modern humans and mid-Pleistocene *Homo*, and Salé groups with modern humans in the CDA. However, there was clear separation in the PCA between *H. sapiens* and mid-Pleistocene *Homo* on one hand and *H. erectus* and *H. neanderthalensis* on the other, with Salé more closely

resembling the first set of taxa. It does not appear, at least on the basis of temporal bone anatomy, that Salé was a member of *H. erectus*.

The morphological “gap” between Homo sapiens and earlier Homo species

A morphological ‘gap’ between *H. sapiens* and earlier *Homo* taxa was apparent in analyses of the two more complete cranial landmark sets (the standard and no-metopion landmark sets). This ‘gap’ has been noted in previous studies and explained in terms of differential expansion of the parietal, (Bruner *et al.*, 2003), temporal and / or occipital lobes (Lieberman *et al.*, 2002) of the brain. The vector of shape change from *H. habilis* to early *H. sapiens* was characterized by increasing expansion of the neurocranium along the mid-sagittal plane from glabella to lambda and a decrease in width across the lateral temporal base in combination with increased width across the temporal and frontal squamae (including frontotemporale) and a superior shift of the anterior cranial base. When recent *H. sapiens* specimens were included in the analysis, this vector of modernization also included a more globular neurocranium, narrower posterior cranium, steeper frontal squama and less developed supraorbital region. The increased globularity of the modern human skull resulted from the interaction between endocranial growth and cranial base breadth (Lieberman *et al.*, 2000). With regards to these aspects of cranial shape, the Asian *H. erectus*, Daka and D 3444 specimens resembled later *Homo* species more closely than did D 2280 and the older *H. erectus* fossils from East Turkana (ER 3733 and 3883).

Mid-Pleistocene *Homo* individuals bridged this gap in the no-opisthion/no-mid-parietal landmark set and in most analyses which used only fossil *Homo* specimens. This pattern suggested that mid-Pleistocene *Homo* shared a less globular cranial shape and a more prominent supraorbital region with earlier *Homo* taxa but also exhibited greater outward expansion of the superior vault, a narrower base and a wider anterior and mid-vault, features which aligned this species more closely with *H. sapiens*. The changes seen in mid-Pleistocene *Homo* cannot be attributed simply to an increase in brain size because both mid-Pleistocene *Homo* and *H. neanderthalensis* show increased in endocranial volume relative to *H. erectus*. Rather, these changes may represent the initial changes in the direction of a more globular cranium, despite the greater antiquity of the mid-Pleistocene *Homo* specimens compared to Neanderthals and the Ngandong / Sambungmanan fossils.

Evolution of neurocranial shape in the genus Homo

Examination of shape change along the less speciose phylogenetic tree highlighted the timing of key events on the lineage leading to modern humans. The mid-sagittal profile of *H. erectus* remained low as in ER 1813 but increased in length and became much wider, particularly at the posterior and mid-vault. The frontal bone also increased in length and the supraorbital torus became much more prominent. The general trends that characterize many evolutionary transitions in *Homo* are the expansion of the neurocranium superiorly and posteriorly in the midline and the increase in relative length of the parietal bone. These changes may reflect the underlying increase in brain size in

more recent species of *Homo*, although these changes were not as apparent in the mid-Pleistocene *Homo* – *H. neanderthalensis* transition. There was also a decrease in the inferior projection of the entoglenoid, the constriction across frontotemporale and an increase in the height of the temporal squama over time. Again, Neanderthals did not exhibit this last trend when compared to the mid-Pleistocene *Homo* fossils. *H. sapiens* was the first species to exhibit a decrease in the size of the supraorbital torus and a wider mid-vault than posterior vault.

Ceprano (*H. mauritanicus*) is intermediate in some respects between *H. erectus* and younger Middle Pleistocene hominins. For example, the neurocranium is *erectus*-like in its low mid-sagittal outline and wide posterior vault, and *heidelbergensis*-like in its frontal bone shape. However, it is also autapomorphic in several aspects of cranial morphology, specifically its short parietal length, very wide mid-vault, high temporal squama and laterally positioned temporal base structures. If this specimen is representative of the species that gave rise to both *H. rhodesiensis* and Neanderthals, then perhaps the unique morphological traits were geographic specializations not seen in those populations which were directly ancestral to later species.

Evolution of the frontal, occipital and temporal base regions of the skull in Homo

By focusing on limited regions of the skull, it was possible to increase both the landmark density and sample size for these analyses. Some broad evolutionary trends could be identified for these cranial regions. However, it is important to consider the

orientation and relative proportions of these regions in relation to the rest of the skull when interpreting the results.

The shape of the frontal bone in *H. erectus* and mid-Pleistocene *Homo* was very similar in its receding mid-line profile and less domed coronal section. In contrast, the frontal bone of both Neanderthals and modern humans was more rounded both side-to-side and along the mid-sagittal plane. *H. erectus* exhibited some aspects of frontal bone morphology which were apparently unchanged from earlier taxa, including greater postorbital constriction, and others that were unique, such as the very straight superior profile of the supraorbital torus with no posterior torsion. At the same time, both the African / Georgian and Asian samples of *H. erectus* shared different aspects of frontal bone shape with early *H. sapiens*. Recent Asian *H. erectus* (but not S 17) resembled *H. sapiens* in its more expanded mid-sagittal squama with less postorbital constriction whereas the African and Georgian *H. erectus* shared with *H. sapiens* a relatively shorter squama with a wider, taller and more arched torus. If the African populations of *H. erectus* were ancestral to later *Homo* taxa, as suggested by several workers (e.g., Stringer, 1984; Wood, 1984, 1994; Rightmire, 1990; Clarke, 1990, 2000a; Strait *et al.*, 1997; Foley, 2002), then the expansion of the frontal squama along the midline and at frontotemporale evolved in parallel in the Asian *H. erectus* lineage. With the exception of Bodo, whose frontal bone shape was very similar to that of earlier *Homo* species, mid-Pleistocene *Homo* and especially *H. neanderthalensis* evolved a more arched supraorbital tori and less constriction at frontotemporale. The frontal bone of Ceprano is indistinguishable from younger mid-Pleistocene *Homo* specimens like Dali, Kabwe and Petralona, which may indicate that the frontal bone was one of the first regions to change

in this species. However, Bodo, exhibits a slightly more primitive configuration of the frontal bone. Either Bodo was not part of this same lineage as Ceprano, or there was variation among early members of the mid-Pleistocene *Homo* sample in the morphology of this region. The more vertical forehead, greatly reduced supraorbital region, and lack of constriction across frontotemporale appeared in modern humans only after ~100 Ka as this shape complex was not fully developed in the Skhul, Jebel Qafzeh and Jebel Irhoud early modern human specimens.

The temporal base is the one region of the skull that did not separate recent humans from other *Homo* taxa. In fact, the temporal base, contrary to expectations (Lockwood *et al.*, 2004), did not provide good separation of taxa nor did it recover the expected phylogenetic relationships when used to generate distance trees. Lockwood *et al.* (2004) were able to recover the true (i.e., genetic) relationships among *H. sapiens* and the great apes using phenetic tree methods applied to 3D landmark data of the temporal bone. They argued that temporal bone shape was particularly useful in phylogeny reconstruction because “Its functional complexity should minimize the possibility that a single behavioral shift in unrelated taxa could lead to homoplastic similarity across a suite of features” Lockwood *et al.* (2004, p. 4356). These researchers further suggested that the temporal bone may prove particularly useful in elucidating relationships among Pleistocene *Homo* taxa (p. 4360). The failure of the temporal base landmarks to recover the expected relationships among Pleistocene *Homo* in this study may be a reflection of 1) an insufficient number of temporal landmarks (a result of incomplete preservation of the temporal bone in fossil specimens) or 2) the inability of the temporal bone to recover

the correct phylogenetic relationships among closely related species within a single genus.

The shape seen in recent humans may be fairly conserved as it was also found in most mid-Pleistocene *Homo* fossils and was similar to that seen in African *H. erectus* specimens. The short and narrow tmj and long anterior face of the tympanic tube set Asian *H. erectus* apart from other *Homo*. The differences seen in the Asian branch of *H. erectus* may have evolved through isolation and drift or as a result of local selection. However, the Dmanisi hominins exhibited a somewhat intermediate pattern of temporal base shape and it is possible that they were ancestral to both the African and Asian *H. erectus* lineages.

It appears that a moderately wide occipital bone that is slightly angled in the mid-sagittal plane with a transverse occipital torus characterized *H. habilis* (as seen most clearly in the occipital bone of ER 1813) and was therefore the primitive condition for *Homo*. This pattern was taken to a more extreme form in *H. erectus*, particularly the Indonesian specimens, whereas *H. sapiens* have a narrower occipital with an extended and gently rounded mid-sagittal profile. It is possible that this more modern morphology evolved first in African populations of mid-Pleistocene *Homo*, as seen in ER 11693 from Eliye Springs. The Neanderthal occipital shape was not obviously different from other Middle and Late Pleistocene *Homo*, in agreement with the findings of Gunz and Harvati (2006), but the higher position of opisthocranium did distinguish them from *H. erectus*. WT 15000, the only subadult individual in the analysis, had the least angled occipital sagittal bone of all *H. erectus* specimens which may indicate that this morphology was

partially due to *in vivo* development. However, additional subadult specimens are needed to properly address the development of the occipital bone.

Santa Luca (1980) hypothesized that the evolution of the occipital bone proceeded through a few stages. According to him, the occipital bone began small with a proportionally large nuchal plane and inion and opisthocranium were coincident. In the second stage, the occipital plane increased while the nuchal plane decreased in size. Finally, the occipital plane increased in size, became more vertically oriented and rounded and opisthocranium moved into a position superior to inion. The findings here confirm that an elongated, more vertical and rounded occipital plane, as well as the vertical separation of inion and opisthocranium, did characterize the transition from ‘archaic’ *Homo* to recent *H. sapiens*, but suggest that the occipital profile of recent Indonesian *H. erectus* does not fall along this trajectory.

The overlap in general cranial shape among *H. erectus* individuals supports a single species that shared a very similar cranial shape despite the wide geographic and temporal range that characterized this species. Regional analyses highlighted some geographic variation in this species. Unique aspects of frontal bone, occipital bone and temporal base shape in the Asian *H. erectus* fossils supports the hypothesis that the Asian populations were not directly ancestral to later species included in the mid-Pleistocene *Homo* group or to *H. sapiens*. However, this phylogenetic scenario would require the parallel evolution of a more expanded midsagittal profile (as well as some discrete traits, Andrews, 1984) in the Asian *H. erectus* lineage and *H. heidelbergensis*. Although *H. erectus* is well-represented in these analyses, more complete samples for other taxa, such

as the Neanderthals, could change the results and these conclusions should be viewed as preliminary.

The evolutionary fate of the Homo erectus lineage

The dataset here does not support an ancestor – descendant relationship between the Ngandong hominins and modern humans in the Southeast Asia / Australia region. This does not mean that no gene flow occurred between the Ngandong and early modern human populations, but whatever genetic contribution may have occurred was not detectable in terms of general cranial shape. While many researchers have attributed similarities between the Ngandong and modern humans in Southeast Asia and Australia to either artificial cranial deformation or pathology (e.g., Brothwell, 1975; Brown, 1989; Webb, 1990; Antón and Weinstein, 1999), neither problem affected the results of this analysis. Cranial deformation has not been reported for any of these three individuals and while hyperostosis affected the cranial bone thickness of WLH-50, this was not a factor in this study.

Hawks *et al.* (2000) found that WLH-50 was classified with the Ngandong sample in a discriminant function analysis (DFA) of linear measurements. Based partially on this result, (Hawks *et al.*, 2000, p. 11) argued that:

“WLH-50 is metrically and morphologically more like the Ngandong sample than it is like hominids from the other two regions [Africa and the Levant]. We might expect these findings if WLH-50 is a descendant of all three groups, whether or not the influence of Ngandong was stronger than the other two as the data suggest. The results involve two different analyses of many different variables, and are not possible if the Levant and African samples are

uniquely ancestral to WLH-50 while Ngandong, or some other sample like it, is not.”

While the CDA here was not identical to the DFA of Hawks *et al.*, there was broad overlap between the two analyses in terms of the samples and the basic cranial shape captured in both studies. The results of the PCA performed here directly contradicts the assertion that WLH-50 resembles the Ngandong sample in its cranial morphology, while the CDA assigned all three specimens to *H. sapiens* rather than late Indonesian *H. erectus*. The second analysis to which they refer was a pairwise difference analysis (PDA) which was criticized on by Bräuer *et al.* (2004), both methodologically (see also Collard and Franchino, 2002) and in terms of the quality of the discrete data employed by Hawks *et al.* (2000).

The results reported here reflect the advantage of using scale-free cranial shape rather than linear measurements which capture both size and shape information. As noted by Brown (1992), the WLH-50 cranium, like many terminal Pleistocene Australians, was large, particularly in its length. The linear measurements utilized by Hawks *et al.* (2000) captured both similarity in size between WLH-50 and the Ngandong crania, as well as thick cranial vault bones which differ histologically between WLH-50 (which is thickened due to pathological hyperostosis: Brown, 1989; Webb, 1990) and Indonesian *H. erectus* (Brown, 1994). Neither size nor the non-homologous cranial bone thickening are convincing phylogenetic links, and it is clear that the actual shape of the cranium was very different from the Ngandong series, as observed by Brown (1992). The three modern human crania used here have been referenced specifically by proponents of the multiregional model as exhibiting similarities to the Ngandong cranial fossils in both discrete cranial traits as well as aspects of cranial shape (e.g., Thorne,

1975; Wolpoff *et al.*, 1984; Frayer *et al.*, 1993; Hawks *et al.*, 2000; Wolpoff *et al.*, 2001). Indeed, Brown (1992) suggests that other crania, such as Lake Mungo 1 and 3 and Keilor bear even less resemblance to Indonesian *H. erectus*. In addition, the landmarks used here, particularly in the Australians only landmark set, reflected closely the measures used by Hawks *et al.* (2000) and included information about the shape of the frontal midsagittal profile and the position of frontotemporale, other aspects of cranial shape which have been used to argue for regional continuity in southeast Asia and Australia (e.g., Weidenreich, 1943; Wolpoff *et al.*, 1984; Wolpoff, 1992; Frayer *et al.*, 1993). Therefore, although the design of this analysis favored a result in line with the multiregional model, the results clearly refute the claim of Hawks *et al.* (2000) to have disproved the Recent out of Africa model of modern human evolution.

It was, however, interesting that both the Wajak skull and WLH-50 did not group with other recent humans (including native Australians), but rather grouped with the early *H. sapiens* from Skhul, Jebel Qafzeh and Jebel Irhoud. It seems unlikely that either pathology or artificial deformation can be used to explain this finding, particularly in Wajak 1. This less derived anatomy could be the result of an early migration of populations that resembled those from Skhul, Jebel Qafzeh and Jebel Irhoud. The ways in which Wajak 1 and WLH-50 differ from other recent human populations are very similar to the ways in which early and recent modern humans differ: in the lower profile of the neurocranium in the midsagittal plane and the more prominent supraorbital torus. However, it is possible that these individuals are only ~14 ka (WLH-50, Simpson and Grün, 1998) or less than 10 ka (Wajak 1, Storm, 1995) and, as such, would represent very recent members of a much older lineage. Alternatively, the more primitive features

might have resulted from some degree of genetic exchange between early populations of modern humans in this region and late-surviving populations of *H. erectus* (such as Ngandong) (Bräuer, 1992; Stringer, 1992a). A third alternative is that these traits (re-)evolved as the result of isolation and drift in this region.

Although the populations of Indonesian *H. erectus* did not contribute greatly to modern humans in this region, they may have been ancestral to *H. floresiensis*. The shape of the LB1 cranium was consistent with predictions of a scaled down version of *H. erectus* based on a PCA in size-shape space. While this finding does not definitively establish the Flores hominins as a population of insular dwarfed *H. erectus*, it does establish that the cranial shape of LB 1 was consistent with a small *H. erectus* individual (but not *H. sapiens* or *H. heidelbergensis*), based on allometric shape change in this species.

Conclusions

H. erectus represented a species distinct from both modern and extinct *Homo* taxa. Using 3D geometric morphometric methods it was possible to differentiate *H. erectus* from other *Homo* species from the shape of both the overall cranium and various regions of the cranium (particularly the frontal and occipital bones). The aspects of cranial shape which act to differentiate *H. erectus* can supplement previous, character based definitions of *H. erectus*. ER 42700 did not exhibit a cranial shape which was consistent with the *H. erectus* pattern, a result which can not be attributed only to its small size as the Dmanisi hominins who are also small resemble *H. erectus* much more

closely in their overall cranial shape. The temporal bone anatomy of Salé also appears to argue for its exclusion from *H. erectus*, although this conclusion is based on a very limited region of the cranium. The species status of Ceprano is less clear, although its frontal anatomy does not adhere to the *H. erectus* pattern, as noted previously by Manzi *et al.* (2001) and Bruner and Manzi (2006). *H. erectus* is thus represented by cranial fossils from the African sites of East Turkana, West Turkana, Olororgesailie, Daka and Olduvai Gorge and the Asian sites of Sangiran, Ngandong, Sambungmacan, Ngawi and Zhoukoudian. Although not addressed here, fossils from additional sites in South Africa, Algeria and China may also represent *H. erectus*.

If, as has been suggested, *H. habilis* is close to the ancestry of *H. erectus* (Strait *et al.*, 1997; Foley, 2002; Bermudez de Castro *et al.*, 2004), then numerous changes in cranial anatomy characterized the origin of *H. erectus*, including a posterior projection of the occipital bone, a higher temporal squama and a wider neurocranium. Later transitions along the lineage leading to modern humans involve continued posterior projection at lambda, a decrease in the projection of the entoglenoid process, a decrease in postorbital constriction and a series of changes in frontal bone anatomy. The Asian populations are more-derived than the African populations of *H. erectus* in their temporal base and occipital bone shape and hence may not be on the direct lineage leading to *H. sapiens*, although this would require the parallel evolution of certain other aspects of cranial shape. The cranial shape evidence does not bear out the predications of the multiregional model of human origins, based on the lack of resemblances between WLH-50, KS 17 and Wajak 1 to the Ngandong population.

The initial description of LB1 suggested that the Liang Bua hominins represented an insular dwarfed population of *H. erectus*. Using allometric shape change in *H. erectus*, it was shown that the shape of LB1 was within the predicted range for a similarly small *H. erectus* neurocranium. Although this does not definitively confirm that the Flores population was a relic dwarf population, it does indicate that a small version of *H. erectus* could resemble LB1.

Geometric morphometric techniques are powerful tools in elucidating both evolutionary and ontogenetic integration in the cranium (Lieberman *et al.*, 2002; Bookstein *et al.*, 2003) and future work must address the functional and developmental basis of the unique aspects of *H. erectus* cranial shape identified here. The first step in this process will be to add an ontogenetic component to the analysis, in order to compare the ontogenetic trajectories of *H. erectus* with those seen in other species of *Homo*, as has been done with *H. neanderthalensis* (Ponce de León and Zollikofer, 2001). The inclusion of an ontogenetic series will also clarify whether the unique aspects of cranial shape seen in *H. erectus* were established early in ontogeny and therefore have a strong genetic component.

Chapter 4: Geographic, Temporal and Size-Related Variation in *Homo erectus*

Introduction:

Despite claims for homogeneity and stasis within *Homo erectus* (Rightmire, 1984; Bilsborough, 2000), it is clear that variations exist within this fossil *H. erectus* sample, and this diversity has implications for the interpretation of the taxonomy and evolutionary history of *H. erectus* (s.l.). Major *H. erectus* finds are from sites across the Old World, including East Africa, the Caucasus, China, Indonesia and possibly South Africa and Italy. The discovery of new specimens, re-dating of African, Chinese and Indonesian sites and new analyses have brought forward new ideas concerning the taxonomy, evolution and dispersal of *H. erectus*. The main topic which must be taken up in order to address these hypotheses is that of variation within this sample. A large dataset of three dimensional (3D) cranial shape landmarks and curves from a representative sample of *H. erectus* will be used to explore the patterns of variation in this taxon. The results of this analysis will clarify areas of uncertainty in the evolutionary history of this widespread and long-lived taxon.

The first question to be asked is whether the variation in this sample supports a single or multiple species model for *H. erectus*. Currently, cranial shape variation in the *H. erectus* sample is interpreted as either intraspecific or interspecific variation. Two evolutionary patterns are compatible with the former interpretation: *H. erectus* as a single, long-lived, polymorphic species (e.g., Rightmire, 1990, 1998a; Asfaw *et al.*, 2002; Antón, 2003) or *H. erectus* as a grade within *H. sapiens* (Thorne and Wolpoff, 1981;

Wolpoff *et al.*, 1984, 1994; Frayer *et al.*, 1993; Wolpoff, 1999). If the variation is instead viewed as interspecific variation, then the evolutionary history of this taxon is considerably ‘bushier’ and presumably includes many lineages which went extinct without leaving any ancestors.

The identification of autapomorphies in the Asian *H. erectus* sample has led to the recognition of a separate species, *H. ergaster* or *H. leakeyi*, for the early African fossils (Groves and Mazák, 1975; Andrews, 1984; Stringer, 1984; Wood, 1984, 1991, 1994; Groves, 1989; Clarke, 1990, 1994) while the presence of primitive characters in the Dmanisi sample has prompted some to erect a new nomen, *H. georgicus*, for the Georgian sample, (Gabounia *et al.*, 2002; de Lumley *et al.*, 2006). *H. ergaster*, as originally conceived by Groves and Mazák (1975), included mostly mandibular and dental specimens (most notably the type specimen, ER 992) plus the cranial specimens ER 734 and 1805. They also noted resemblances between the “*Telanthropus capensis*” remains from Swartkrans, which includes the fragmentary cranium SK 847, and *H. ergaster* but left the Swartkrans fossils as *Homo incertae sedis*. The reconfiguration of this species by Wood (1991, 1994) to include ER 3733, 3883 and WT 15000 (Nariokotome Boy), while excluding ER 1805, has been more widely accepted. However, while both sets of workers excluded the larger African specimen, OH 9, from *H. ergaster*, other workers have supported a simpler African (including OH 9) versus Asian dichotomy (Stringer, 1984; Andrews, 1984).

In contrast to these ‘cladistic’ approaches to alpha taxonomy, most quantitative investigations of variation within *H. erectus* have reached the opposite conclusion: morphological variation in the *H. erectus* hypodigm is within the range of a single

species. Variation in cranial measurements has been quantified relative to modern humans, other fossil hominins and a wide range of extant and fossil primates (including modern humans) (Bilsborough and Wood, 1986; Kramer, 1993, Kidder and Durband, 2004; Villmoare, 2005, Baab, in review).

While an understanding of the relative magnitude of variation within a taxon is important in evaluating whether one or more species is present, a 'grade'-based approach to species definition is also concerned with the structure of morphological variation within a taxon. This second approach is adopted here and should be seen as complementing earlier work by Baab (in review). As discussed below, results of both analyses are in accord with many previous (particularly metric) examinations of *H. erectus* taxonomy: *H. erectus* represents a single, widespread and polymorphic species (Bilsborough and Wood, 1986; Rightmire, 1990; Kramer, 1993, Kidder and Durband, 2004; Villmoare, 2005).

As a consequence, the second part of this analysis involves the interpretation of variation in this sample within the framework of a single species. Several major sources of intraspecific variation can be identified: geographic, temporal, allometric, ontogenetic, sexual and individual. The restricted geographic distribution, incomplete preservation and small sample sizes usually limit the examination of intraspecific variation in fossil hominin species. However, workers have successfully explored and quantified variation in such species as *Australopithecus afarensis*, *A. africanus*, *Paranthropus boisei*, and *H. habilis* s.l. (Kramer *et al.*, 1995; Suwa *et al.*, 1997; Lockwood, 1999; Lockwood *et al.*, 2000), and in many ways *H. erectus* represents an ideal fossil taxon in which to examine intraspecific variation. It has a wide geographic range, with numerous sites in several

circumscribed regions (e.g., East Africa, China), it has considerable time depth (nearly 2 Myr) and there is a high degree of size variation, both across time and space and within more restricted temporogeographic samples like Dmanisi (Skinner *et al.*, 2006; van Arsdale, 2006). Also, there are a relatively high number of reasonably well-preserved fossil calvaria and crania assigned to *H. erectus*, and these generally preserve similar aspects of morphology: the vault (including the supraorbital region) and the lateral basicranium.

H. erectus presents several challenges as well. The pitfalls associated with assigning sex to individual fossils derived from samples of different geological ages and across a wide spatial spread are widely acknowledged (Armelagos and Van Gerven, 1980). It is possible to quantify variation associated with size, and within limited temporogeographic samples this probably corresponds to sexual variation. However, size variation outside of these circumscribed samples must be viewed as a combination of sexual and allometric variation. A second challenge is that geographic, temporal and size-related variation may be conflated in *H. erectus*. The earliest *H. erectus* fossils are all from the western part of its range (Africa and Georgia) and are also among the smallest. However, there is size variation within both the Sangiran and African samples. For example, S 2 is considerably smaller than the majority of Sangiran specimens, such as S 17. Recent discoveries have also highlighted the size variation that existed in Africa from 1.5 Ma (WT 15000 and OH 9 vs. ER 42700) to 1 Ma (Daka vs. OL 45500) (Walker and Leakey, 1993; Asfaw *et al.*, 2002; Leakey *et al.*, 2003; Potts *et al.*, 2004). There is also overlap between several of the Zhoukoudian crania and the “large-brained” Ngandong fossils (Rightmire, 2004), despite the potential difference in age of 300 – 800

kyr (Bartstra *et al.*, 1988; Swisher *et al.*, 1996; Grün *et al.*, 1997; Shen *et al.*, 2001).

Together, this suggests that while it will be difficult to distinguish geographic from temporal effects, it will be possible to separate these influences from size-related allometric effects within this sample.

This study addresses variation in the shape of the cranium as a whole as well as the shape of particular regions of the skull, like the frontal base. The use of 3D shape variables allows for the study of the shape of biological structures, rather than just a limited set of linear measurements. The relationship between cranial shape variation and several external variables, specifically geography, geological age and cranial size, is explored using principal components and multiple regression analyses. Previous multivariate investigations of cranial metrics have quantified and described geographic variation in *H. erectus* populations (Antón, 2002; Antón *et al.*, 2002b; Kidder and Durband, 2004). However, only a few workers have quantified anagenetic change in cranial shape (Bräuer, 1994) and size-related shape variation (Spoor *et al.*, 2005). This study represents the first systematic, quantitative examination of diachronic and size-related variation across both Asian and African *H. erectus*.

The final goal of this study was to assess the broader implications of these analyses in terms of the evolutionary history of *H. erectus*. Major questions concerning the evolution of this species include: 1) does the East Turkana or Dmanisi population most closely approximate the basal *H. erectus* condition (Andrews, 1984; Wood, 1984, 1991; Lordkipanidze *et al.*, 2006); 2) is there a strong African – Asian dichotomy vs. a widespread but more unified species (Asfaw *et al.*, 2002; Manzi *et al.*, 2003; Gilbert *et al.*, 2003); 3) were the Javanese hominins characterized mainly by *in situ* evolution or

whether there were multiple immigrations (Antón, 2002, 2003; Kaifu *et al.*, 2005); and 4) should Sambungmacan be viewed as a population intermediate between Sangiran and Ngandong or was it more closely related to Ngandong (Jacob, 1975; Wolpoff, 1999; Antón, 2003). While the analysis of this dataset can not definitively answer all of these questions, the careful examination of the structure of intraspecific variation can shed light on some of these points of disagreement.

Background

Homo erectus morphology

Traditionally two major types of data, metric (size and shape) and nonmetric (discrete), have been used to describe and quantify cranial variation. Metric analyses in particular have highlighted several aspects of cranial shape that together define *H. erectus* relative to other species: the cranium is long and low (dolicocephalic) with an angled occipital bone, the vault walls are supero-medially converging with greatest width across the temporals, and the frontal bone is low and receding with a prominent torus.

Numerous discrete traits are also found exclusively or in higher frequencies in *H. erectus*, such as midline keeling on the frontal and/or parietals, an angular torus, a thick petrosal crest, an occipital torus and a strong supramastoid crest. It is equally clear from investigations of cranial morphology that aspects of shape vary within this group. For example, the Zhoukoudian skulls have an occipital bone that is more posteriorly elongated and narrower than other *H. erectus* (Weidenreich, 1943; Antón, 2002; Kidder

and Durband, 2004). The frontal squama and supraorbital torus shape also show inter-regional differences with the Indonesian fossils exhibiting a flatter frontal squama that flows into the supraorbital torus without a supratral sulcus (Weidenreich, 1943; Rightmire, 1990; Antón, 2002). Some discrete characters also exhibit a discontinuous distribution within *H. erectus*: both the supramastoid crest and the presence of a fissure between the mastoid process and the tympanic plate (the mastoid fissure) are more common in the Asian specimens than in the African.

Geographic variation

Geographic differentiation within single species is a widespread primate phenomenon (Albrecht, 1978; Albrecht and Miller, 1993; Shea *et al.*, 1993; Frost *et al.*, 2003; Guy *et al.*, 2003), and *H. erectus* is no exception. Some of the most frequently cited and carefully evaluated differences within *H. erectus* appear to correspond to geographic variation within the sample. On the basis of perceived geographic variation, Andrews (1984) suggested that name *H. erectus* be restricted to the more derived Asian fossils. Similar arguments were made by Stringer (1984), Wood (1984) and Clarke (1990), though Wood also included OH 9 in *H. erectus* based on its overall similarity to the Asian fossils. Andrews (1984) evaluated the potential *H. erectus* autapomorphies proposed by both Stringer (1984) and Wood (1984) and restricted the list to the following: thicker cranial bones, midline keeling on the frontal and parietals, an angular torus at the mastoid angle of the parietal, inion separated from endinion in Frankfurt horizontal and fissures both between the mastoid and the petrous crest (mastoid crest) and

the entoglenoid process and tympanic plate. He also concluded that all of these characters were restricted to the Asian fossil sample. Workers like Bräuer (1990, 1994), Kennedy (1991) and Bräuer and Mbua (1992), however, argued that these traits were more widely distributed both within and outside of *H. erectus* and hence could not be considered autapomorphic for the Asian fossils. More recently Villmoare (2005) suggested that the supramastoid crest is consistently more marked in the Asian sample than the African, though his analysis also suggested that other traits like midline keeling on the frontal and an angular torus were not restricted to the Asian hominins.

In addition to geographic distribution of non-metric characters in *H. erectus*, morphometric analyses of the cranium have also highlighted certain regional patterns of cranial size and shape. In contrast to the East Turkana hominins (ER 3733 and 3883), the Asian *H. erectus* fossils have a shorter occipital plane (Wood, 1984; Delson *et al.*, 2001) and a more acute angle between the occipital and nuchal planes (Wood, 1984). The face is also shorter and wider with a broader interorbital region (Stringer, 1984). Various aspects of the supraorbital torus and supratrochlear sulcus have also been suggested to differentiate between regional groups, and there is less postorbital constriction in the Asian, and particularly the late Indonesian, sample. Bräuer (1994) also noted a narrower mandibular fossa and longer parietal antero-posteriorly in a relatively small sample of Asian *H. erectus*. The Zhoukoudian population had a narrower biasterionic breadth and a wider biauricular breadth than other *H. erectus*. While the smallest cranial capacities have been recorded for African and Georgian crania, there is a great degree of overlap among the regional samples (Rightmire, 2004).

While highlighting overall resemblances between the Zhoukoudian and Javanese (Sangiran plus Ngandong) samples, Weidenreich (1943) also noted a few important differences between the two Asian samples. The Zhoukoudian fossils have a more marked frontal tuberosity (frontal bossing) and continuous post-toral sulcus while the frontal squama was flatter and ran smoothly onto the supraorbital torus in the Indonesian hominins. However, the Indonesian group displayed greater height in the area of obelion relative to the flattening present in their Zhoukoudian counterparts. When viewed superiorly, the Zhoukoudian occipitals were narrower and more elongated compared to the broader and more rounded occipitals of the Sangiran hominins (Weidenreich, 1943; Bilsborough, 2000; Delson *et al.*, 2001). The glenoid fossa was less narrow antero-posteriorly and positioned higher, above the Frankfurt Horizontal, in the Zhoukoudian sample compared to the Indonesian hominins (Picq, 1990).

In addition to inter-regional distinctions, there is also important variation within most regional samples. Although some of the earliest Sangiran specimens are quite robust (Antón, 2003), they are also very fragmentary and distorted, complicating their interpretation. The most apparent differences within the Indonesian sample are likely related to the increase in cranial capacity seen in later specimens, particularly those from Ngandong. For example, both the decrease in postorbital constriction and the increase in frontal squama steepness noted by Sartono (1975) are probably the result of increasing brain size, although these traits are also apparent in the smaller-brained Sm 3. Earlier and later Indonesian specimens also differ in more detailed aspects of their morphology, including the heavier occipital torus with the inferiorly projecting protuberance at inion found in the larger Ngandong hominins. However, a similar morphology is also found in

the early S 4 fossil and, as Antón (2003) points out, the more variable earlier fossils encompass the variation seen in the later, more homogenous populations.

Within China, Zhoukoudian and Nanjing in particular have been singled out as having a unique cranial shape relative to Hexian. This cranial shape featured a narrow occipital and frontal compared to the wider midvault (Kidder and Durband, 2000, 2004; Antón, 2002). Several explanations have been proffered: either the metric pattern evident in the Zhoukoudian and Nanjing populations was a result of environmental adaptation, genetic isolation (genetic drift) or the measurements for Hexian are incorrect (Wolpoff, 1999; Antón, 2002; Kidder and Durband, 2004). Though Nanjing and Hexian are geographically close together (~100 km) and at the same latitude (contra Antón, 2002), they may differ in their paleoecology. Both sites include northern faunal elements like those at Zhoukoudian, but Hexian also incorporates more southern subtropical taxa (*Ailuropoda*, *Stegodon*, *Megatapirus*) (Huang *et al.*, 1982; Xu and You, 1984; Etler, 1996). Some workers see this as a fundamental difference between these two sites, one which may explain the greater similarities between Zhoukoudian and Nanjing 1 (Etler, 1996; Kidder and Durband, 2004; Durband *et al.*, 2005). However, the Nanjing fauna also incorporates at least one southern Chinese faunal element, *Stegadon* (Xu, 2002), throwing this conclusion into doubt.

Although Wood (1991) considered the Koobi Fora and Olduvai Gorge crania to represent separate species, few studies have addressed variation within the African sample. This may be due in part to the smaller number of crania found in Africa attributable to *H. erectus*. The addition of three new fossil specimens since 1998 from

Ethiopia and Kenya changes this picture and it may now be possible to examine temporo-geographic trends in African *H. erectus*.

Temporal variation

Chronological framework: In order to rigorously test for diachronic changes in *H. erectus*, it is necessary to first establish a fossil chronology. While a secure chronostratigraphic framework has been established for *H. erectus*-bearing sites at Olduvai Gorge, East and West Turkana and Dmanisi in East Africa and Georgia, the situation at many Asian sites is less clear cut. Many of the Javanese fossils were recovered by local inhabitants *ex situ*, further complicating attempts to determine both relative and actual ages for these fossils. In general, the oldest *H. erectus* fossils are from eastern (Koobi Fora) and possibly southern Africa (SK 847) and from Dmanisi, Georgia. Many of these fossils are older than 1.5 Myr. Fossils closer to 1 Ma are from East Africa (OH 9, Daka, Buia and Olororgesailie) and the Sangiran dome. Middle Pleistocene *H. erectus* are best known from Zhoukoudian, China, though numerous other Chinese sites are of similar age or older. It is possible that fossils from Ngandong and Sambungmacan are also of Middle Pleistocene age, although most evidence supports a late Pleistocene age (at least for Ngandong).

Pliocene / Early Pleistocene *Homo*: Several of the fossils from sites in East (ER 730, 3733 and 3883) and West (WT 15000) Turkana are well-dated to the early Pleistocene (Feibel *et al.*, 1989; Brown and McDougall, 1993) ER 3733, originally thought to be

1.78 Ma (Feibel *et al.*, 1989) was recently redated to 1.65 Ma on the basis of a revised stratigraphy (Gathogo and Brown, 2006). However, this younger date was recently criticized on the basis of paleomagnetic stratigraphy by Feibel *et al.* (2007). A thick-walled occipital fragment with an occipital torus from Koobi Fora, ER 2598) may represent the first appearance of *H. erectus* at 1.88-1.9 Ma (Wood, 1991), but could also represent another species such as *H. rudolfensis*. A recent find by Leakey *et al.* (2003), ER 42700, is also assigned an early Pleistocene age of 1.5 Ma, despite the much smaller size of its calvaria compared to the similarly aged ER 3883, WT 15000 and OH 9. The partial cranium SK 847 from Swartkrans, often assigned to African *H. erectus* (Clarke *et al.*, 1970; Clarke and Howell, 1972; Clarke, 2000a; Groves and Mazák, 1975; Tobias, 1978; Walker, 1981 but see Grine *et al.*, 1996), is around 1.7 Ma (Delson, 1984, 1988; Brain, 1993). Since 1991, the site of Dmanisi, Georgia has yielded four mandibles and four crania (plus postcranial specimens) that have been attributed to *H. erectus* (Gabunia and Vekua, 1995; Gabunia *et al.*, 2000b; Vekua *et al.*, 2002; Rightmire *et al.*, 2006). This site has been dated to the earliest Pleistocene (Gabunia *et al.*, 2000b; Gabunia *et al.*, 2002). Later early Pleistocene specimens found in East Africa, including the two from Olduvai Gorge (OH 9, ~1.4 and OH 12, ~1.1 Ma; Hay, 1990; Delson and van Couvering, 2000), the new partial calvaria from Olororgesailie (0.9 Ma, Potts *et al.*, 2004) and the two specimens from the Afar triangle – Buia and Daka, both around 1 Ma (Abbate *et al.*, 1998; Asfaw *et al.*, 2002).

Early Pleistocene sediments in the Sangiran dome have also yielded fossil hominin remains, though many are fragmentary. The upper “Black Clays” of the Sangiran (Pucangan) Formation are either just over 1 Ma or older than 1.5 Ma (Itihara *et*

al., 1994; Larick *et al.*, 2001). The best-preserved cranial specimen from these layers is Sangiran 4 (S 4) which consists of a rear neurocranium and separate lower face.

Early / Middle Pleistocene: Overlying the Sangiran Formation in the Sangiran dome (Central Java) is the Bapang (Kabuh) Formation. Because most Sangiran dome hominins were not recovered in situ in controlled excavations it is difficult to order them stratigraphically as attested to by the numerous schemes presented in the literature (Pope, 1988; Itihara *et al.*, 1994; Larick *et al.*, 2001; Rightmire, 2004). There is also considerable disagreement about the age of these deposits and hence the age of most Javanese *H. erectus*. In particular, two different sets of dates have been proposed for the Sangiran dome which is the source of many cranial fossils including the very complete S 17 but also S 2, 3, 4, 10 and 12 as well as more recently described fossils from Grogol Wetan (Widianto and Grimaud-Hervé, 2000), Tanjung (Arif, 2005) and Sendangbusik / Bukuran (Widianto *et al.*, 1994; Grimaud-Hervé *et al.*, 2005). With the exception of S 4, and possibly Hanoman 1 from the Sendangbusik / Bukuran region, all of these fossils are thought to be from the younger Bapang (Kabuh) Formation. Faunal correlation (de Vos, 1985; van den Bergh *et al.*, 2001), paleomagnetism (Hyodo *et al.*, 1993, 2002; Itihara *et al.*, 1994), fission-track dating (Suzuki *et al.*, 1985) and the recognition of Australasian strewnfield tektites (Itihara *et al.*, 1985, 1994) have converged on a range of dates for the Sangiran dome hominins between about 1.0 and 0.7 Ma. Earlier dates have been proposed by Swisher (1997) and Larick *et al.* (2001) which place the fossil hominins between 1.5 and 1.0 Ma by based on $^{40}\text{Ar} / ^{39}\text{Ar}$ dates from hornblende samples. Supporters of the earlier chronology have criticized the paleomagnetic and fission-track

results on methodological grounds (Swisher et al., 1994; Antón, 2003; Bettis et al., 2004) and the paucity and provenance of tektites in the lithostratigraphic record (Antón, 2003; Bettis et al., 2004).

Similarly, two different chronologies have been proposed for Modjokerto (Perning). A very early $^{40}\text{Ar} / ^{39}\text{Ar}$ date of 1.8 Ma was reported for a layer just above the Parning I juvenile fossil calvaria by Swisher *et al.* (1994). This date was criticized as incompatible with the faunal (de Vos and Sondaar, 1994) and tektite records (Langbroek and Roebroeks, 2000) and a date of less than 1 Ma was suggested by the latter study. The location of the Parning I find site has also been questioned (Huffman *et al.*, 2006).

These two viewpoints, that some hominins in Java may be older than 1.5 Ma or they are all younger than 1 Ma, are not compatible and suggest very different scenarios for early hominin migrations. If the earlier ages are accepted, then many African and Asian *H. erectus* populations overlapped in time. The more recent set of ages suggests that most African *H. erectus* existed prior to the Javanese *H. erectus*. The observation that the earliest dentognathic remains from the Sangiran formation are more primitive in their morphology than the East Turkana *H. erectus* fossils (Kaifu *et al.*, 2005) may support an early Pleistocene arrival of hominins in Java, though whether the first hominins were *H. erectus* or an earlier species of *Homo* is yet unknown (Robinson, 1953; Tobias and von Koenigswald, 1964; Krantz, 1975; Howell, 1978; Franzen, 1985; Clarke, 1990; Swisher *et al.*, 1994; White, 1995; Wang and Tobias, 2001; Asfaw *et al.*, 2002; Dennell and Roebroeks, 2005).

Middle Pleistocene: While the best-known Chinese *H. erectus* fossils from the northern Chinese site of Zhoukoudian have traditionally been assigned to the later Pleistocene (400 to 280 Ka; Yuan et al., 1991; Grün et al., 1997), the most recent dating evidence based on U-series dating of speleothems rather than fossil teeth or antlers has pushed the dates back to between 800 and 400 Ka (Shen and Jin, 1991; Shen et al., 2001). The older dates of Shen and colleagues are better technically because the use of speleothems requires less assumptions than U-series or ESR dating of enamel or antler. This suggests that the Zhoukoudian hominins either overlapped the Sangiran hominins in time or were younger, depending on which set of dates are applied for Java. As is well known, most Zhoukoudian fossil hominins were lost during World War II but excellent casts are available at the American Museum of Natural History.

Numerous other sites in China have yielded *H. erectus* fossils, but they are not as accessible to researchers. Some very fragmentary cranial, dental and postcranial fossils were recovered from Yiyuan, also located in the north and dated to around 440 Ka by faunal correlation (Lu et al., 1989). Well-preserved partial crania have been uncovered from Hexian (Huang et al., 1982; Wu et al., 2006) and Nanjing (Wu et al., 2002a; Liu et al., 2005), both located ca. 900 km southeast of Zhoukoudian. ESR / U-series dating work suggested a middle Pleistocene age of 400 ka for Hexian (Grün et al., 1998) and although initial age estimates for Nanjing were similar (~350 ka, Chen et al., 1996), more recent thermal ionization mass spectrometric (TIMS) dates on speleothems and amino acid racemization of fossil mammal teeth have concluded that the fossils are older than 500 or 580 ka and may be in the range of 638-624 ka (Wang et al., 2002; Liu et al., 2002; Zhao et al., 2001). These sites may therefore overlap in time with Zhoukoudian. Further

west, sites in Lantian county (Gongwangling and Chenjiawo) (Wu and Poirer, 1995; Brown, 2001) and at Yunxian (Li and Etler, 1992) have also yielded fossilized crania and mandibles attributed to *H. erectus*. There are a wide range of dates assigned to Gongwangling from ~750 ka to 1.15 Ma (An and Ho, 1989; Wu *et al.*, 1989; An *et al.*, 1990) which makes this one of the oldest Chinese *H. erectus* sites. Chenjiawo is younger than Gongwangling. The middle Pleistocene fauna of Yunxian appears consistent with the ESR date of 581 ka from tooth enamel (Li *et al.*, 1991; Chen *et al.*, 1997). Two central upper incisors which may be *H. erectus* have been found at the southern Chinese site of Yuanmou (Zhou and Hu, 1979). While the site of Yuanmou is important because it may be as old as 1.7 or 1.3 Ma (paleomagnetism and ESR; Qing, 1985; Qian *et al.*, 1991), the possibility that these teeth represent a hominin other than *H. erectus* cannot be ruled out, and there are also issues with the stratigraphy and exact provenience of the incisors (Brown, 2001). Similarly, the affinities of the fossils from Yiyuan and Yunxian may belong with later “archaic” *Homo* from China like Dali or Jinniushan (Wu and Poirer, 1995; Zhang, 1998). Archaeological sites from both northern (Nihewan basin) and southern (Bose basin) China appear to be securely dated to 1.66-1.1 and 0.8 Ma, respectively (Hou *et al.*, 2000; Zhu *et al.*, 2001, 2004). As no hominin remains have yet been uncovered, it would be premature to assume these sites represent the presence of *H. erectus* and not earlier or later *Homo*. Taken together, the evidence for an early Pleistocene *H. erectus* presence in China is weak.

Middle /Late Pleistocene: The best evidence for late Pleistocene *Homo* comes from Java at the site of Ngandong, though fossils from Sambungmacan and Ngawi may also be of

similar age. The fossils from Ngandong appear to represent the latest surviving representatives of *H. erectus*, especially if the date of 53-27 ka proposed by Swisher *et al.* (1996) is true. The very young age range of 53-27 ka was based mainly on ESR dating of bovid teeth. U-series dating provided older ages, but this was attributed to a loss of uranium from the teeth late in their burial history (Swisher *et al.*, 1996, but see Grün and Thorne, 1997). These dates are supported by earlier U-series dates of 101 to 31 ka obtained from fauna from the site of Ngandong by Bartstra *et al.* (1988).

However, some workers contend that the Ngandong fossils are not contemporaneous with the surrounding fauna and may be of middle Pleistocene age (Santa Luca, 1980; Grün and Thorne, 1997; Westaway *et al.*, 2003). They stress that the taphonomy of the Ngandong hominins differs in color and texture from the nearby fossil fauna, suggesting they are not the same age. However, Von Koenigswald (1951, p. 218) stated that the hominins were contemporaneous on the basis of “their preservation which is exactly the same as in the numerous animal bones found in the same deposit.” He based on this observation on the original fauna found with the Ngandong hominins which has since disappeared. This contention is supported by Bartstra *et al.* (1988) and Swisher *et al.* (1996) who argue further that the probability of so many hominin fossils being reworked without other contemporaneous, faunal elements is highly unlikely. However, Dennell (2005) and Dennell and Roebroeks (2005) find it equally unlikely that cranial elements would comprise such a high frequency of the total hominin remains unless they were preferentially relocated by fluvial transport, making them older than their surrounding deposits. While Rightmire (1990) notes a lot of surface abrasion, possibly

the result of water transport, Swisher *et al.* (1996) note that the preservation of delicate structures like the pterygoid plates argue against extensive water transport.

If, as appears likely, the Ngandong calvaria were found in situ, then they are of Late Pleistocene age (though how late continues to be a source of contention) (Table 4.3). If, however, they were re-deposited in the High Terraces from older deposits, then their age would remain unknown. The Ngawi calvaria may also derive from terraces of the same age as Ngandong, although it could also be from the Kabuh Formation (Sartono, 1990). While a tooth from the Sambungmacan 1 (Sm 1) find site was also dated to between 50 and 32 ka by Swisher *et al.* (1996), the provenance of this tooth has been questioned (Matsu'ura *et al.*, 2000) and the other two Sambungmacan calvaria are of unknown age (Delson *et al.*, 2001; Baba *et al.*, 2003; Rightmire, 2004).

Diachronic change

Given the long time span of *H. erectus*, there is great potential for anagenetic change to have occurred within this species. However, in contrast to geographic variation, it has been more difficult to detect temporal trends within *H. erectus*. The most obvious temporally mediated development was the increase in cranial capacity through time (Wolpoff, 1984; Leigh, 1992; Antón and Swisher, 2001; Rightmire, 2004). There has been no systematic attempt to correlate the increase in endocranial volume with morphological change in the cranium, although Antón (2003) has speculated that an increase in vault height and in minimum frontal breadth resulted from increasing brain size, at least within the Indonesian sample.

In addition to an increase in endocranial capacity, there is also limited evidence of additional diachronic changes in cranial morphology including a decrease in postorbital constriction, a narrowing of the glenoid fossa and an increase in the antero-posterior length of the parietal bone (Bräuer, 1994). There was also apparent anagenetic change in several features associated with the temporomandibular joint (tmj). In particular, Picq (1990) recognized a sequence from early *Homo* through a 'pre-*erectus*' group (ER 3733, 3883 and 1805) that was further continued in *H. erectus* (beginning with OH 9 and on through Indonesia, up to Ngandong). The postglenoid process became reduced in size, the glenoid fossa became antero-posteriorly constricted and the anterior wall of this fossa became long and antero-inferiorly sloping. This general pattern did not, however, apply to *H. erectus* from Zhoukoudian.

Aside from alterations in the tmj, there is not strong evidence of any temporal trends within Africa, though this may change with the addition of recently described fossils (Antón, 2003). Within Indonesia, diachronic change occurred from the Sangiran to the Ngandong / Sambungmacan calvaria. These changes included an increase in the size of the mastoid processes, a higher frequency of a glabellar depression and the presence of a supramastoid sulcus became a fixed trait (Antón, 2003). Wolpoff (1999) described Sm 1 as intermediate between the Sangiran hominins from the Kabuh layers and the Ngandong / Ngawi sample. In the latter populations he observed the development of a lateral frontal trigone (a triangular flattening of the frontal squama posterior to the lateral corner of the supraorbital torus) and an expansion of both the frontal (resulting in a less receding frontal squama and narrower medial supraorbital

torus) and occipital regions. The size of the upper plane of the occipital also increased in proportion to the lower plane, and the transverse occipital torus increased in size.

There were also changes between the Early and Middle Pleistocene Javanese populations that were not continued into the Late Pleistocene, like an increase in basal pneumatization (Wolpoff, 1999). Changes in the dentition and mandibles of hominins from the Sangiran dome were documented between samples from the Sangiran and the Bapang Formations, with the earlier samples being quite primitive for *H. erectus* while the later population resembled later *H. erectus* (Kaifu *et al.*, 2005). Based on these observations, they argued that the first hominin migrants into Java were not descended from early African *H. erectus* (i.e., from East Turkana) but rather from an even less derived form of *H. erectus* (like that seen at Dmanisi). Either *in situ* anagenetic change produced the observed differences or population replacement occurred.

Size variation

As discussed previously, it is difficult to determine sex for the majority of the fossil specimens because temporal and geographic variation can easily be mistaken for sexual variation. Thus, while variations within the East Turkana, Sangiran, Ngandong and Zhoukoudian sites have been attributed to sexual differences (e.g., Weidenreich, 1943; Santa Luca, 1980; Wolpoff, 1999), these conclusions must be viewed cautiously. One exception is the site of Dmanisi, where the hominin-bearing sediments were deposited in a relatively short period of time and the fossils therefore constitute a single population (Gabunia *et al.*, 2000b; Rightmire *et al.*, 2006). A high degree of size

variation in the size of the mandible has been observed; D 2600 is very large compared to the other Dmanisi mandibles, suggesting a high degree of sexual dimorphism in this population (Gabounia *et al.*, 2002; Skinner *et al.*, 2005). In general, cranial superstructures like supraorbital, occipital and angular tori as well as mastoid and supramastoid crests are more strongly developed in presumed males than females (Wolpoff, 1999; Marquez *et al.*, 2001).

By comparing smaller to larger crania, the problem of assigning sex is avoided, although allometric effects may also be responsible for observed differences. This tack was taken by Rightmire (1990) who found overall similarities among smaller-brained specimens from Africa and Indonesia versus large-brained fossils from Africa, Indonesia and China. Within Indonesia, small-brained fossils differed in a small number of features from the large-brained specimens, regardless of age (Sartono, 1975; Antón, 2002). These findings are in agreement with recent work that highlighted the effect of size on certain aspects of cranial shape often used to define *H. erectus*, like occipital angulation, cranial bone thickness and degree of postorbital constriction (Sporer *et al.*, 2005). The work by Spoor *et al.* (2005) is the first systematic attempt to quantify character variation as an effect of size, but further work is needed as there is a great deal of size variation encompassed not just in *H. erectus s.l.* but in both the Dmanisi and Javan *H. erectus* samples. Compared to geographic and temporal variation, less attention has been paid to size-related variation.

Materials

3D landmark data were acquired from original *H. erectus* cranial fossils in Africa and Indonesia and from casts of the Zhoukoudian fossils. See Table 4.1 for sample details. Casts were also used for Sangiran 12, 17, Ngawi, D 2280, 2700 and 3444 (Dmanisi) the originals of which were unavailable for study. The reconstruction of Zhoukoudian by Tattersall and Sawyer (1996) was used only in the analysis of facial morphology as there are no complete faces in the Zhoukoudian sample. This specimen is an amalgam of the neurocranium (including the supraorbital torus) of Zkd 12 and facial fragments from several other individuals. Zkd 12 is one of the larger specimens from the Zhoukoudian collection and all facial fragments used in the reconstruction were also relatively large (Tattersall and Sawyer, 1996). The very young individual from Mojokerto (=Peking) was not included in any analysis. The subadult WT 15000 was likely less than 12 years of age and possibly as young as six or seven years at death (Smith, 1993, 1994; Dean *et al.*, 2001). Thus, WT 15000 was not included in most analyses but the affinities of this individual were evaluated separately. The age of Zkd 3 is unclear. It may be a young subadult (8-9 years of age) (Weidenreich, 1943), an older subadult (Black, 1929, 1931; Antón, 2001) or an adult (Mann, 1971). It was therefore included in analyses when possible, but its possible subadult status must be kept in mind when discussing this specimen. Ceprano was not examined as the results of Chapter 3 suggested that it was better viewed as a member of a later species of *Homo*. ER 42700 also did not share close resemblances to *H. erectus* but its taxonomic affinities remain very unclear. Also, the sphenoccipital synchondrosis of ER 42700 is nearly fused so that it likely represents an older subadult or young adult (Leakey *et al.*, 2003). Therefore,

this fossil was not generally included in analyses but was evaluated separately to clarify how its cranial shape compared to *H. erectus*.

Sample composition

I endeavored to maintain approximately equal sample sizes from each region in any particular time band so as not to bias the analyses. The Ngandong (=Solo) series of calvaria are both numerous and well-preserved. As a result there were often a disproportionately large number of specimens from this site (four or five) which could be incorporated into any given analysis. In contrast, there were usually only one or two well-preserved specimens from the other temporogeographic samples (i.e., East Turkana,

Table 4.1: List of fossil specimens used in this study and their respective cranial capacities.

Region	Specimen	Cranial Capacity (cm ³)	Correction for Subadult Status
Africa	ER 3733	848 ¹	909 ²
	ER 3883	804 ¹	
	ER 42700	N/A	
	WT 15000	880 ²	
	OL 45500	N/A	
	OH 9	1065 ³	
	Daka	995 ⁴	
Georgia	D 2280	775 ⁵	612 ⁸
	D 3444	650 ⁶	
	D 2700	600 ⁷	

China	Zkd 3	915 ⁹
	Zdk 5	1140 ⁹
	Zdk 11	1015 ⁹
	Zkd 12	1030 ⁹
Early Indonesia	S 2	813 ¹⁰
	S 4	908 ¹⁰
	S 12	1059 ¹⁰
	S 17	1004 ¹⁰
Late Indonesia	Sm 1	1100 ¹¹
	Sm 3	917 ¹²
	Ng 6	1251 ¹³
	Ng 7	1013 ¹³
	Ng 10	1135 ¹³
	Ng 11	1172 ¹³
	Ng 12	1090 ¹³
	Ngawi	1000 ¹⁴

1, Holloway, 1983; 2, Begun and Walker, 1993; 3, Holloway, 1973; 4, Asfaw *et al.*, 2002; 5, Gabunia *et al.*, 2000b; 6, Lordkipanidze *et al.*, 2006; 7, Vekua *et al.*, 2002; 8, Rightmire *et al.*, 2006; 9, Weidenreich, 1943; 10, Holloway, 1981a; 11, Jacob, 1975; 12, Marquez *et al.*, 2001; 13, Holloway, 1980; 14, Widiyanto and Zeitoun, 2003

Dmanisi, Zhoukoudian, Sangiran and Sambungmacan). Therefore, to avoid biasing the relationships between cranial shape and age or size (because the Ngandong fossils are among the youngest and largest *H. erectus* crania), only two specimens from each temporogeographic sample were included. Because the greatest source of variation within a single population is sexual variation, when more than two Ngandong specimens were sufficiently preserved to be included in the same analysis, only the largest (Ng 6) and smallest (Ng 12 or 7) specimen available were used. Ng 7 was smaller than Ng 12 but was only complete enough to include in the occipital profile analysis. Different combinations of two Ngandong specimens resulted in very similar results, the biggest difference being greater overlap of Daka with the Indonesian specimens (particularly S

17) when Ng 6 was not included. When more than two specimens from either Zhoukoudian or Dmanisi were incorporated into the analysis, then Ng 10 was also included. The use of Ng 10 or 11 did not change the results in any meaningful way.

Methods

Data acquisition

Geometric morphometric methodologies were applied to 3-D data in order to explore cranial shape variation within *H. erectus*. Multivariate analyses of linear measurements are equivalent to “classic comparative anatomy with metric summaries substituted for qualitative, ‘by eye’ assessments of ... anatomies” (Albrecht and Miller, 1993, p. 128). The use of 3D geometric morphometric data is fundamentally the same, but it retains the original geometry of the specimen, and it is therefore possible to visualize the results of the statistical analysis (Adams *et al*, 2004).

A total of 131 midline and bilateral 3-D landmarks (such as standard osteometric points like bregma) were recorded from each cranial specimen with a Microscribe 3D-X digitizer. In addition, three midline and nine bilateral curves were recorded from each individual when possible. Each curve is a series of landmarks (termed semilandmarks) taken along a cranial contour like the midsagittal plane or along the temporal squama. For all specimens, each curve was then resampled to the same number of semilandmarks using weighted linear interpolation. The landmark protocol included landmarks and curves from all regions of the vault, face and base and was similar to landmark sets employed by Frost *et al*. (2003), Harvati *et al*. (2004) and McNulty *et al*. (2006). Not all

landmarks were analyzed. One landmark (metopion) was not collected as a separate landmark but rather was calculated as the midpoint of the ‘curve’ taken between glabella and bregma. See Table 4.2 for a list of landmarks used here with definitions and abbreviations.

Landmark mirroring and reconstruction

While most *H. erectus* calvaria and crania preserve the cranial vault and the lateral basicranium (particularly the mastoid and tempormandibular joint [tmj] regions), the exact structures preserved vary among individuals. As in any morphometric analysis, only individuals with no missing data could be included in any analysis. Two strategies were invoked in order to maximize the number of specimens studied. First, missing bilateral landmarks were ‘mirrored’ and secondly, multiple different landmark configurations were examined.

Prior to superimposition by generalized Procrustes analysis (GPA, explained below), bilateral landmarks missing unilaterally were mirrored to the other side for all specimens. The procedure is straightforward. First, a ‘reflection’ is created for each specimen – this is a second landmark configuration where the midline landmarks are preserved as in the original but the right and left landmarks are reversed. In the second step the original and its reflection are superimposed by GPA. The reflected contralateral landmark is then substituted for the missing landmark in the original, creating a more complete landmark configuration. This step is particularly essential in including incompletely preserved fossil specimens. The remaining bilateral landmarks were then

averaged with their reflected configurations in order to minimize the effects of bilateral asymmetry, especially in fossil specimens (Bookstein, 1996; McNulty *et al.*, 2006).

Because landmark mirroring does assume a high degree of symmetry in the original specimens, adjustments to fossils exhibiting marked asymmetries due to taphonomic processes were necessary. In the case of WT 15000, plastic deformation of the cranium has resulted in a misalignment of the midline of the upper face, palate and the midsagittal plane of the neurocranium (Walker and Leakey, 1993). Therefore the facial landmarks inferior to the supraorbital torus, the right lateral supraorbital torus landmarks as well as right PN, AS and PT were removed so that the landmarks included in the GPA and subsequent mirroring steps were reasonably symmetrical. The final result was a relatively complete neurocranium where the removed bilateral landmarks were replaced with those from the opposite side. The supraorbital torus landmarks were also not symmetrical with regard to the midline for OL 45500. Therefore, those recorded on the left were deleted and mirrored from the right side. Similarly, ER 3883 suffered from plastic deformation (Wood, 1991), resulting in asymmetries of the left and right temporal and occipital bones. The left basal landmarks, as well as left PO, PN, AS and PT were deleted and mirrored from the right side.

As a result of the misalignment between the face and the remainder of the cranium in WT 15000, the facial landmarks for all four specimens in the “Face” analysis (WT 15000, ER 3733, S 17 and the 1996 reconstruction of Zhoukoudian (Tattersall and Sawyer, 1996)) were isolated and then mirrored and averaged separately from the neurocranium.

Although OH 9 is missing all midline landmarks on the superior neurocranium (lambda, bregma and metopion), the frontal squama is broken just anterior to bregma. Therefore, bregma was estimated as described in Chapter 2. A slightly different procedure was used for Zkd 5. Portions of both temporal bones were recovered in the mid-1930s and described by Weidenreich (1935, 1936/37, 1943). In 1966, members of the Institute of Vertebrate Paleontology and Paleoanthropology recovered both a frontal and an occipital bone that also belong to Zkd 5 (but see Schwartz and Tattersall, 2003). Together these form a nearly complete cranium lacking its superior aspect. While most of the frontal squama is present, the posterior border is not complete. This specimen has been reconstructed in the area, of bregma but no sutures are preserved. The midsagittal curve was recorded from glabella to the general region of bregma and Zkd 2, 3, 10, 11 and 12 were used only to estimate the position of bregma along this curve.

Generalized Procrustes analysis

GPA was used to remove variation due to location and orientation of the original specimens during data collection as well as scale (though shape variation related to size is not removed) (Rohlf, 1990; Rohlf and Marcus, 1993; O'Higgins, 2000; Adams *et al.*, 2004). GPA alignment works by first superimposing centroids at the origin and scaling all configurations to a unit centroid size. They are then rotated until the residual sum-of-squares can no longer be improved. This fit is accomplished through an iterative approach whereby all specimens are initially aligned to an individual specimen (which acts as a temporary average shape) using a least-squares approach, the average shape is

then recalculated and the specimens are realigned to this new average and scaled, and the preliminary residual sum-of-squares is calculated. This least-squares process is repeated until the differences in the residual sum-of-squares falls below a set tolerance level (Gower, 1975; Rohlf and Slice, 1990). The superimposed landmarks are then treated as (shape variables) in standard multivariate statistical analyses (Kent, 1994).

Study design

There were four geographic groups recognized in this analysis: Indonesia, China, East Africa and Georgia. In order to statistically investigate the effects of time on the fossil sample, specimens were assigned to one of five time bands of 400 kyr each from 2.0 Ma to the present. Although there is uncertainty regarding the age of some sites, each specimen was assigned to a single time band based on evaluation of the available data (Table 4.3) and centroid size was calculated for all individuals in each analysis. Centroid size is the square root of the sum of the squared distances between all landmarks and their centroid (Slice *et al.*, 1996) and acts a multivariate proxy for size (Bookstein, 1996).

Cranial capacity was initially included as a fourth independent variable, but it accounted for similar shape variation as did geological age and centroid size. Therefore, only limited results relating to the effect of cranial capacity are reported. Data on cranial capacity was culled from the literature. For the composite Zhoukoudian reconstruction, the cranial capacity for Zkd 12 was used, as this was the neurocranium used in the reconstruction. See Table 4.1 for details.

Table 4.2: Landmarks and curves: definitions and abbreviations.

Landmark / Curve	Abbr.	Definition	Ref.
<i>Dorsal Landmarks</i>			
Inion	IN	point at which the superior nuchal lines merge in the external occipital protuberance (or linear tubercle)	2
Lambda	LA	the apex of the occipital bone at its junction with the parietals, in the midline	1
Bregma	BR	posterior border of the frontal bone in the midline;	1
Midline post-toral sulcus	PTS	minima of concavity on midline post-toral frontal squama	6
Glabella	GL	most anterior midline point on the frontal bone, usually above the frontonasal suture	2
Nasion	NA	the intersection of the fronto-nasal suture and the median plane	1
Alveolare	AL	midline point at the inferior tip of the bony septum between the upper central incisors	2
Alare	ALR	the most lateral point on the margin of the nasal aperture	2
Zygoorbitale	ZO	point where the orbital rim intersects the zygomaticomaxillary suture	2
Dacryon	DA	point where the lacrimomaxillary suture meets the frontal bone	2
Supraorbital notch	SON	point of greatest projection of notch into the orbital space, taken on the medial side of the notch	6
Frontomalare temporale	FMT	point where the frontozygomatic suture crosses the temporal line (or outer orbital rim)	2
Frontomalare orbitale	FMO	point where the frontozygomatic suture crosses the inner orbital rim	2

Mid-torus inferior	MTI	point on inferior margin of supraorbital torus roughly at the middle of the orbit (on superior margin of orbit)	3
Mid-torus superior	MTS	point on superior aspect of supraorbital torus, directly above mid-torus inferior on anterior aspect of torus	3
Anterior pterion	AP	where coronal suture intersects sphenofrontal or sphenoparietal suture	
Jugale	JG	the point in the depth of the notch between the temporal and frontal processes of the zygomatic	2
Porion	PO	uppermost point on the margin of the external auditory meatus	2
Auriculare	AU	a point vertically above the center of the external auditory meatus at the root of the zygomatic process	2
Malar root origin	MR	point where malar root arises from the maxilla (often a point of convexity between malar juga and malar root)	6
Frontotemporale	FT	the point where the temporal line reaches its most anteromedial position on the frontal	2
Parietal notch	PN	on posterosuperior border of the temporal where the squamosal and parietomastoid sutures meet	2
Asterion	AS	the common meeting point of the temporal, parietal, and occipital bones, on either side	1
<i>Ventral Landmarks</i>			
Opisthion	OP	midline point at the posterior margin of the foramen magnum	2
Tympanomastoid junction	TM	point where tympanic tube and mastoid fissure meet laterally	
Medial petro-tympanic crest	MPT	most medial point of petrotympanic crest at level of carotid canal	5

Lateral petro- tympanic crest	LPT	lateral origin of petrotympanic crest	5
Stylomastoid foramen	SF	posterior border of stylomastoid foramen	4
Postglenoid	PG	Infero-lateral most point posterior to glenoid fossa and anterior to ectotympanic tube (corresponds to postglenoid process)	3
Entoglenoid	EG	most inferior point on the entoglenoid pyramid	4
Lateral articular foss	LAF	deepest point on the lateral margin of the articular eminence	4
Center of mandibular fossa	CMF	the intersection of the perpendicular axes through the longest and widest parts of the mandibular fossa	
Medial squamo- tympanic fissure	MST	intersection of squamotympanic fissure with medial edge of mandibular fossa	
Lateral squamo- tympanic fissure	LST	Intersection of squamotympanic fissure with lateral edge of mandibular fossa	
Foramen spinosum	FS	point on posterior margin of foramen spinosum	
Temporospheno- id suture	TS	point where temporospheno- id suture passes from squama to cranial base (often on infratemporal crest)	
Lingual canine margin	LC	most lingual aspect of canine alveolar process	6
M1-M2 contact	M1-2	point of contact projected onto buccal alveolar margin	3
M2-M3 contact	M2-3	point of contact projected onto buccal alveolar surface	6
Metopion	ME	point midway between glabella and bregma in midline, calculated <i>a postieri</i>	2

Curves

Midsagittal Frontal Profile	MFP	from bregma to glabella along midline
Midsagittal Occipital Profile	MOP	from lambda to opisthion along midline
Superior Frontal Torus	SFT	from frontomalarotemporale to midline, along the supero-anterior edge of the frontal torus

¹ Howells, 1973 ² White and Folkens, 2000 ³ Frost, 2001 ⁴ Harvati, 2001 ⁵ Harvati, 2003 ⁶ McNulty, 2003

Because an individual could only be included in an analysis if all landmarks were preserved, several different landmarks sets were designed to maximize fossil inclusion. The neurocranial landmark sets capture the overall shape of the vault including the supraorbital torus. There were four regional analyses which focus on the frontal bone, temporal base, occipital profile and the facial skeleton. The fossil samples for each landmark set differ based on individual fossil preservation. Tables 4.4 and 4.5 provide details on the composition of samples and landmarks in each analysis. Within the neurocranial and frontal bone analyses, individual landmarks were excluded in order to accommodate additional specimens. Results were reported for each landmark set separately, but interpretations of geographic, anagenetic and size-related variation were based on the combined results of these analyses.

Table 4.3: Geological time bands for *Homo erectus* sites / specimens (preferred ages Outlined).

Site / Specimen	Time Band 1: <2.0 -1.6	Time Band 2: <1.6 - 1.2	Time Band 3: <1.2 - 0.8	Time Band 4: <0.8 - 0.4	Time Band 5: <0.4
ER 3733	1.78 ¹ or 1.65 ²				
Dmanisi	1.77 - 1.81 ³⁻⁷				
ER 3883		1.57 ¹			
WT 15000		1.56-1.51 ⁸			
S 4		>1.5 ⁹	1.07-0.99 ^{10, 11}		
ER 42700		1.5 ¹²			
OH 9		1.48-1.33 ¹³			
S 17		1.3-1.24 ¹⁴	0.99 - 0.78 ^{10, 11}		
S 12			1.2-0.98 ¹⁴	~0.78 ¹⁰	
S 2			1.2-0.98 ¹⁴	~0.78 ¹⁰	
Daka			~1.0 ¹⁵		
OL 45500			0.97-0.9 ¹⁶		
Zhoukoudian (all but 5)				0.6-0.4 ¹⁷ or 0.8-0.6 ¹⁸	
Zkd 5				>0.4 ¹⁸	0.29 ¹⁹
Sambungmacan			~1.0 (Kabuh or Jaramillo) ²⁰⁻²²	<0.78 (Bruhnes) ²⁰	0.05-0.032 ²³
Ngawi			Kabuh ²⁴	Kabuh ²⁴	High Terraces (same age as Ngandong) ²⁴
Ngandong				Middle Pleistocene ²⁵	0.05-0.032 ²³ or 0.1 ²⁶

1, Feibel *et al.*, 1989; 2, Gathogo and Brown, 2006; 3, Gabunia *et al.*, 2000b; 4, Gabounia *et al.*, 2002; 5, Vekua *et al.*, 2002; 6, de Lumley *et al.*, 2002; 7, Lordkipanidze *et al.*, 2006; 8, Brown and McDougall, 1993; 9, Antón, 2003; 10, Itihara *et al.*, 1994; 11, Hyodo *et al.*, 1993, 2002; 12, Leakey *et al.*, 2003; 13, Delson and van Couvering, 2000; 14, Larick *et al.*, 2002; 15, Asfaw *et al.*, 2002; 16, Potts *et al.*, 2004; 17, Grun *et al.*, 1997; 18,

Shen et al., 2001; 19, Yuan et al, 1991; 20, Jacob et al., 1978; 21, Matsu'ura et al., 2000; 22, Baba et al., 2003; 23, Swisher et al., 1996; 24, Sartono, 1990; 25, Santa Luca, 1980; 26, Bartstra and Baoseki, 1989

Table 4.4: Neurocranial analyses: composition of samples and landmark sets.

Analysis	Fossils	Landmarks ¹
Original	ER 3733, ER 3883, Daka, D 2280, Zkd 11, Zkd 12, S 17, Ng 12, Ng 6, Sm 3	IN, LA, BR, MET, PTS, GL, SON, FMT, FMO, AP, PO, AU, FT, PN, AS, OP, TM, PG, EG, TS ²
Dmanisi	+ D 3444, D 2700, Ng 10 ³	
ER 42700	+ ER 42700, D 2700	- MET ⁴
Zhoukoudian	+ Zkd 3, 5, Ng 10	- OP, TS
Ngawi	+ Ngawi	- PG
OH 9	+ OH 9	- LA, AP
WT 15000, S 2, Sm 1	+ WT 15000, S 2, Sm 1	- MET, PTS, GL, SON

1, Abbreviations refer to Table 4.2.

2, See Figure 4.1 for an illustration of the original neurocranial landmark set.

3, + indicates the addition of these fossils to the original sample.

4, - indicates the exclusion of these landmarks from the original landmark set.

Table 4.5: Regional analyses: composition of samples and landmark sets.

Analysis	Fossils	Landmarks ¹
Frontal	ER 3733, ER 3883, Daka, OL 45500, D 2280, Zkd 3, Zkd 5, Zkd 11, Zkd 12, S 17, Sm 3 ² , Ngawi, Ng 6, Ng 12	BR, GL, NA, FMT, FMO, MTI, AP, FT twelve semilandmarks ³
OH 9 Frontal	+ OH 9 ⁴	- AP ⁵
Temporal Base	ER 3883, Daka, OH 9, D 2280, Zkd 3, Zkd 5, Zkd 11, S 2, S 4, S 17, Sm 1, Ng 6, Ng 12	TM, MPT, LPT, SF, PG, EG, LAF, CMF, MST, LST, TS ⁶

Occipital	ER 3733, ER 3883, Daka, D 2280, Zkd 11, Zkd 12, S 2, S 4, S 12, S 17, Sm 1, Sm 3, Ngawi, Ng 6, Ng 7	LA, OP Eight semilandmarks ⁷
Facial	ER 3733, WT 15000, Zkd reconstruction, S 17	NA, AL, ALR, ZO, DA, FMT, FMO, MTI, MTS, JG, MR, LC, M1-2, M2-3 ⁸

1, Abbreviations refer to Table 4.2.

2, Nasion was taken at the broken inferior edge of the frontal bone but may be slightly superior to the actual frontonasal suture.

3, Six evenly spaced semilandmarks were resampled from the MFP curve and three each were resampled from the left and right SFT curves. See Figure 4.17.

4, + indicates the addition of these fossils to the Frontal sample.

5, - indicates the exclusion of these landmarks from the Frontal landmark set.

6, See Figure 4.23.

7, Eight semilandmarks were resampled from the MOP curve between lambda and opisthion (see Figure 4.27).

8, See Figure 4.30.

Both the frontal and occipital bone analyses included semilandmarks and landmarks. For the frontal bone analysis, the semilandmarks were resampled from two curves: the midsagittal frontal profile (MFP) and the superior supraorbital torus (SFT, left and right). MFP was resampled to eight semilandmarks, including glabella and bregma. SFT right and left were resampled to five semilandmarks each, which included frontomalarotemporale as the first landmark. Because the supraorbital curves ended at the midline which was also captured by the midsagittal line, the last of these five semilandmarks was dropped from each of the supraorbital curves. Because the curves included several ‘real’ landmarks (i.e., glabella, bregma, frontomalarotemporale), only 12 actual semilandmarks were used for a total of 25 landmarks and semilandmarks. The occipital bone analysis was focused exclusively on the curvature of the bone in the midline. The midline occipital profile (MOP) curve was taken from lambda to opisthion in the mid-sagittal plane. In addition to lambda and opisthion, eight semilandmarks were

analyzed that were evenly spaced between these two landmarks, for a total of 10 semilandmarks and landmarks.

Another set of analyses focused more specifically on variation within the restricted geographic portions of the hypodigm. Analyses that quantify and describe variation within the Asian part of the hypodigm are consistent with the work of Antón and colleagues using linear measurements (Antón, 2002; Antón *et al.*, 2002b; see Table 4.6). Very few studies have examined variation within the African fossil sample, likely due to the smaller sample size. However, with the addition of newly described fossils from Africa and Georgia (see Table 4.7), the temporal and possibly geographic patterns of shape variation in early *H. erectus* can be explored.

Table 4.6: Asian neurocranial analyses: composition of samples and landmark sets

Analysis	Fossils	Landmarks ¹
Indonesian	Zkd 11, 12, S 2, 17, Ng 6, 12, Sm 1, 3	OP, IN, LA, BR, FMO, FMT, FT, AP, PO, AUR, TM, EG, PG, PN, AS, TS
Zhoukoudian	Zkd 3, 5, 11, 12, S 17, Ng 6, 11, 12, Sm 3	IN, LA, BR, ME, PTS, GL, SON, FMO, FMT, FT, AP, PO, AUR, TM, EG, PG, PN, AS

1, Abbreviations refer to Table 4.2.

Table 4.7: Afro-Georgian neurocranial analyses: composition of samples and landmark sets.

Analysis	Fossils	Landmarks ¹
Original	ER 3733, ER 3883, Daka, D 2280, D 3444	IN, LA, BR, MET, PTS, GL, SON, FMT, FMO, AP, PO, AU, FT, PN, AS, OP, TM, PG, EG, TS
OH 9	+ OH 9 ²	- LA, AP ³
Subadult	+ WT 15000, D 2700, OH 9	- MET, PTS, GL, SON, LA, AP

1, Abbreviations refer to Table 4.2.

2, + indicates the addition of these fossils to the original sample.

3, - indicates the exclusion of these landmarks from the original landmark set.

Statistical analysis

TpsSmall (Rohlf, 2003) was used to test the correspondence between the datasets in Kendall's shape space and the Euclidean space which is tangent to Kendall's shape space at the mean configuration (Marcus *et al.*, 2000). The very tight correlations ($R^2 = 0.99999 - 1.0$) between the pairwise Procrustes distances (calculated in Kendall's shape space) and the pairwise Euclidean distances for all landmark sets described in Tables 4.5-4.8 permitted statistical analyses to be carried out in GPA space (*sensu* Slice, 2001, 2005).

Multivariate regression: The primary objective of this study is to examine the relative effects of geographic distance, anagenetic change and size on cranial shape variation in *H. erectus*. Unfortunately, the effects of geographic distance and geological age are difficult to separate because all of the African and Georgian specimens fall at the older end of the age spectrum, while all of the Asian fossils, with the exception of S 4 and S 17,

are younger (see Table 4.3). It is, however, possible to address whether temporal / geographic variation or size variation has a greater effect on *H. erectus* cranial shape. While older African and Georgian fossils are generally smaller compared to more recent Asian specimens, there are some notable exceptions to this trend. Sm 3, Daka and ER 42700 all represent small specimens at later time periods, while S 17 and OH 9 are older specimens that are fairly large.

Regressions of the coordinates of the superimposed landmarks on the four geographic groups (East Africa, Indonesia, China and Georgia - coded as dummy variables), geological age measured as millions of years before present (ln-transformed, based on the midpoint of each band) and centroid size (ln-transformed) were performed. The total variance remaining in the sample after the shape variables were adjusted for each independent variable was calculated and presented as a proportion of the total variance of the sample (the trace of the covariance matrix). Regressions were performed for all landmark sets. The angle (and cosines of the angle) between the vectors of regression coefficients for geological age and centroid size was reported in order to quantify the magnitude of correlation between these two factors. The vectors of regression coefficients are the beta coefficients from the separate regressions of the coordinates of the superimposed landmarks on log(geological age) and log(centroid size). The closer an angle is to 90°, or the smaller the cosine, the less correlated is the variance explained by the two factors. An angle closer to 0° indicates a positive correlation between the variance accounted for by each factor, while an angle closer to 180° is negatively correlated. If landmarks were removed in order to accommodate individual specimens, new regressions were performed and all results were reported.

Principal components analysis: Principal components analysis (PCA) was performed for each landmark set. PCA reduces the dimensionality of the data by rotating the original data (space coordinates) so that the new axes (principal components) are orthogonal to one another and are ordered by the amount of variance explained.

Multiple regression: Multiple regressions of the principal component scores were performed on $\ln(\text{geological age})$ and $\ln(\text{centroid size})$. In order to also examine the interaction between the two independent variables, the general linear model was used. The analysis results in both a probability associated with the F value for the overall model, as well as t-tests for the independent variables and their interactions.

Visualization

Regressions of the shape variables on the natural logs of geological age and centroid size were performed. In order to visualize the shape change associated with temporal or size variation, the vectors of regression coefficients were added to and subtracted from the consensus landmark configuration. This provides the shape at the extremes of the observed range of the independent variable at along the regression slope and provides an intuitive way of examining shape change associated with time or size.

In comparisons of the shape associated with each geographic region, the average of all specimens from a single region was compared to the average of all specimens from the other regions. This approach was deemed preferable to a comparison of the mean

from each region to the grand mean for all *H. erectus* fossils because the former method emphasized the small scale variations among geographic groups.

Shape variations along each principal component axis were not provided because they corresponded in large part to the differences illustrated in the geographic, temporal and allometric comparisons described above.

Results

Neurocranium

Original: The original neurocranial landmark set captured the cranial profile from glabella to opisthion, cranial breadth across anterior, middle and posterior cranial vault and the basic orientation of several basal temporal bone structures as illustrated in Figure 4.1. The fossil sample was representative of *H. erectus* geographic and temporal variation and was summarized in Table 4.4.

Geography explained 43% of variation in the Procrustes superimposed shape variables while geological age accounted for 21% and size for 13% (Table 4.8). Shape variation explained by age and size was correlated but not identical as indicated by the angle of 47° between their respective vectors of regression coefficients. The total variance accounted for by geographic and temporal variation was 55%; this indicates that geographic and temporal factors account for some of the same shape variance because this is less than 64% (the sum of the percentages accounted for by each variable independently).

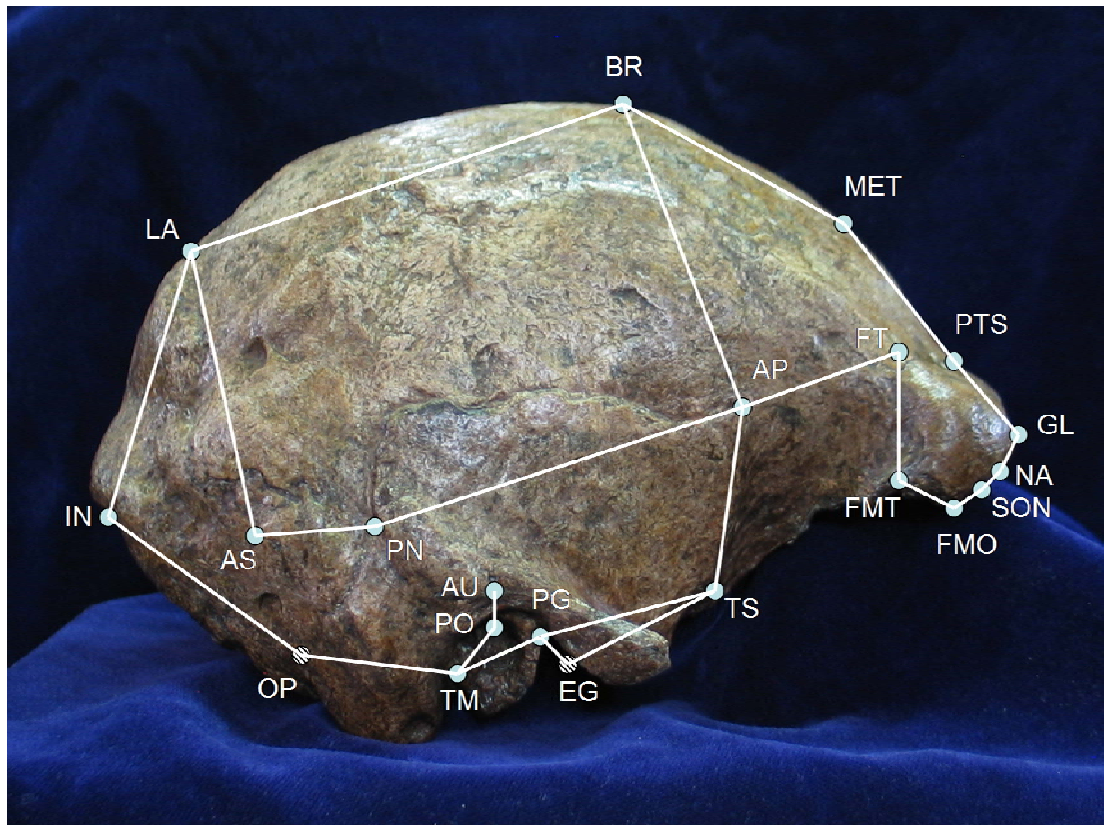
The youngest fossils from Indonesia grouped together at one end of PC 1 as seen in Figure 4.2. At the other end of the first component were the fossils from East Turkana and D 2280. While Daka, S 17 and the Zhoukoudian fossils occupy more intermediate positions on PC 1, the latter (Chinese specimens) are closer to the African / D 2280 end of the component while the former (Daka and S 17) are closer to the recent Indonesians. The proportion of variance accounted for by each component is listed in Table 4.9 for all neurocranial analyses. The ordering of these specimens did not perfectly mirror either the age or geographic origin of the fossils, although geological age did predict 70% of variation in PC 1 scores (see Table 4.9). Variation along the second PC was not easily interpreted in terms of any of the independent variables.

The differences among the African, Chinese and Indonesian fossils are illustrated in Figure 4.3. The African sample was distinct in having a less expanded frontal squama with less anterior projection at glabella, especially compared to the Indonesian sample. The African specimens also had relatively wider supraorbital tori. The more anteriorly positioned bregma and lambda and more inferiorly located opisthion resulted in longer upper and lower scales of the occipital. Both the entoglenoid and postglenoid processes were more posteriorly situated. The Chinese had a much more posteriorly projecting occipital at inion and a high relative position of inion, creating a longer occipital plane compared to the other groups. There was also greater width across the postglenoid and entoglenoid processes, as well as the temporosphenoid suture and auriculare. The supraorbital torus of both the Chinese and Indonesian groups is relatively narrow and it more down-turned laterally in the latter group. The Chinese also have a long frontal squama and short parietal squama as a result of the more posterior placement of bregma.

Table 4.8: Neurocranial analyses: proportion of total variance explained by geography, geological age and centroid size

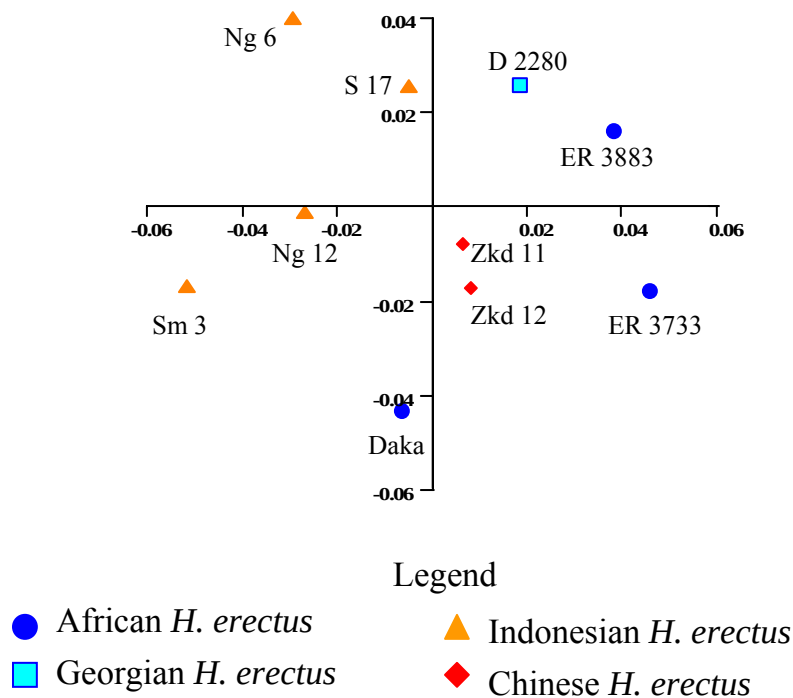
Factor	Original		Dmanisi		ER 42700		Zhoukoudian	
	Variance	% of Total	Variance	% of Total	Variance	% of Total	Variance	% of Total
Total	0.00369	100	0.00381	100	0.00403	100	0.00357	100.0
Geography	0.00159	43.2	0.00150	39.5	0.00148	36.8	0.00170	47.7
ln(geological age)	0.00078	21.1	0.00075	19.6	0.00069	17.2	0.00062	17.3
ln(centroid size)	0.00046	12.5	0.00055	14.5	0.00055	13.7	0.00030	8.5
Geog. & ln(geol. age)	0.00204	55.2	0.00188	49.3	0.00184	45.7	0.00201	56.3
Geog. & ln(cent. size)	0.00211	57.2	0.00189	49.6	0.00213	52.9	0.00192	53.7
ln(geol. age) & ln(cent. size)	0.00115	31.1	0.00115	30.1	0.00119	29.6	0.00086	24.0
Geog., ln(cent. size) & ln(geol. age)	0.00253	68.6	0.00226	59.3	0.00255	63.2	0.00222	62.2
Angle / cosine of angle between ln(cent. size) & ln(geol. age)		47° / 0.68		39° / 0.78		61° / 0.48		45° / 0.71
Factor	Ngawi		OH 9		WT 15000, S 2, Sm 1			
	Variance	% of Total	Variance	% of Total	Variance	% of Total		
Total	0.00359	100	0.00383	100	0.00410	100		
Geography	0.00154	43.0	0.00171	44.7	0.00136	33.1		
ln(geological age)	0.00083	23.0	0.00086	22.4	0.00078	19.0		
ln(centroid size)	0.00039	10.8	0.00034	8.9	0.00049	12.0		
Geog. & ln(geol. age)	0.00196	54.6	0.00209	54.5	0.00186	45.3		
Geog. & ln(cent. size)	0.00203	56.6	0.00220	57.4	0.00167	40.6		
ln(geol. age) & ln(cent. size)	0.00117	32.6	0.00123	32.1	0.00107	26.1		
Geog., ln(cent. size) & ln(geol. age)	0.00241	67.2	0.00256	66.9	0.00218	53.1		
Angle / cosine of angle between ln(cent. size) & ln(geol. age)		56° / 0.56		70° / 0.34		37° / 0.80		

Figure 4.1: The neurocranial analyses included up to 34 landmarks (including both midline and bilateral). These landmarks are illustrated below on Ngandong 12. The lines between landmarks are for visualization purposes only. Landmark abbreviations refer to Table 4.2. Opisthion (OP) and entoglenoid (EG) can not be seen from this perspective and their positions are estimated.



group. The Indonesians were unique having a long parietal because of the more posteriorly positioned lambda. Inion was more antero-inferiorly located so that the upper scale was longer than the nuchal plane. There was less constriction across frontotemporale which was also more posteriorly positioned. The parietomastoid suture between the parietal notch and asterion becomes elongated at both ends in the Indonesian specimens. The entoglenoid was located on the same coronal plane as the postglenoid process rather than being posteriorly situated as in the other groups.

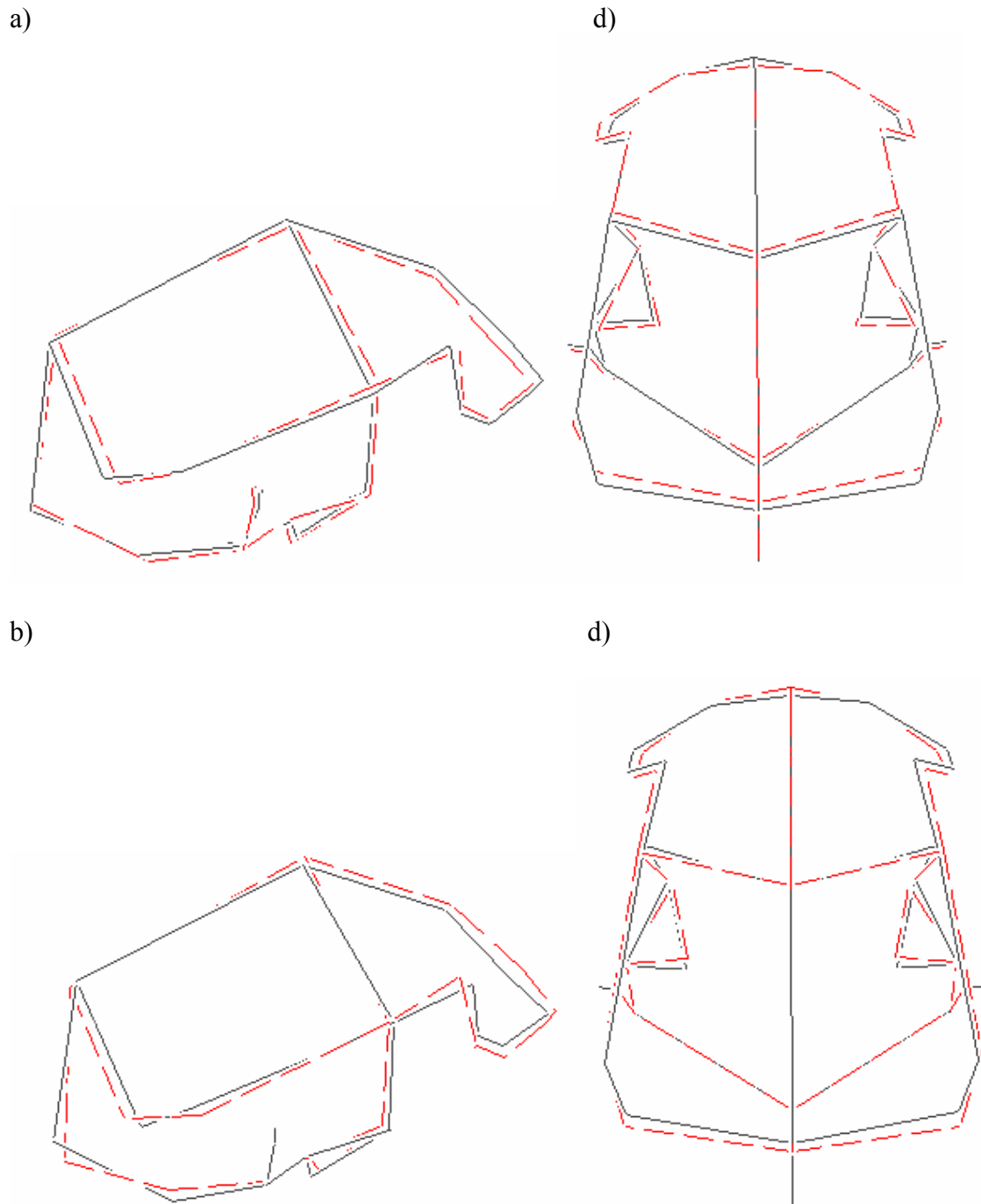
Figure 4.2: PCA of original neurocranial landmark set. PC 1 and 2 are plotted below. The greatest differences are between the early African and recent Indonesian fossils. There is overlap of geographic groups along both components.



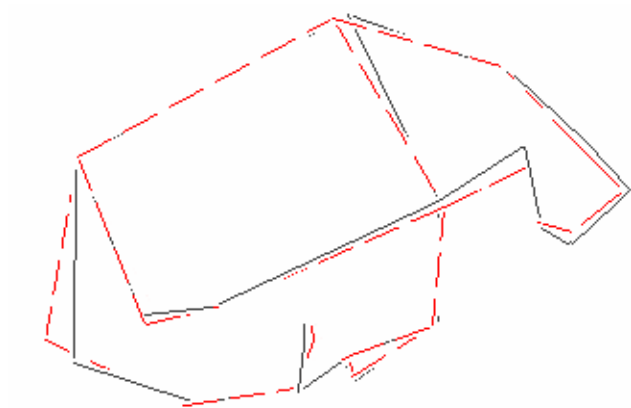
As seen in Figure 4.4, the shape changes associated with decreasing geochronological age involved a more expanded cranial vault (at lambda, bregma, metopion and the midline post-toral sulcus), a wider frontal squama (both across anterior pterion and especially across frontotemporale) and a narrower supraorbital torus. In terms of the supraorbital region, glabella was more superiorly situated in younger individuals, while the inferior margin was more inferiorly positioned both at midorbit and laterally. These changes were accompanied by a shorter and more horizontally inclined of the nuchal plane (rather than antero-inferiorly angled). The parietomastoid suture was longer and more horizontally oriented (rather than postero-inferiorly angled) in younger fossils. The temporosphenoid suture also crossed onto the squama in a more posterior and yet more medial position, indicating a narrower anterior base. The entoglenoid and

postglenoid processes were more anteriorly positioned in younger specimens and the entoglenoid process was less inferiorly projecting.

Figure 4.3: Geographic shape variation in original neurocranial data set. The dashed red line illustrates the mean of each geographic group relative to the means of the remaining groups in lateral and superior view: African (a, d), Indonesian (b, e) and Chinese (c, e).



c)



e)

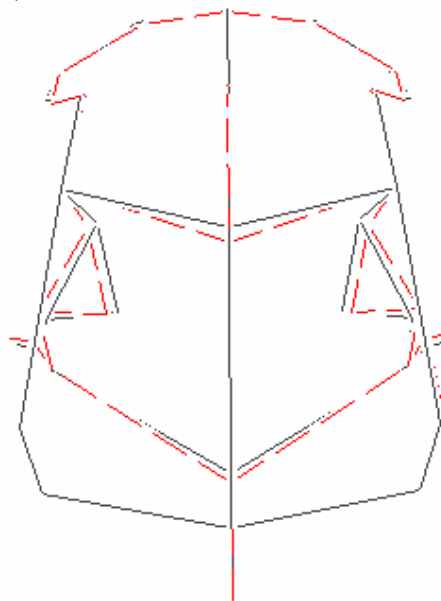
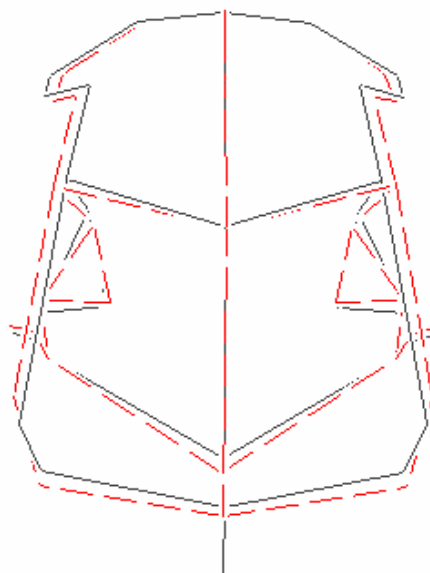
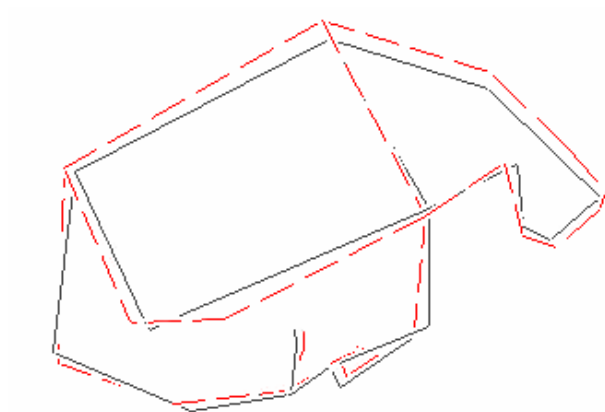


Figure 4.4: Neurocranial shape change associated with decreasing geochronological age (solid black to dashed red) of *H. erectus* is shown below.

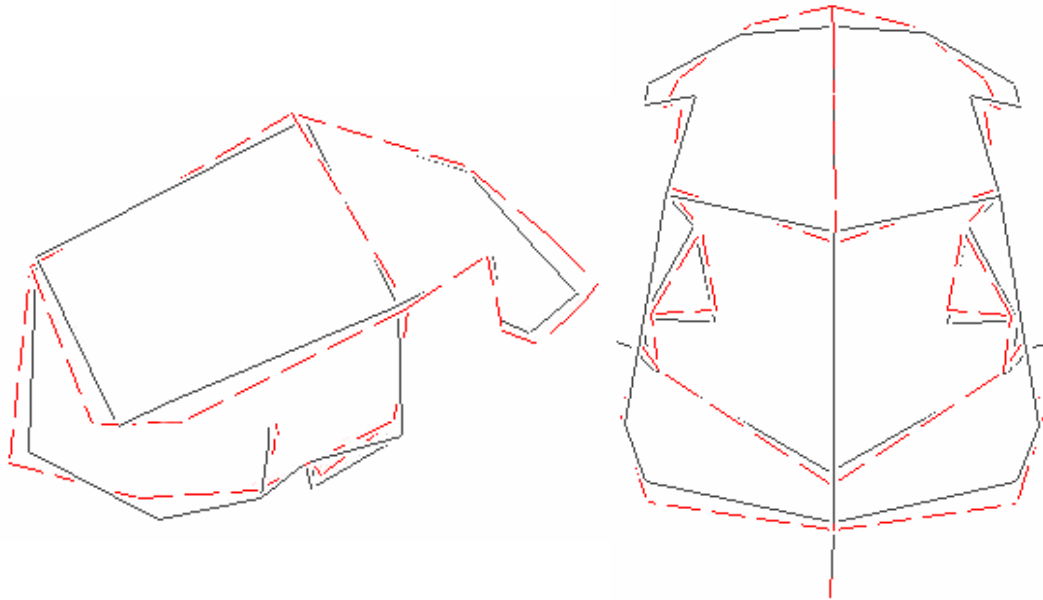


The major difference in shape between smaller and larger individuals was the great antero-posterior elongation in the latter as shown in Figure 4.5. This takes the form of both a more posteriorly positioned inion and a more anteriorly positioned glabella. Larger specimens had a disproportionately large frontal bone with a more prominent supraorbital region. Larger specimens were also relatively narrower across their frontal tori, porion, auriculare and the postglenoid processes. Similar to the changes seen over time, both opisthion and the entoglenoid processes were more superiorly positioned and there was greater distance between the parietal notch and asterion in larger fossils. The superior position of opisthion resulted in a shorter posterior neurocranium. Larger specimens also had more inferiorly directed lateral supraorbital tori.

Table 4.9: Neurocranial analyses: results of PCA and multiple regression of PC 1 and 2 scores on geological age and centroid size

Analysis	PC	% of Variance	Overall Model ANOVA		Parameter Estimates (Pr > t)		
			R ²	Pr(R ²) > F	ln (geol. age)	ln(centsize)	Interaction
Original	1	0.25	0.7	0.0023	0.0023	-	-
	2	0.18	-	N/S	-	-	-
Dmanisi	1	0.21	0.64	0.001	0.001	-	-
	2	0.2	0.55	0.0038	-	0.0038	-
ER 42700	1	0.2	0.59	0.0174	0.0061	0.0319	-
	2	0.19	0.59	0.0035	-	0.0035	-
Zhoukoudian	1	0.31	-	N/S	-	-	-
	2	0.17	0.75	0.0048	0.0149	0.1834	0.0156
Ngawi	1	0.27	0.74	0.0006	0.0006	-	-
	2	0.17	-	N/S	-	-	-
OH 9	1	0.29	0.65	0.0027	0.0027	-	-
	2	0.15	-	N/S	-	-	-
WT 15000, S 2, Sm 1	1	0.24	0.54	0.004	0.004	-	-
	2	0.17	0.4	0.0208	-	0.0208	-

Figure 4.5: Size-related shape variation in original neurocranial data set. The shape differences between smaller (black solid line) and larger (dashed red line) fossils are illustrated below.



Dmanisi: Both D 3444 and D 2700 preserved the original landmark set but are unusual in being an old, edentulous individual and a young, subadult individual, respectively.

Increasing the sample size of individuals from the site of Dmanisi also allowed for the addition of Ng 10 to the Ngandong sample (see Table 4.4).

As seen in Table 4.8, the inclusion of these additional fossils had the effect of decreasing slightly the amount of variance accounted for by geography (40%) and geological age (20%) while increasing the amount of shape variance explained by centroid size (15%). Figure 4.6 demonstrates that the relative positions of individuals along PC 1 were very similar to the original PCA with D 2700 falling quite near to D 2280 but D 3444 scoring more similarly to the recent Indonesian fossils. Both D 2700

and D 3444 scored lower on PC 2 than the remainder of the sample and D 2280 also scored fairly low (similarly to S 17). The first two components accounted for nearly the same percentage of variance in the total sample (~20%), which means that the shape differences between ER 3733 / 3883 and Ngandong / Sm 3 were of a similar magnitude as those separating the Dmanisi individuals from the rest of the sample. 64% of variation in PC 1 scores is accounted for by geological age while 55% of variation in PC 2 scores is explained by differences in centroid size (Table 4.9).

Figure 4.6: PCA of the Dmanisi landmark set. PC 1 is plotted against PC 2 below. See Table 4.5 for details on the Dmanisi neurocranial sample and landmarks. The Dmanisi specimens exhibit some shape similarities along the second component, with only D 2280 overlapping S 17.

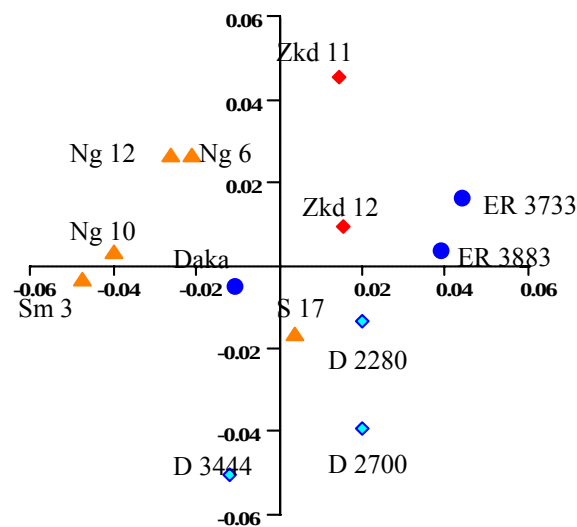


Figure 4.7 illustrates that the Georgian sample differed from other *H. erectus* specimens in having a long parietal and short frontal with a less posteriorly projectinginion. Both opisthion and the entoglenoid were more inferiorly situated in the Dmanisi hominins and there was greater constriction across frontotemporale and greater width across the basal temporal structures (temporosphenoid suture, postglenoid and

entoglenoid processes). A final difference was the more superior positioning of the parietal notch, above the level of asterion.

The temporal changes were similar to those described above, with even greater constriction across frontotemporale and greater width across the basal temporal bone in the earlier specimens as see in Figure 4.8. There was also slightly less of a change in height at bregma due to the higher position of this landmark when D 3444 and 2700 were included in the sample of earlier specimens. Figure 4.9 illustrates that the size related shape differences were more apparent when D 2700 and 3444 were incorporated into the

Figure 4.7: Geographic shape variation in the Dmanisi neurocranial data set. The average configuration for the Dmanisi fossils (dashed red line) was compared to the mean of the remaining *Homo. erectus* specimens (black solid line).

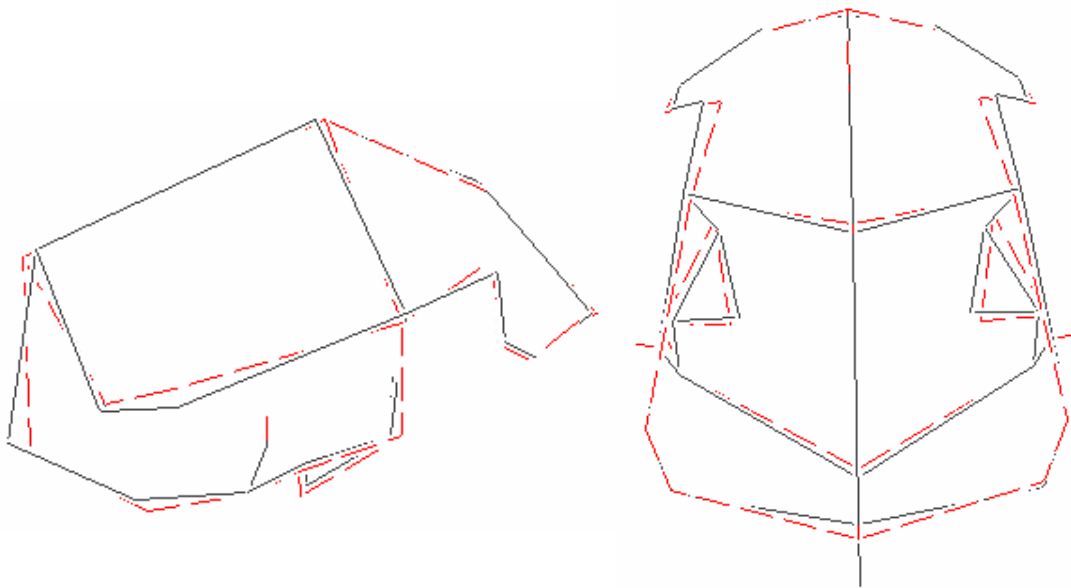


Figure 4.8: Shape change associated with decreasing geochronological age (solid black to dashed red) of *Homo erectus* using the Dmanisi landmark set is shown below.

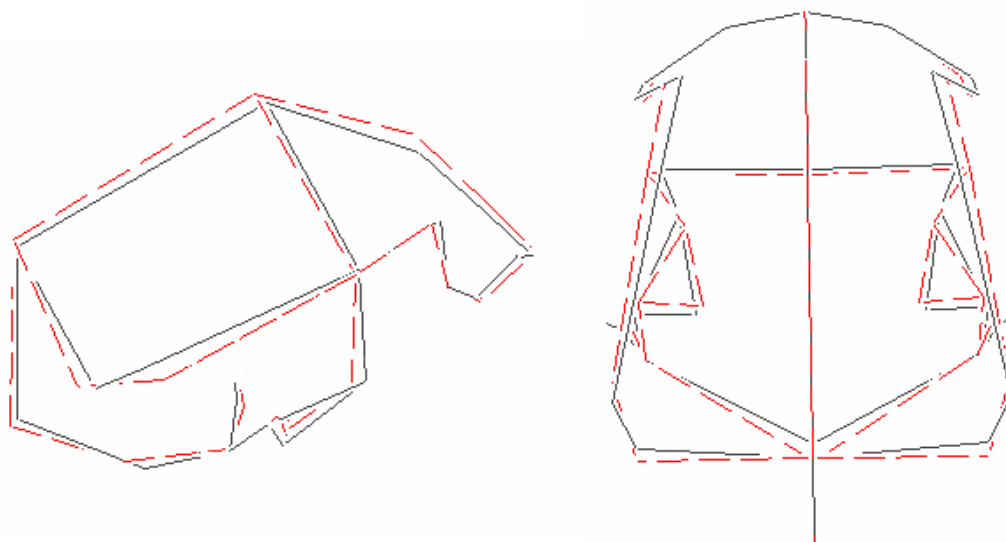
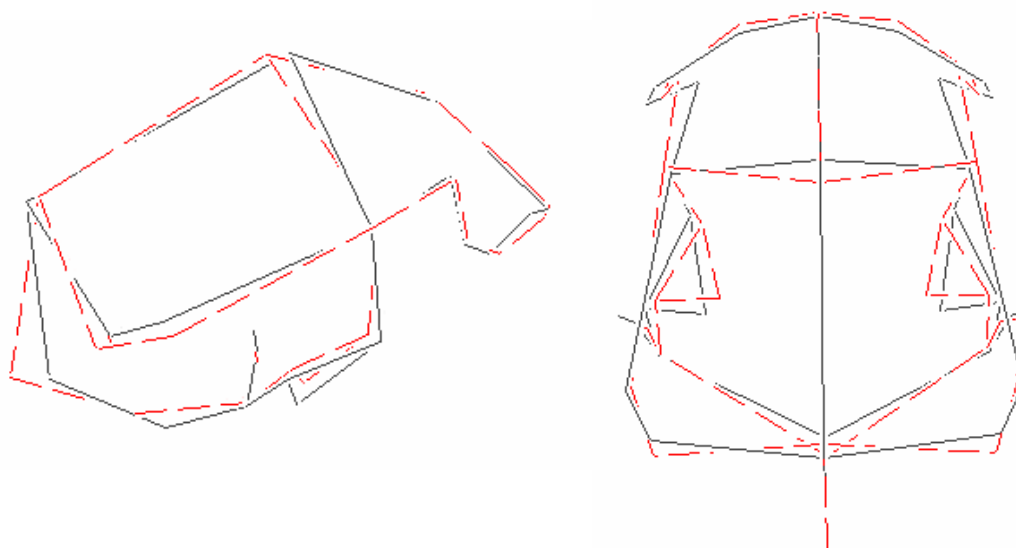


Figure 4.9: The solid black corresponds to smaller specimens while the red dashed outline indicates shape differences related to larger size in the Dmanisi neurocranial analysis.



analysis. In smaller individuals inion was even less posteriorly situated while glabella was more anteriorly projecting. Therefore, while there is still an increase in the overall length of the cranium, the expansion all occurs posteriorly. Smaller crania are comparatively even wider across the temporal bone, including the basal structures, porion and auriculare. Also, the frontal bone is relatively shorter and the parietal is longer due to a more anterior position of bregma and posterior position of lambda. The lateral ends of the supraorbital torus were positioned at the same height in smaller and larger fossils. Other changes from smaller to larger crania remain unchanged, such as a lengthening of the parietomastoid suture between asterion and the parietal notch, a more superiorly situated opisthion, a narrower supraorbital torus and less constriction across frontotemporale.

ER 42700: By excluding metopion, ER 42700 could be incorporated into the analysis (see Table 4.4). D 2700 was also incorporated into the analysis as it was another small specimen with which to compare ER 42700. As seen in Table 4.8, geography and geological age both accounted for less of the total shape variance than in the original analysis, but size explained approximately the same proportion (14%). ER 42700 was at the extreme of both PC 1 and 2 in the PC plot shown in Figure 4.10. On PC 1, both ER 42700 and Sm 3 scored low in opposition to the East Turkana and D 2280 fossils, based mainly on the greater superior expansion at bregma and posterior expansion at lambda. On PC 2, the African fossils and D 2700 generally scored lower than the Asian and D 2280 specimens with the exception of Zkd 12. D 2700 scored plotted most closely to ER 42700 on PC 2. Geological age and centroid size together accounted for 59% of variation

in PC 1 scores and size alone accounted for 59% of variation in PC 2 scores (see Table 4.9).

By comparing ER 42700 to the average *H. erectus* configuration in Figure 4.11, it was clear that ER 42700 did not appear to be simply a scaled down version of a classical *H. erectus* but had a higher cranial profile and a less angled occipital bone. There was much greater expansion at lambda (posteriorly) and bregma (postero-superiorly). The occipital plane was angled supero-posteriorly which was unique and the nuchal plane was also elongated due to a more anteriorly positioned opisthion. The supraorbital torus was less anteriorly projecting above the orbit and at the lateral corners. The position of frontotemporale was low and the temporosphenoid suture crossed onto the squama in a relatively anterior position.

Figure 4.10: PCA of ER 42700 data set. PCs 1 and 2 are plotted below. It is clear from the plot that ER 42700 represents an outlier relative to other *Homo erectus* specimens.

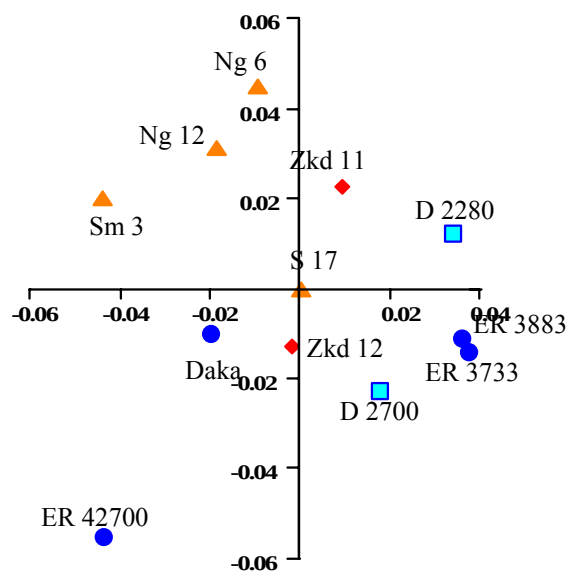
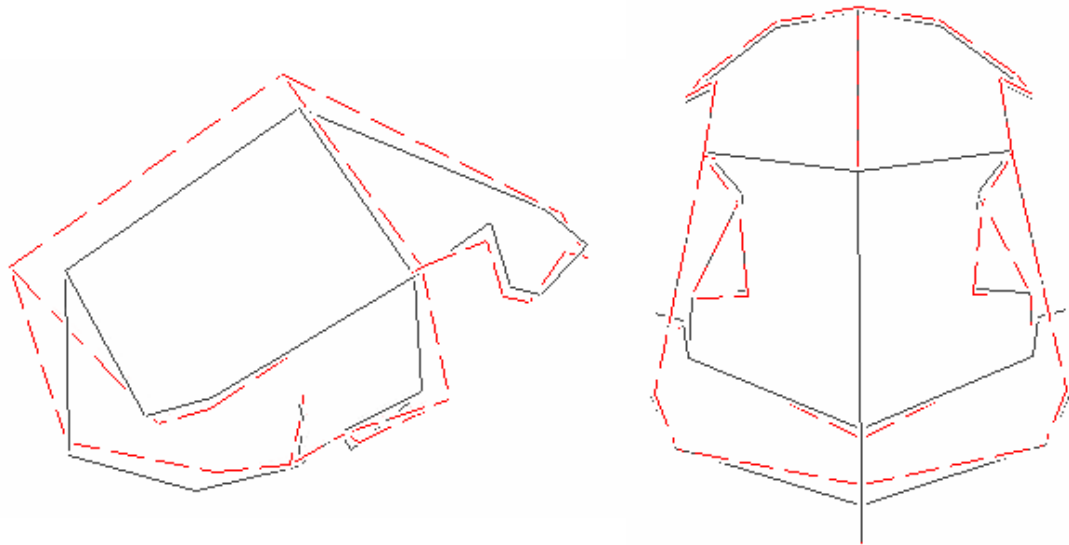


Figure 4.11: The differences in cranial shape between ER 42700 (dashed red line) and the average *Homo erectus* configuration (solid black line), shown in lateral and superior view. ER 42700 has a fundamentally different midsagittal profile due to the great superior expansion at bregma and the more posterior positioning of lambda.



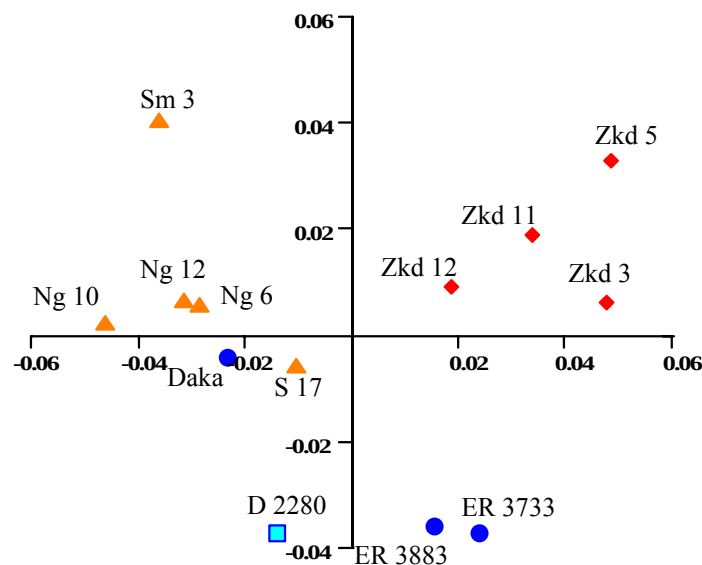
The addition of this specimen to the analysis obscured a clear pattern of temporal change, and the differences between smaller and larger specimens were mainly those that separated ER 42700 from the other specimens. For this reason, ER 42700 was treated as an outlier and not included in the further analyses.

Zhoukoudian: This analysis was intended to increase the sample size and temporal depth of the Zhoukoudian sample by including Zkd 3 and 5. Zkd 5 was 200-400 Ka younger than the other Zhoukoudian specimens (Shen *et al.*, 2001). Because there were three Zhoukoudian fossils from the same time period, Ng 10 was also incorporated into this analysis. Both opisthion and the temporosphenoid suture were dropped as described in

Table 4.4. Both Zkd 3 and 5 were missing opisthion. The location of the temporosphenoid suture in Zkd 5, although in proper relation to other basal landmarks, was located too far superiorly relative to the frontal bone. This may be related to a misalignment of the various fragments in the reconstruction, and therefore the temporosphenoid landmark was also excluded from the analysis.

Nearly half of the differences in cranial shape could be attributed to geographic origin while 17% of the variance was accounted for by the age of the fossils and only 9% is accounted for by size (Table 4.8). As seen in Figure 4.12, the recent Indonesian sample was contrasted with the Chinese and East Turkana fossils on PC 1. Daka fell closest to the recent Indonesian specimens while S 17 and D 2280 were fairly intermediate. Zkd 3 and 5 scored lowest, rather than ER 3733 and 3883. Zkd 3 fell well within the boundaries of cranial shape variation for Zhoukoudian, despite its possible subadult status. Within each of three major regions (Indonesia, China and Africa) the

Figure 4.12: PCA of Zhoukoudian data set (see Table 4.5 for details). The first two components are plotted below.

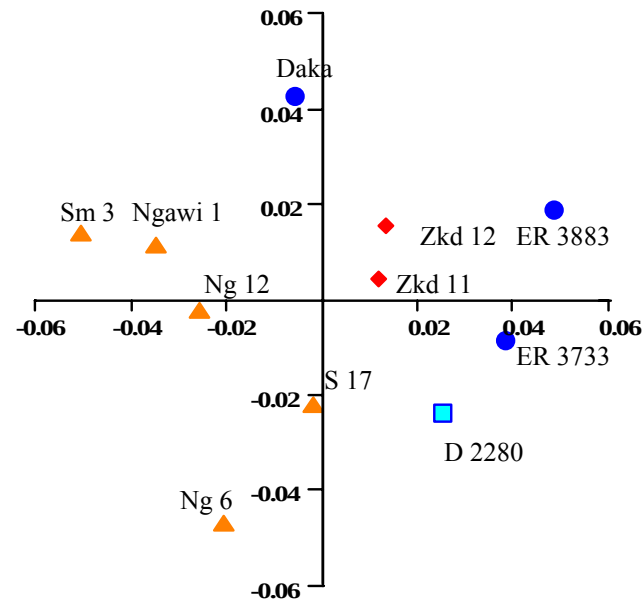


oldest specimens scored lowest on PC 1 and the youngest generally scored highest. Therefore, Zkd 5 and Daka scored higher than the other members of their respective groups and S 17 has the lowest score of the Indonesians. It is interesting, therefore, that Sm 3 scores higher than the other Indonesian hominins. On PC 2 the East Turkana and D 2280 specimens were separate from the other specimens and contrasted most with Sm 3. As seen in Table 4.9, factorial regression analysis indicated that there was a significant interaction between geological age and centroid size on PC 2. This is a complicated interaction: in the oldest and youngest time spans the larger individuals score lower, whereas this relationship is reversed in the intermediate time spans. The overall model accounted for 75% of total variance in PC 2 scores. Geological age by itself accounts for 49% of variation ($p = 0.0076$).

Despite some differences in the PCA plot, the patterns of geographic, temporal and size-related variation in cranial shape are almost identical to those seen in the original analysis, with very minor differences. However, the length and orientation of the nuchal plane cannot be assessed in the absence of opisthion.

Ngawi: The inclusion of Ngawi produced very similar results to the original neurocranial analysis. Only the postglenoid landmark was excluded in this analysis as summarized by Table 4.4. Geography, age and size each explained a similar proportion of shape variation as in the original analysis (Table 4.8). In the PC plot of Figure 4.13, Ngawi fell close to the specimens from Sambungmacan and Ngandong along the first two PCs. Shape variation related to geography, time and size are not noticeably different from those described in the first neurocranial analysis (Table 4.9).

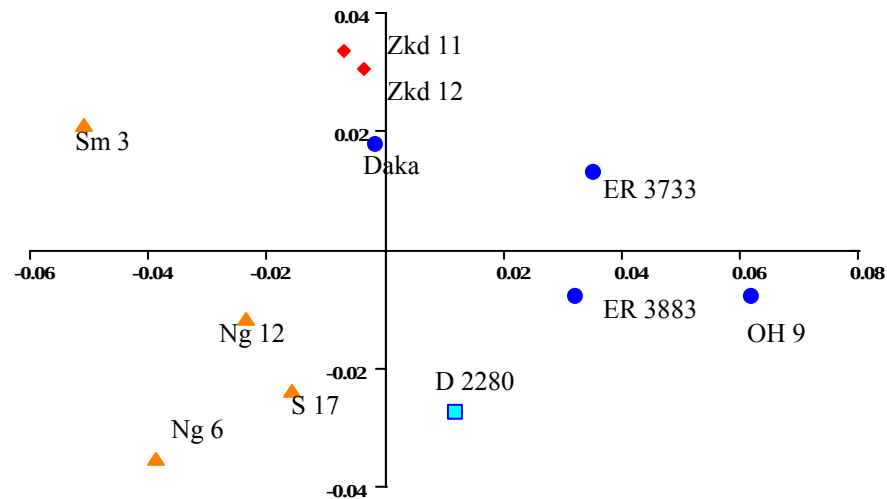
Figure 4.13: PCA of Ngawi data set (see Table 4.5 for details). PC 1 and 2 are shown below.



OH 9: Three landmarks, lambda and anterior pterion (right and left) were excluded in order to accommodate OH 9 in the analysis (Table 4.4). As seen in Table 4.8, the addition of OH 9 results in a similar proportion of shape variance explained by geography and geological age (45% and 22%, respectively) but less of the variance was attributable to size differences (9%).

Figure 4.14 illustrates that the relative positions along PC 1 were similar to the original analysis with OH 9 falling closest to the East Turkana hominins and furthest from the recent Indonesian specimens. 65% of variation in PC 1 scores can be explained by the geological age of the fossils (Table 4.9). There were greater differences along PC 2. OH 9 and Ng 10 scored lowest, in contrast to the two Zhoukoudian specimens who scored high.

Figure 3.14: PCA of OH 9 data set (see Table 3.5 for details). The first two PCs are plotted below.



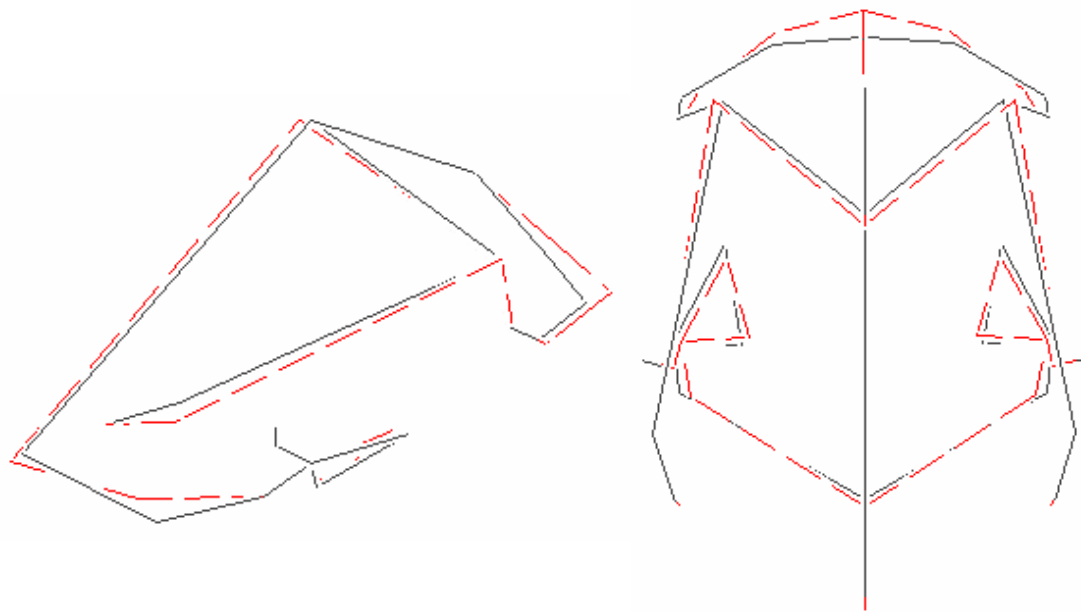
Although the relative positions of anterior pterion and lambda cannot be evaluated, the shape changes associated with geography and time are very similar to those already described with some very small differences apparent in the placement of the midline post-toral sulcus and glabella, likely due to the exaggerated supraorbital torus of OH 9. For example, there was less expansion over time in this region when OH 9 was included in the analysis.

The differences associated with size, however, showed more apparent differences as illustrated by Figure 4.15. There was no longer superior expansion at bregma and there was even greater anterior projection at glabella in the large specimens. The nuchal plane was shorter and more horizontally inclined in larger specimens as before and the parietomastoid suture was more horizontal but not elongated relative to the smaller specimens. There was less of a difference in the relative bi-frontotemporale constriction

between smaller and larger fossils, although larger ones were still wider across frontotemporale. An increase in size remained correlated with a narrowing across the temporal base. The inferior entoglenoid processes were equally inferiorly projecting across different sizes and the lateral corners of the supraorbital torus were no longer inferiorly angled, although the supraorbital torus was still slightly narrower in larger fossils.

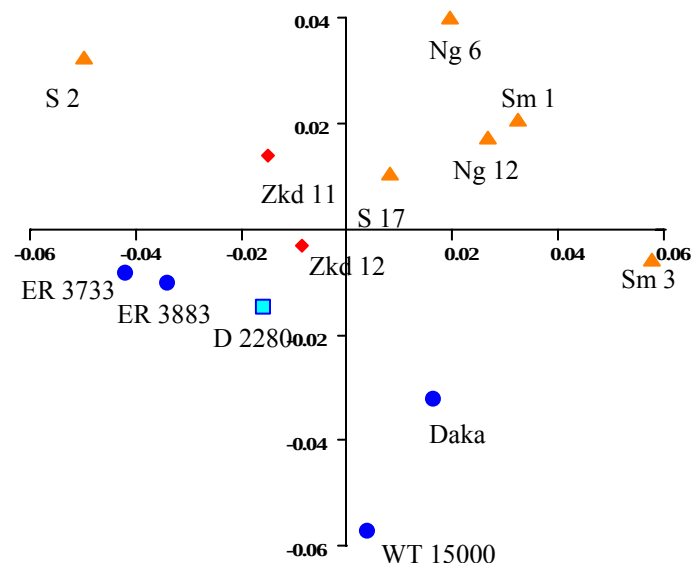
WT 15000, S 2 and Sm 1: By excluding several landmarks in the supraorbital region, it was possible to incorporate three additional specimens: WT 15000, S 2 and Sm 1 as described in Table 4.4.

Figure 4.15: Size-related shape variation in OH 9 neurocranial data set. Cranial shape change associated with size variation between small (solid black line) and large (dashed red line) individuals, shown in lateral and superior view.



As seen in Table 4.8, the results were similar to the original analysis, with 19% of shape variance explained by geological age and 12% by centroid size. However, geographic origin explained considerably less variation (33%) than in previous analyses. The relative positioning of fossils along PC 1 was equivalent to the original analysis (the fact that the axis is ‘flipped’ is not meaningful), but S 2 fell at the negative end of PC 1 with the East Turkana fossils (see Figure 4.16). WT 15000 occupied a fairly intermediate position, close to Daka and S 17. On PC 2 the Asian specimens, with the exception of Sm 3 all scored higher than the Afro-Georgian sample. WT 15000 was particularly isolated at the negative end of the component, in greatest contrast to Ng 6 and S 2. A little over half of the variation in PC 1 scores was explained by geological age while centroid size accounted for 40% of PC 2 variation (Table 4.9). PC 1 was therefore less clearly associated with temporal change than in previous analyses because S 2 scored lower than expected and WT 15000 scored higher than predicted based on their relative ages.

Figure 4.16: PCA of WT 15000, S 2, Sm 1 data set. The first two PCs are plotted below. See Table 4.5 for details on the landmarks and fossil sample used in this neurocranial analysis.



The shape change through time and between smaller and larger specimens was very similar to that described previously (for those regions that were preserved). However, the supraorbital torus was even wider and there was slightly less constriction across frontotemporale in the earlier specimens.

WT 15000 was unique mostly in the more postero-lateral position of its lateral torus. It was less posteriorly projecting at inion (which was also more inferiorly situated) and opisthion was inferiorly located compared to ER 3733 and 3883, resulting in a more open occipital angle. Daka was closest to WT 15000 on PC 2 and so mostly closely approached the West Turkana hominin in these traits.

S 2 differed from other Indonesian specimens in the more superior and posterior location of inion, and less transverse breadth across frontotemporale and anterior pterion. There was also less superior expansion at bregma and the parietal notch was closer to asterion. In these characters it resembled the East Turkana specimens. However, it had a narrower supraorbital torus, resulting in less drastic constriction behind the orbits. This feature, along with a more superior position of opisthion, was a trait shared with other Indonesian hominins.

Frontal bone

As described in Table 4.5, the frontal bone analysis included 14 individuals from all geographic regions. The landmark configuration, seen in Figure 4.17, consisted of both landmarks and semilandmarks.

As summarized by Table 4.10, both geography and geological age explained a similar proportion of variance in frontal shape as they did in the neurocranial analyses (47% and 19%, respectively) while size accounted for a greater percentage (18%). Both age and size explained similar shape variation (33° between their vectors).

There was strong geographic subdivision between the African fossils and Chinese individuals on PC 1, seen in Figure 4.18. The Indonesian sample was separate from the others on PC 2. Both S 17 and D 2280 grouped with the other Indonesian fossils on PC 2 but have low scores like the African sample on PC 1. Zkd 3 again fell within the range of variation exhibited by other Zhoukoudian specimens, despite its possible subadult age. Geological age predicted 38% of variation in PC 2 scores (Table 4.11). Size of the frontal bone similarly predicted 37% of PC 2 variance, but these two effects were not independent and accounted for essentially the same variance. OL 45500 was unique on PC 3 in its extreme constriction across frontotemporale relative to its greater width across the posterior frontal squama and its thinner torus with a very inferiorly positioned nasion and greatly inflated glabellar region.

Figure 4.17: Landmarks (labeled) and semilandmarks used in the frontal bone analysis illustrated on Sm 1. Blue circles are landmarks and yellow circles are semilandmarks. See Table 4.6 for landmark abbreviations and details about the semilandmarks.

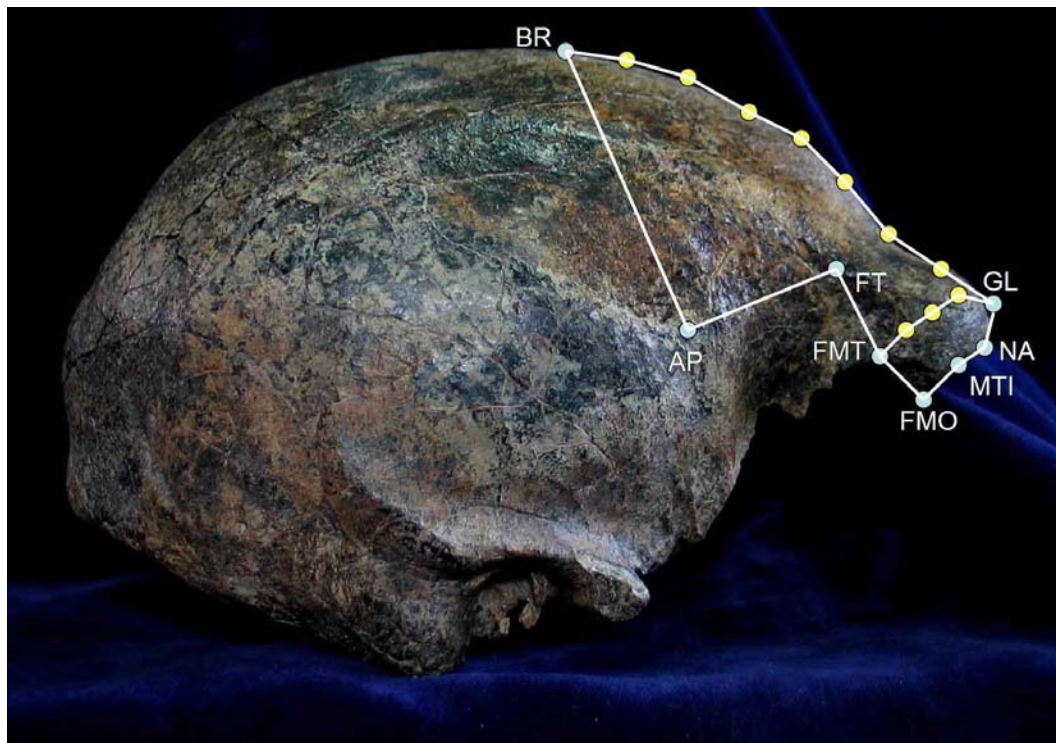
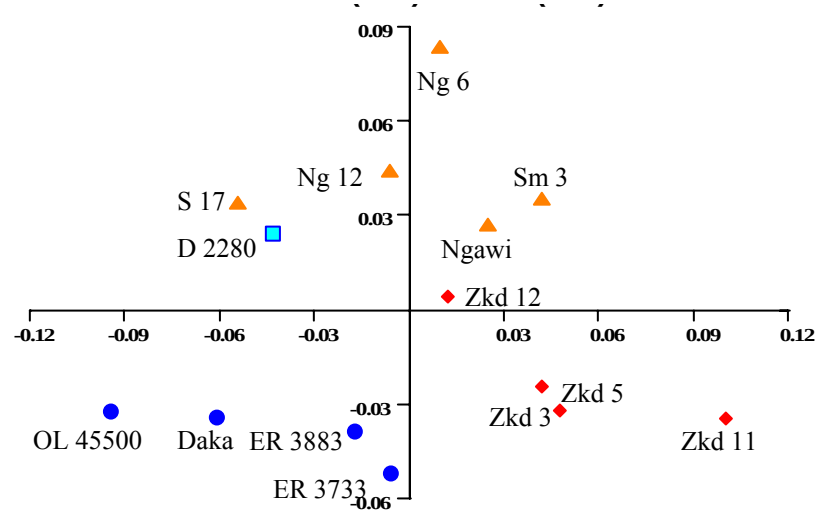


Table 4.10: Regional analyses: proportion of total variance explained by geography, geological age and centroid size

	Frontal		Temporal Base		Occipital		Face	
Factor	Variance	% of Total	Variance	% of Total	Variance	% of Total	Variance	% of Total
Total	0.00727	100	0.03466	100	0.00283	100	0.00865	100
Geography	0.00343	47.2	0.01536	44.3	0.00057	20.1	0.00643	74.4
ln(geological age)	0.00136	18.7	0.00503	14.5	0.00044	15.6	0.00320	36.9
ln(centroid size)	0.00131	18.0	0.00425	12.3	0.00016	5.7	0.00320	37.0
Geog. & ln(geol. age)	0.00386	53.1	0.01761	50.8	0.00114	40.1	0.00865	100
Geog. & ln(cent. size)	0.00400	54.9	0.01798	51.9	0.00071	25.1	0.00865	100
ln(geol. age) & ln(cent. size)	0.00205	28.2	0.00880	25.4	0.00063	22.1	0.00572	66.1
Geog., ln(cent. size) & ln(geol. age)	0.00443	60.9	0.02014	58.1	0.00127	44.9	0.00865	100
Angle between ln(cent. size) & ln(geol. age)		33		63		113		171

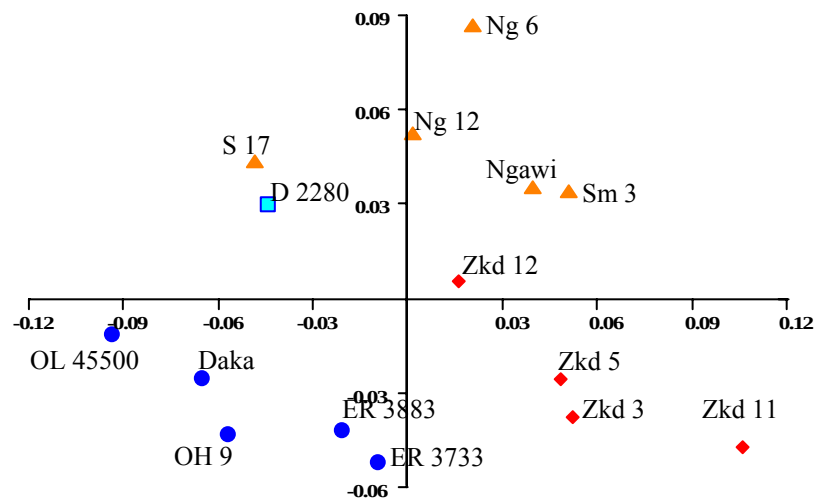
Figure 4.18: PCA of frontal landmark set (see Table 4.6 for details). The first two components are plotted below. The African, Indonesian and Chinese groups are distinct on the first two components, with the greatest differences apparent between the African and Zhoukoudian specimens. D 2280 overlaps the African and Indonesian specimens on these components.



Although PC 1 scores were not significantly related to the size of the frontal bone, the age or the endocranial volume of the individual fossils, there was an insignificant trend within the African group for younger fossils to have more extreme (negative) scores on PC 1. The incorporation of OH 9 (by dropping the anterior pterion landmark) resulted in a similar ordering along PC 1 and a weak but significant relationship between age and PC 1 as illustrated in Figure 4.19. As a group the Zhoukoudian specimens generally score lower than predicted for their age. The addition of OH 9 also made the relationship between PC 1 and age within the African group reach significance ($R^2 = 0.78$, $p = 0.0481$) (Table 4.11).

The shape differences among geographic groups include the relative expansion along the midline, the shape of the supraorbital torus and the position of frontotemporale as seen in Figure 4.20. The Africans had a relatively short frontal bone (glabella to bregma), especially compared to the Chinese mean. In the Indonesian specimens

Figure 4.19: PCA of OH 9 frontal landmark set (see Table 4.6 for details). The first two PCs are plotted below. The results are similar to the original Frontal PCA. OH 9 clearly groups with other African specimens on PC 1 and 2.



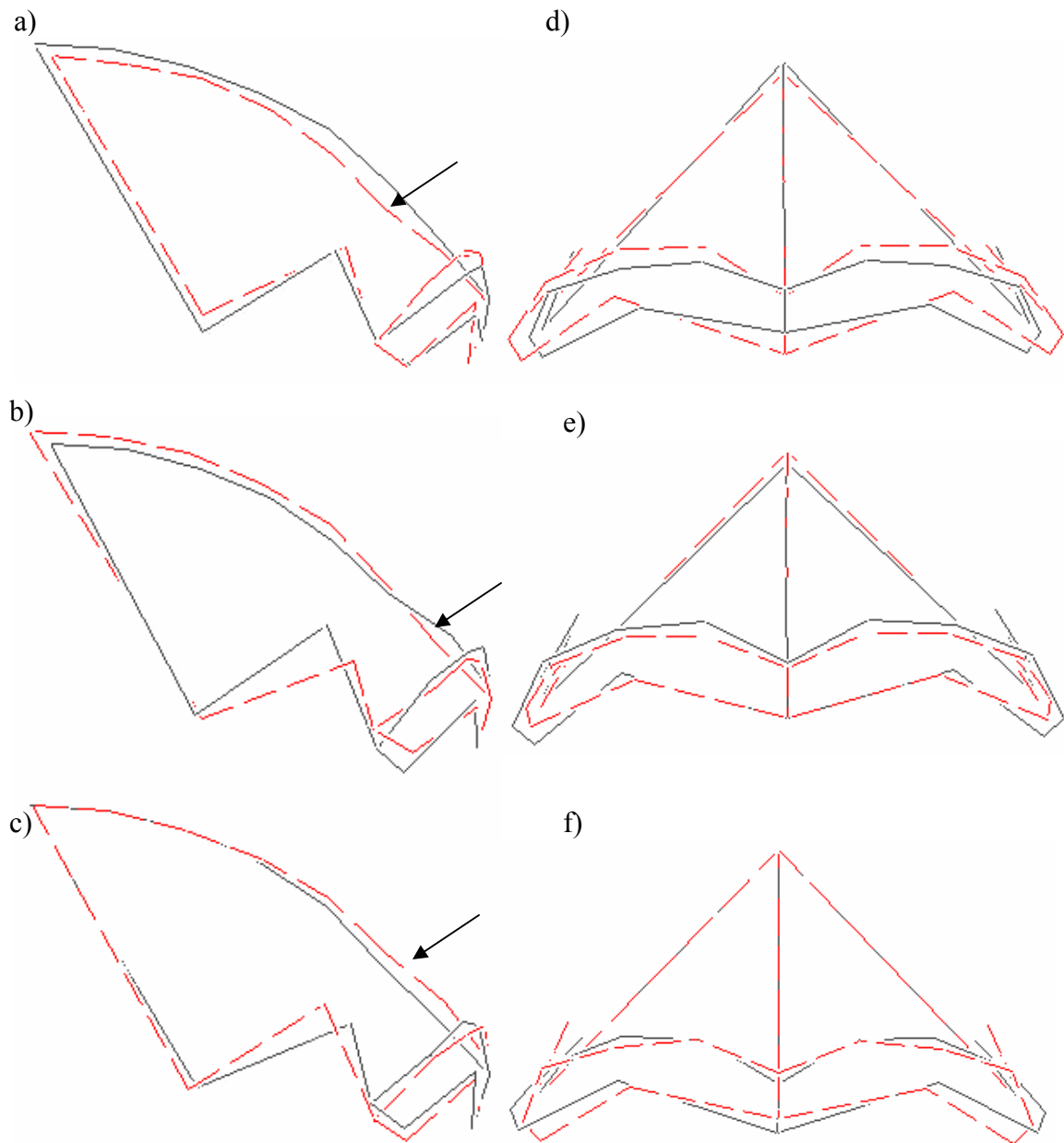
frontotemporale was more postero-supero-laterally situated whereas the African fossils and D 2280 were relatively narrower across frontotemporale. Frontotemporale was more anteriorly located, right behind the torus, in the Zhoukoudian fossils. The Indonesian fossils exhibited superior expansion of the midline from glabella to midsquama whereas the Chinese fossils displayed nearly the opposite pattern with expansion superiorly but a more marked post-toral sulcus just posterior to the torus. The African sample had less superior expansion of the entire midline squama, and the post-toral sulcus was developed in a more posterior position than in the Chinese individuals. The Chinese group had a relatively narrower supraorbital torus compared to the wide torus of the African and Georgian fossils. Both the Indonesian and Chinese samples had a more inferiorly

Table 4.11: Regional analyses: results of PCA and multiple regression of PC 1 and PC 2 scores on geological age and centroid size

Analysis	PC	% of Variance	Overall Model ANOVA		Parameter Estimates (Pr > t)		
			R ²	Pr(R ²) > F	ln (geol. age)	ln(centsize)	Interaction
Frontal	1	0.36	-	N/S	-	-	-
	2	0.23	0.38	0.018	0.018	-	-
Frontal (OH 9)	1*	0.39	0.33	0.0248	0.0248	-	-
	2	0.24	0.36	0.0185	0.0185	-	-
Occipital	1	0.49	-	N/S	-	-	-
	2	0.26	-	N/S	-	-	-
Temporal Base	1	0.31	0.31	0.0393	0.0393	-	-
	2	0.16	-	N/S	-	-	-
Face	1	0.46	-	N/S	-	-	-
	2	0.3	-	N/S	-	-	-

* As noted in the body of the text, there was a significant relationship within the African sample between geological age and PC 1 scores ($R^2 = 0.78$, $pr > |t| = 0.0481$)

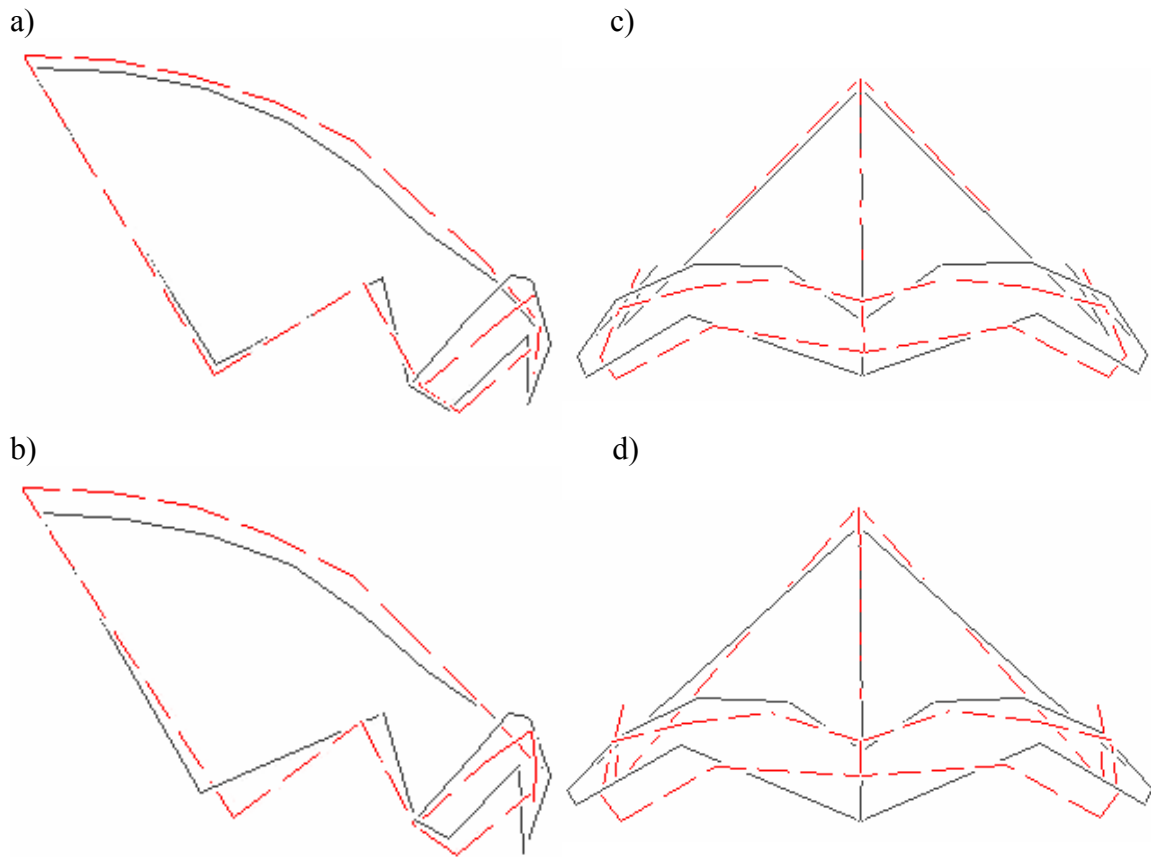
Figure 4.20: Geographic shape variation in the frontal bone. The mean African configuration (dashed red line) compared to the average for all non-African specimens (solid black line) is shown in (a) and (d). The same procedure was used to highlight geographic differences in the Chinese (b, e) and Indonesian (c, f) groups. The configurations are shown in lateral view as illustrated in Figure 4.17 and in frontal view. The arrows illustrates the higher position of the post-toral sulcus (supraglabellar depression) in the African than the Chinese specimens and the lack of a depression in the Indonesian specimens. No depression is evident in the Indonesian configuration.



positioned supraorbital torus at mid-orbit. The lateral corners of the torus were more down-turned in the Indonesian than the Chinese fossils but it was the Africans that displayed the greatest arching over the orbits (torus was higher at mid-orbit than laterally) and thinning of the torus laterally. The Africans also had a more inferiorly situated nasion and glabella. Unlike the other groups, the anterior surface of the supraorbital torus did not extend onto the superior aspect in the Indonesian sample (no torsion of the superficial aspect). The straighter anterior toral profiles of Ngawi and Sm 3 moved them closer to Zhoukoudian along PC 1.

The shape differences between older and younger specimens on one hand and between smaller and larger specimens on the other were quite similar. As noted in Table 4.10, the angle between their respective vectors of regression coefficients was 33° , reflecting a strong correlation between the variance accounted for by each. As seen in Figure 4.21, there was expansion along the middle and superior portions of the midsagittal profile with a less projecting glabella and more superiorly positioned nasion in the younger / larger specimens. Also, the torus was narrower medio-laterally and more inferiorly positioned relative to the frontal squama. In the older / smaller specimens the torus was more arched toward the midline and the lateral corner was less well-developed (thinner) and not as down-turned. The bi-frontotemporale breadth was relatively greater in the larger / younger fossils. The relative position of anterior pterion did differ between the age and size comparisons. In the larger specimens anterior pterion is more anteriorly and medially positioned whereas in younger *H. erectus* fossils there was greater breadth the frontal squama at anterior pterion and it was not more anteriorly positioned.

Figure 4 21: Temporal and size-related shape change in the frontal bone. Frontal bone shape change associated with decreasing geochronological age (solid black to dashed red) of *Homo erectus* is shown below in (a) and (c). Shape differences related to an increase in size from small (solid black outline) to large (dashed red outline) are illustrated in (b) and (d). The images are shown in lateral and anterior views.

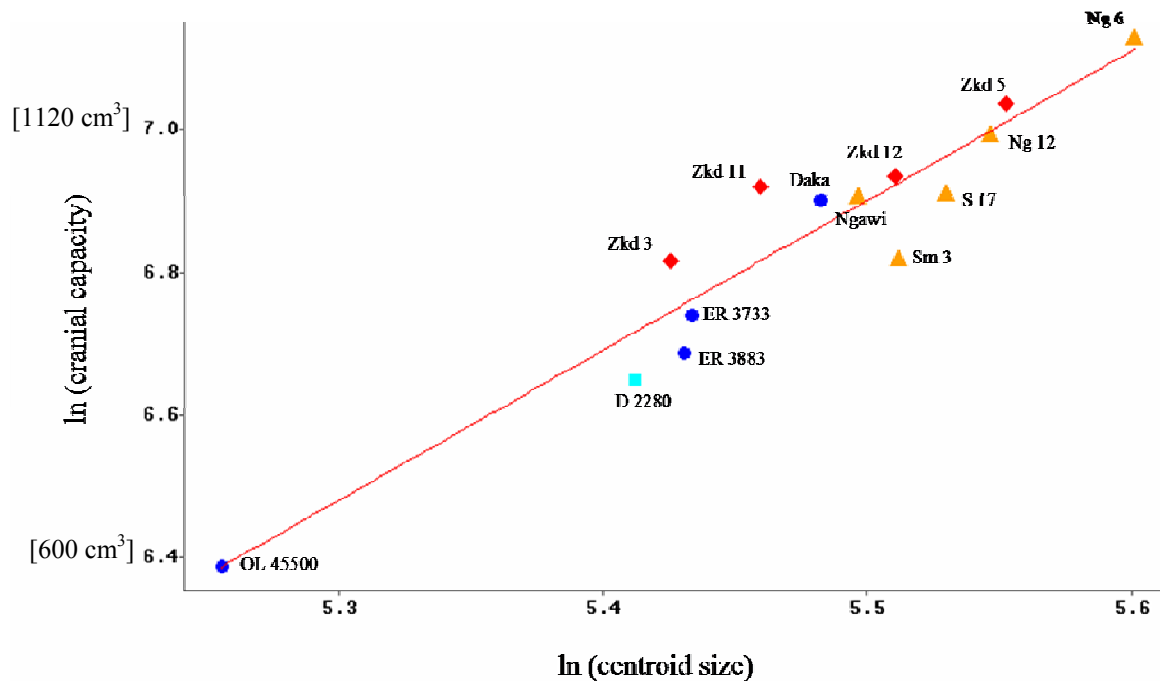


OL 45500 had a strong influence in the size regression because of its very small size. By excluding this fossil from the regression, larger specimens have a much more inflated glabellar region than smaller specimens and the breadth across frontotemporale did not increase, it is just more posteriorly positioned. Therefore, the glabellar region was especially pronounced for such a small frontal bone and the width at frontotemporale was very narrow in OL 45500.

Cranial capacity predicted 81% of variation in the size of the frontal bone ($p = 0.0001$) and vice versa. These regressions were calculated without OL 45500 because this specimen is very incomplete and the endocranial capacity has only been estimated at less than 800 cm^3 (Potts *et al.*, 2004). Using the regression equation, the size of the frontal bone of OL 45500 yields a predicted cranial capacity of 589 cm^3 with a range of $499\text{--}696 \text{ cm}^3$ as shown in Figure 4.22. This value is approximately half that of Ng 6 which has one of the largest endocranial volumes for any *H. erectus* fossil of 1251 cm^3 . Values in the upper half of the range were within the limits recorded for the Dmanisi specimens ($\sim 600\text{--}775$) (Rightmire *et al.*, 2006) and approaching the estimated value of 727 cm^3 for OH 12 (Holloway, 1973). However, if the individual had an endocranial volume in the bottom half of the range then it would be the smallest recorded for *H. erectus*.

Extrapolating values beyond the range of the data is less reliable than interpolation. Therefore, as a means of testing the reliability of these estimates, the endocranial volume was estimated for Ng 6 and D 2280, which had the largest and smallest known endocranial volumes in the sample. In each instance, the fossil being examined was withheld and the regression equation was recalculated and used to predict the endocranial volume of the withheld fossil. When Ng 6 was withheld, the relationship was not quite as strong ($R^2 = 0.73$, $p = 0.0004$) as in the original regression. Using this new regression equation, the cranial capacity of Ng 6 was estimated to be 1219 cm^3 . The actual endocranial volume of Ng 6 was 1251 cm^3 , well within the 95% prediction interval of $1086\text{--}1366 \text{ cm}^3$. Withholding D 2280 resulted in nearly as strong a relationship as originally ($R^2 = 0.77$, $p = 0.0002$). The prediction for D 2280 was 838 cm^3 , which was

Figure 4.22: Predicting cranial capacity of OL 45500 from the centroid size of the frontal bone. The natural log of the frontal bone centroid size is highly predictive of the natural log of cranial capacity within *H. erectus* ($R^2 = 0.81$, $p < 0.0001$). The absolute values which correspond to the log values are shown at the extremes of the y-axis. The very small frontal bone size of OL 45500 results in a predicted cranial capacity of 589 cm³ with a range of 499-696 cm³.



considerably larger than the actual value for D 2280 (775 cm³). In fact, the actual value falls just below the 95% prediction limits of 777 – 904 cm³. Given that the OL 45500 is predicted to be even smaller, and the error seems higher at the small end of the range, it would not be surprising if the calculated value for the Olororgesailie hominin were still too high. These results suggests that an endocranial volume for OL 45500 of less than 500 cm³ is not impossible.

Temporal base

Many *H. erectus* fossils preserve structures of the lateral cranial base, particularly the ventral surface of the temporal bone. This is also an important functional region of the skull because it houses the delicate organs of the middle ear, transmits the facial nerve through the stylomastoid foramen and articulates with the mandible. The temporal bone may also be a particularly phylogenetically informative region of the skull (Lieberman *et al.*, 2000; Lockwood *et al.*, 2004; Harvati *et al.*, 2004). Figure 4.23 illustrates the landmarks used in the temporal base analysis, which capture the shape, orientation and topography of the inferior temporal bone, including the mandibular fossa, the tympanic tube and stylomastoid foramen. A total of 13 fossils were included in the analysis from all geographic regions as summarized in Table 4.5.

Geography explained 44% of the total variance in the Procrustes superimposed shape coordinates while geological age explained 15% and centroid size accounted for 12% (see Table 4.10). As illustrated in Figure 4.24, there was an African – Asian division on the first PC, with D 2280 just overlapping the Asian distribution. As seen in Table 4.11, the three Zhoukoudian fossils scored higher than the other *H. erectus* individuals on PC 2, although OH 9 and Sm 1 scored only slightly lower than Zkd 3. D 2280, Ng 6 and S 17 scored lowest on this PC. About a third of variation along PC 1 was explained by geological age.

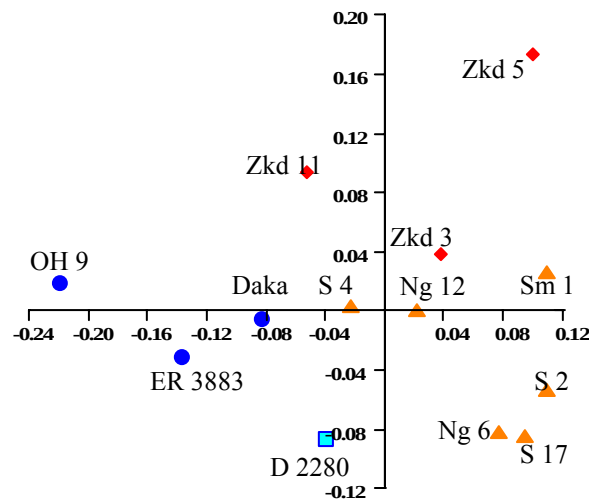
ER 3733 was initially included in this analysis but it was separated from all other individuals on PC 2 as a result of the very medial position of its lateral petrosal crest. This landmark was difficult to identify, possibly as a result of damage to the lateral

tympanic plate as described by Rightmire (1990). The inclusion of ER 3733 did not affect the relative positioning of fossils along PC1, and ER 3733 still grouped with the

Figure 4.23: The temporal base landmarks illustrated on the base of S 4. See Table 4.6 for details about the temporal base analysis and Table 4.2 for landmark abbreviations.



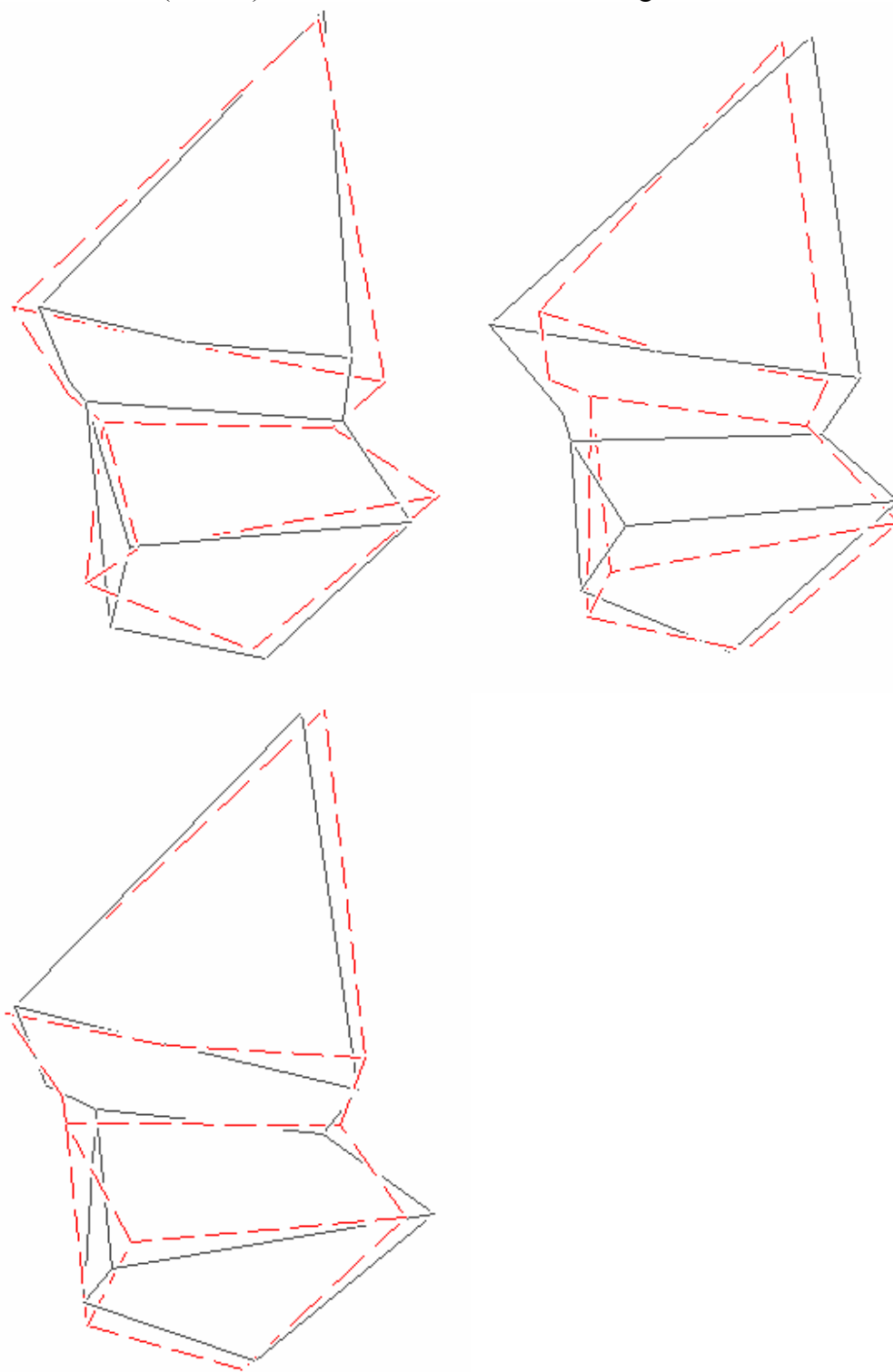
Figure 4.24: PCA of temporal base landmarks (see Table 4.6 for details). PC 1 and 2 are plotted below.



other African fossils. However, this did cause the separation of Zhoukoudian from the other specimens to occur on PC 3 rather than PC 2. Because this unusual morphology may be the result of diagenetic / taphonomic processes, ER 3733 was excluded from this analysis.

As illustrated by Figure 4.25, the African specimens had a wider and longer mandibular fossa which was much deeper medially but shallower laterally. The anterior face of the tympanic tube (from the petrosal crest to the squamotympanic fissure) was steeper laterally, the petrosal crest was extended medially and this end was more antero-superiorly angled. The temporosphenoid suture was more superiorly positioned relative to the center of the mandibular fossa in the African sample. Also, the tympanomastoid junction was more infero-anteriorly situated, so that the height between this and the petrosal crest is quite small. The Chinese fossils had a particularly narrow mandibular fossa which was also shorter antero-posteriorly at its lateral end; the anterior surface of the tympanic tube was long but not very steep. The Indonesian specimens were

Figure 4.25: Geographic shape variation in temporal base. The dashed red outline is the average configuration of each geographic region compared to the mean of the remaining specimens (solid black line) as viewed ventrally: Africa (upper left), China (upper right) and Indonesia (bottom). Shown in ventral view as in Figure 4.23.

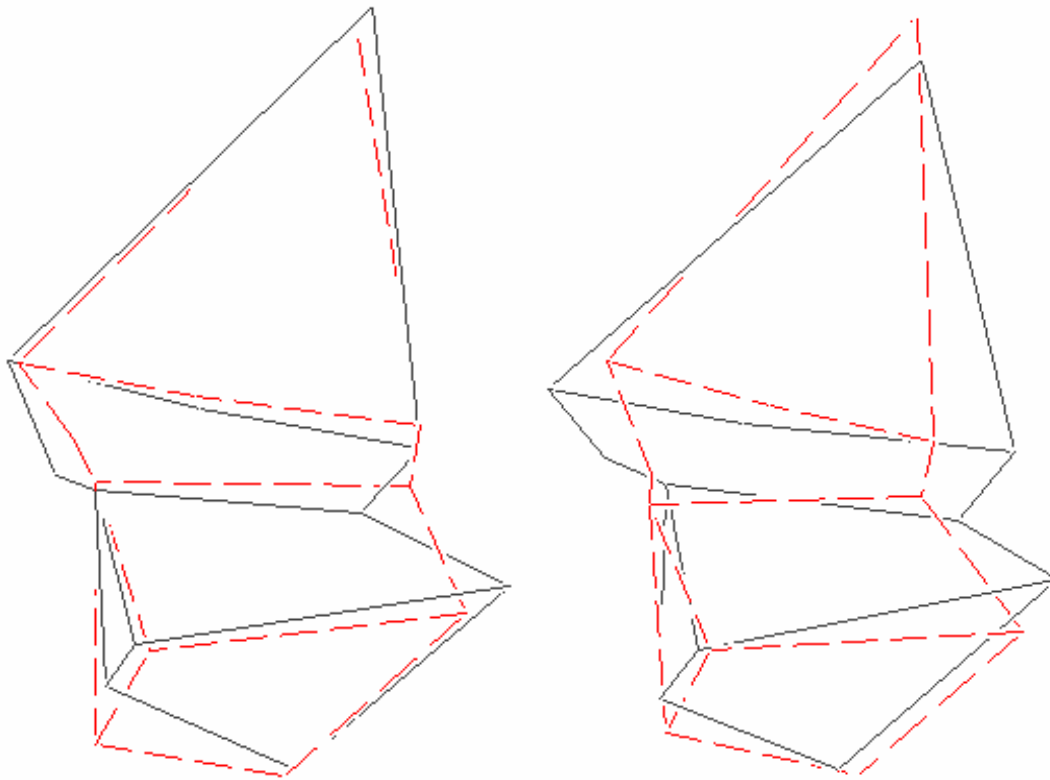


distinguished by the depth of the lateral mandibular fossa and the shallowness of the medial portions mandibular fossa; the squamotypanic fissure was also broad, while the petrosal crest was narrow and more inferiorly positioned at its medial end.

There were marked changes in the morphology of the mandibular fossa that corresponded to geochronological age of specimens. To a large degree they are consistent with the differences between the African and Indonesian fossils. The mandibular fossa was slightly narrower and shorter, and the depth of the fossa was less medially and greater laterally in younger fossils. The anterior face of the tympanic tube increases in length and the petrosal crest becomes narrower and slightly more infero-medially angled. The squamotympanic fissure is deeper medially in older specimens but deeper laterally in younger specimens. The tympanomastoid junction is also more superiorly located in younger specimens, creating greater height between it and the petrosal crest. Finally, the temporosphenoid suture becomes relatively more superiorly positioned over time. See Figure 4.26.

Individuals with larger basal temporal bone centroid sizes are elongated antero-posteriorly and narrower (medio-laterally) across the mandibular fossae. The mandibular fossa is also more superiorly situated. The fossa is less constricted laterally (there is greater antero-posterior distance between the lateral articular fossa and the postglenoid process). In specimens with larger basal temporals, the medial end of the petrosal crest is also angled more postero-inferiorly, increasing the length of the anterior face of the tympanic tube medially. See Figure 4.26.

Figure 4.26: Temporal and size-related shape variation in the temporal base. Shape change associated with decreasing geochronological age (solid black to dashed red) of *H. erectus* is shown on the left. Shape differences between individuals with a smaller (solid black line) and larger (dashed red line) basal temporal bone centroid size shown on right. Shown in ventral view as in Figure 4.23.



Occipital profile

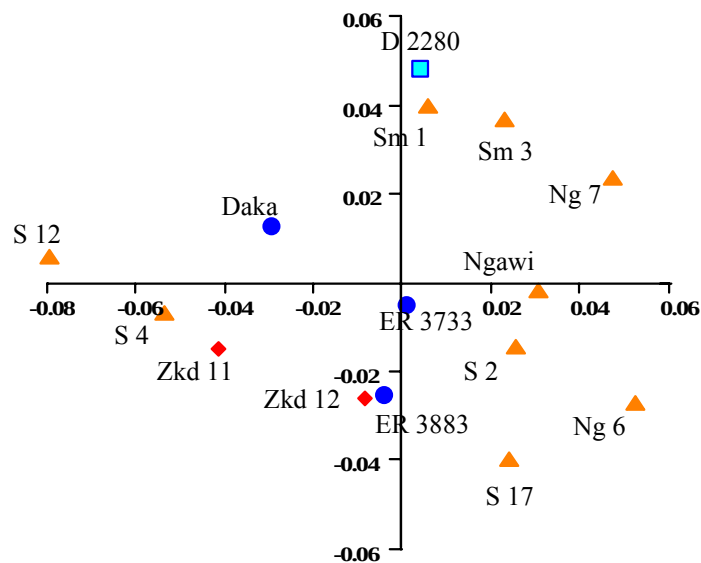
Another analysis focused more specifically on the occipital bone. As illustrated by Figure 4.27, lambda, opisthion and eight semilandmarks were used which together characterized the midsagittal profile of the occipital bone. Specimens from all geographic regions were included, with an especially strong representation of Sangiran fossils (see Table 4.5).

Figure 4.27: Occipital semilandmarks. The ten evenly spaced (resampled) semilandmarks which capture the sagittal profile of the occipital bone from lambda to opisthion shown on Ng 7. The last few semilandmarks are not visible in lateral view but are estimated below. The lines between the points are for visualization purposes only. See Table 4.6 for details on the occipital analysis.



Less of the shape variance is explained by geography (20%) and size (6%) while geological age (16%) explains a similar proportion as in previous analyses (see Table 4.10). Although PC 1 accounts for nearly half of the total shape variance, the pattern is more difficult to interpret than in previous analyses. PC 1 vs. 2 is plotted in Figure 4.28. At the negative end of PC 1 were S 12 and 4 while other Sangiran (S 2, 17) and younger Indonesian fossils had the highest PC 1 scores. Zkd 12, D 2280 and the East Turkana hominins approach the younger Indonesians on PC 1, while Daka and Zkd 11 were more

Figure 4.28: PCA of occipital bone data set. The first two components are shown below. There is great variation within the Indonesian sample, particularly the Sangiran hominins.



similar to S 4 and 12. There was also not a strong geographic pattern on PC 2. D 2280 and the Sambungmacan specimens scored higher than the rest of the sample and are contrasted most strongly with S 17. None of the independent variables explained a significant proportion of variance along PC 1 or 2. However, on PC 1 there was a significant size effect within the later Indonesian group such that the smaller specimens scored higher than the larger ones.

Asterion was also initially included in the analysis in order to incorporate information about the breadth of the occipital bone. However, PC 1 (which mainly reflected variance in the position of asterion) showed very little geographic, temporal or size-related patterning. Therefore, variation in the position of asterion was best explained by inter-individual differences.

As shown in Figure 4.29, the most variable aspect of occipital shape was the extent and positioning of maximum posterior projection (which corresponded to the transverse occipital torus when present). In older individuals maximum posterior protrusion occurred relatively high on the vault while it was less marked and more inferiorly positioned in younger fossils. The occipital plane was also more vertical in younger individuals whereas it angled more gradually from lambda to the torus in lower scoring specimens. These were the same shape changes seen from the negative to positive ends of PC 1.

Figure 4.29: Temporal variation in occipital shape. The solid black line represents older individuals and the dashed red line indicates shape change in the occipital bone over time. Shown in lateral view. All specimens were scaled to the same unit centroid size by generalized Procrustes analysis.



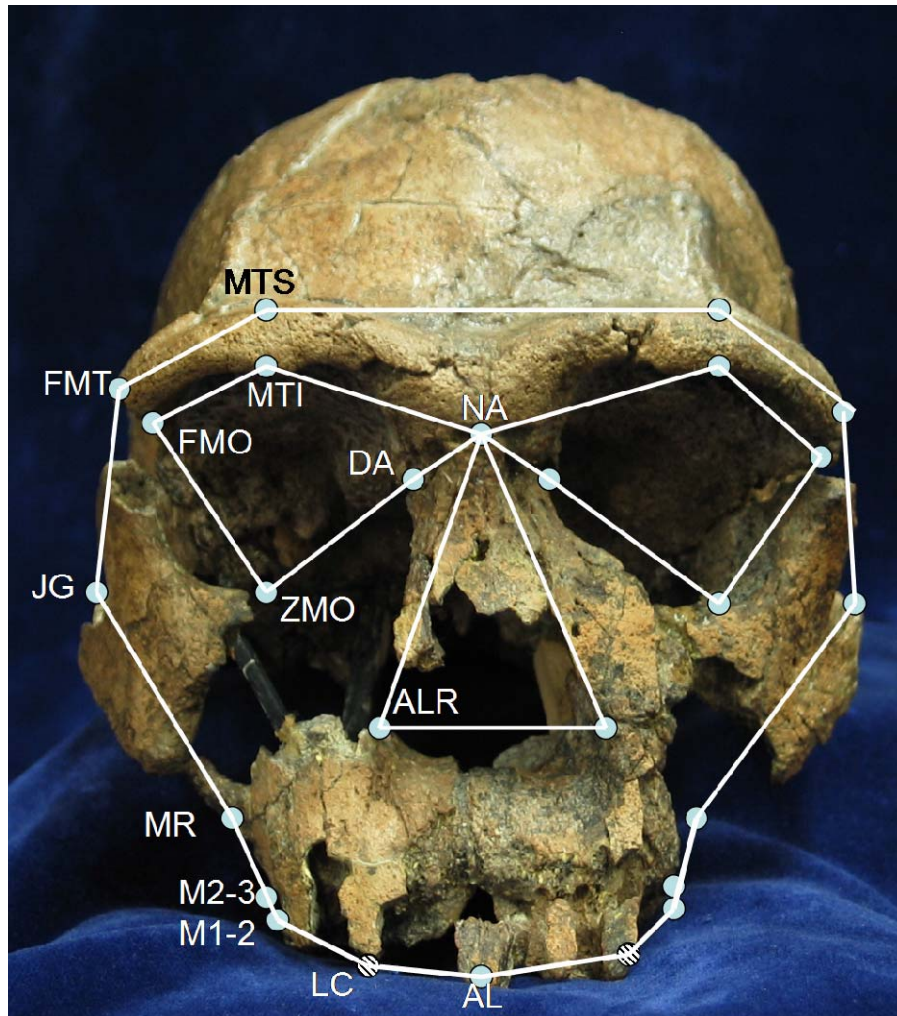
Face

While the face is only infrequently retained in *H. erectus* remains, there are a few well-preserved facial skeletons in both the Asian and African portions of the hypodigm. For this analysis the faces of ER 3733, WT 15000, S 17 and the composite male reconstruction of Zhoukoudian (Tattersall and Sawyer, 1996) were utilized (see Table 4.5). The landmark set shared by all four individuals provided information about the size and position of the orbits, the supraorbital torus, the nasal aperture and the palate. The height, width and depth of the face were also captured by these landmarks as demonstrated in Figure 4.30.

There was a reduction in the absolute size of the face from older to younger specimens ($R^2=0.97$, $p = 0.0150$). There was no clear relationship between cranial capacity and time in these four specimens (S 17 and WT 15000 are similar in age but S 17 has a much larger cranial capacity even if the WT 15000 value is increased to 909 cm^3 to account for further brain growth [Begun and Walker, 1993]). Thus, the decrease in size of the facial skeleton was not related to a change in cranial capacity. The face in the Zhoukoudian reconstruction is much smaller than in the other three specimens, particularly ER 3733, despite its much larger brain size. The faces of WT 15000 and S 17 were nearly identical in centroid size despite the differences in endocranial capacity between the two.

Geography accounts for the greatest proportion of shape change, nearly three quarters of total shape variation while each of the other variables (size and age) account for 37% of variation. The angle between the vectors of correlation coefficients of

Figure 4.30: Facial landmarks are shown below on ER 3733. Lines are for visualization purposes only and do not represent actual data. The lingual canine (LC) landmark is not visible in this view but its approximate position is indicated. Details about the facial analysis can be found in Table 4.6 and landmark abbreviations are located in Table 4.2.



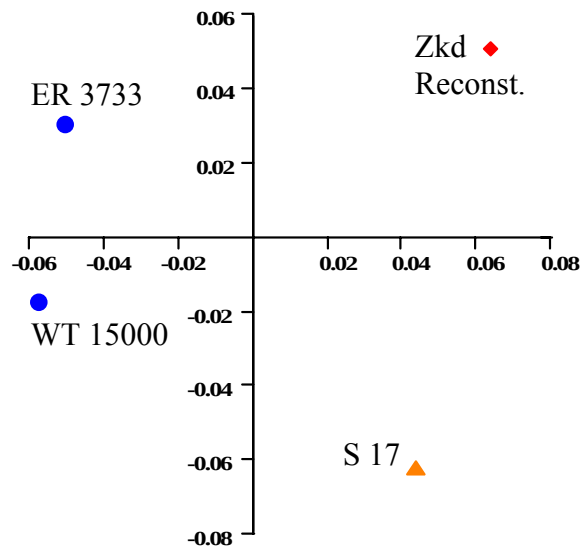
Courtesy of National Museums of Kenya

geological age and centroid size is very large, indicating a high negative correlation which is consistent with the observation that facial size decreases over time. See Table 4.10.

The results of the PCA indicate that the greatest variance (PC 1) separates the African and Asian specimens. The second PC separates the Chinese and Indonesian

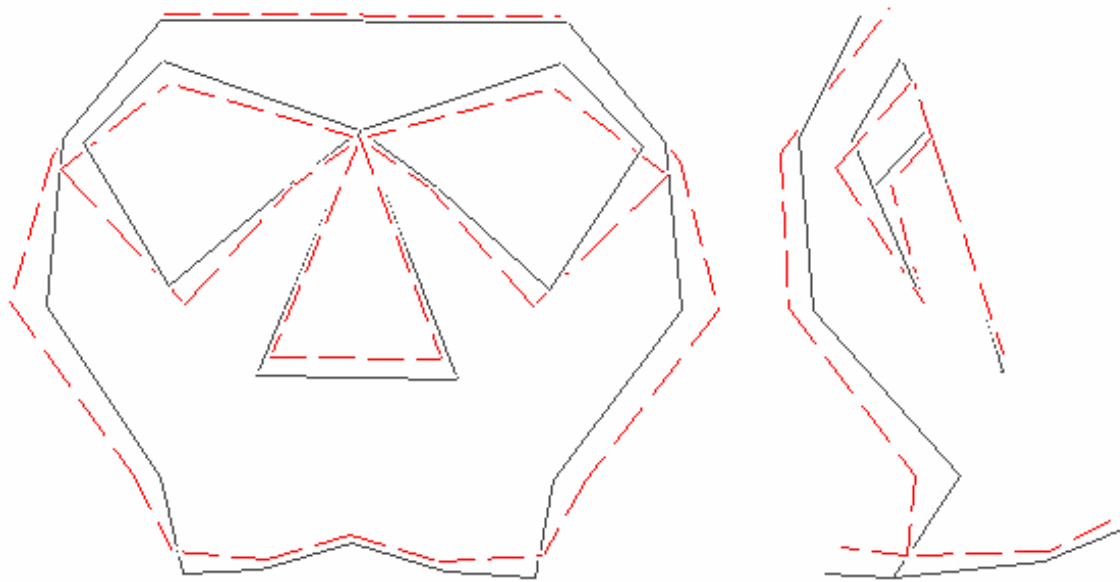
specimens while the two African fossils are more widely separated from on PC 3. See Figure 4.31. Variance in PC 1 scores is almost entirely explained by endocranial volume ($R^2=0.96$, $p = 0.0204$) while neither age or size are significantly correlated with PC 1 or PC 2.

Figure 4.31: PCA of facial landmarks (see Table 4.6 for details). The first PC is 46% of the variance while the second is 30%.



It is important to note that with the exception of WT 15000, all of these faces have been subject to major reconstructive efforts and are unlikely to preserve the original facial anatomy with 100% accuracy. Also, with only four specimens in the analysis, individual variations contribute disproportionately to the PCA. Therefore, direct comparisons between the individual fossils were made, rather than using the regression coefficients and only the most apparent shape differences are reported and illustrated in Figure 4.32.

Figure 4.32: Geographic shape variation in the facial skeleton. The African (solid black line) compared to the Asian (dashed red line) facial skeleton in frontal and lateral views. All specimens were scaled to the same unit centroid size by generalized Procrustes analysis.



Overall the Asian faces were broader across jugale and slightly broader across the origin of the zygomatic processes of the maxillae. The Asians had greater depth at mid-face due to the more posterior location of jugale. The supraorbital tori were also taller in the Asian fossils. The Zhoukoudian reconstruction differs from S 17 in being narrower across the inferior zygomatic processes, but not across jugale. The inferior border of the zygomatic processes is also positioned more superiorly and posteriorly. Alveolare was much more anteriorly positioned and the maximum nasal aperture breadth is wider and more inferiorly situated. They were similar in their supratotal and orbital morphology and in the depth of their faces. The two African specimens had similar facial morphology overall. Compared to ER 3733, WT 15000 had taller and more superiorly positioned supraorbital tori whose lateral corners were more retracted. The orbits were also

relatively taller. There was more anterior projection at nasion, alveolare and alare. The zygomatic processes originated more supero-anteriorly and the palate (as measured to the M1-M2 junction) was posteriorly elongated.

Asia

Two different neurocranial landmark sets were used to examine the relationships within Asian *H. erectus* fossils. The Indonesian analysis maximized representation from sites within Indonesia by incorporating two specimens each from Ngandong, Sambungmacan, Sangiran and Zhoukoudian. In order to include a second fossil from the Sangiran dome region (S 2), it was necessary to exclude the midline frontal bone and medial supraorbital torus landmarks. In the Zhoukoudian analysis, the landmark set was designed to maximize the number of fossils from Zhoukoudian that were included. By excluding opisthion and the temporosphenoid suture, nine individual fossils were included: four from Zhoukoudian, three from Ngandong and one each from Sambungmacan and Sangiran. Landmarks and samples for both analyses are summarized in Table 4.6.

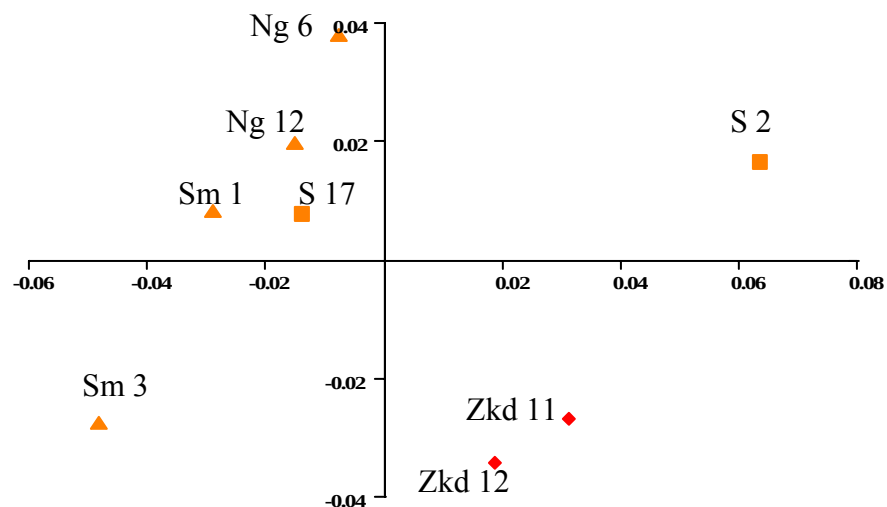
Geography explained approximately twice as much of the neurocranial shape variation in the Zhoukoudian analysis as in the Indonesian analysis (42% versus 19%). In both cases geological age accounted for about a quarter of the variance in the Procrustes superimposed shape coordinates. Size explained a slightly higher proportion of shape variance in the Indonesian analysis (16% versus 11%) (see Table 4.12).

Table 4.12: Asian neurocranial analyses: proportion of total variance explained by geography, geological age and centroid size.

Factor	Asian- Indonesian		Asian- Zhoukoudian	
	Variance	% of Total	Variance	% of Total
Total	0.00361	100	0.00327	100
Geography	0.00070	19.3	0.00138	42.3
ln(geological age)	0.00085	23.6	0.00083	25.3
ln(centroid size)	0.00056	15.6	0.00037	11.4
Geog. & ln(geol. age)	0.00146	40.4	0.00177	54.2
Geog. & ln(cent. size)	0.00125	34.6	0.00165	50.5
ln(geol. age) & ln(cent. size)	0.00129	35.6	0.00115	35.1
Geog., ln(cent. size) & ln(geol. age)	0.00193	53.4	0.00204	62.4
Angle between ln(cent. size) & ln(geol. age)		54		61

Figure 4.33 is a plot of the first two PCs from the Indonesian analysis; the Zhoukoudian crania scored positively on PC 1 while the majority of Indonesian specimens scored negatively. S 2, however, had the highest score of all. The Zhoukoudian fossils and Sm 1 scored lowest on PC 2. While the Chinese fossils grouped together on PCs 1 and 2, the Indonesian specimens do not group together due to the different cranial shapes of S 2 on PC 1 and Sm 3 on PC 2. There was a significant relationship between PC 1 scores and both age and size of the fossils, along with their interaction term as indicated in Table 4.13; in the older age categories smaller fossils scored higher, but in the most recent time band the inverse was true.

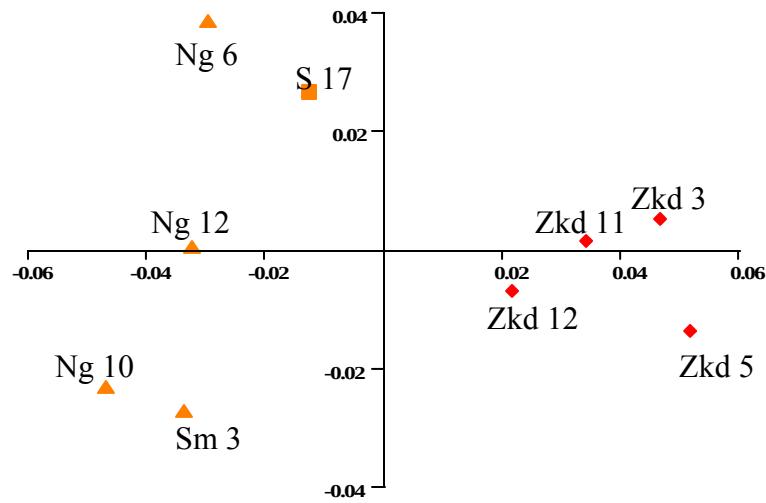
Figure 4.33: PCA of Asian-Indonesian neurocranial data set (see Table 4.6 for details). The first two PCs are plotted below and illustrate the lack of morphological continuity within the Sangiran sample.



In the Zhoukoudian PCA, seen in Figure 4.34, there was a clear Indonesian – Chinese division along PC 1 now that S 2 was not part of the analysis. The relationship

between PC 1 scores and geological age was almost significant ($R^2 = .43$, $p = 0.0549$) and was highly significant when S 17 was not included in the regression calculations ($R^2 =$

Figure 3.34: PCA of Asian-Zhoukoudian neurocranial data set (see Table 4.7 for details). PC 1 and 2 are shown below and demonstrate a division between the Zhoukoudian fossils and the late Indonesian / S 17 samples.

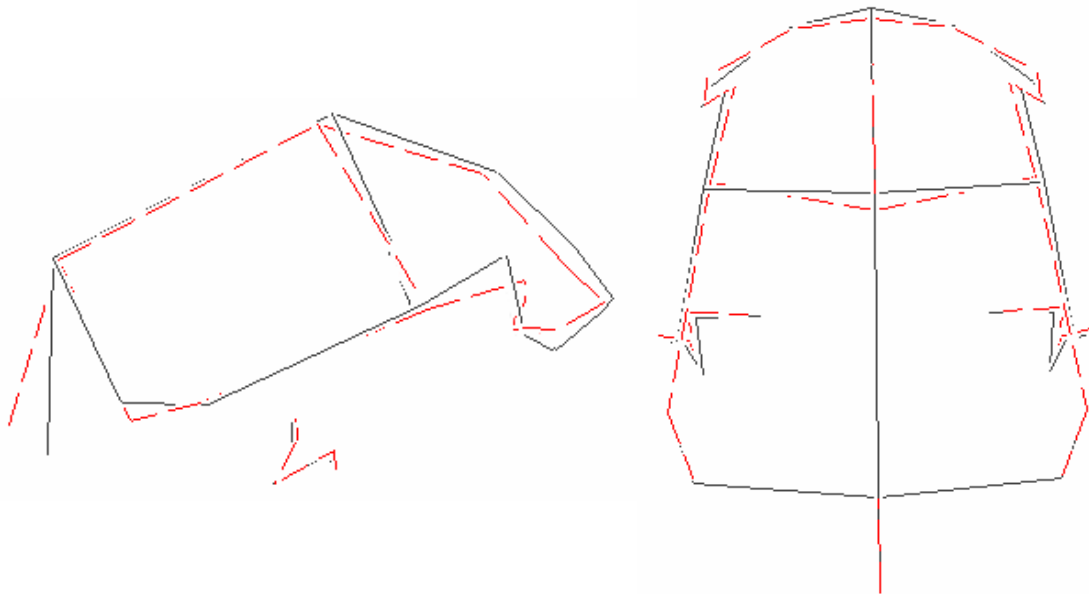


0.94, $p < 0.0001$). This indicates a stronger geographic than temporal pattern of cranial shape in this analysis. There was a significant relationship between size and PC 2 scores within the Chinese sample only ($R^2 = 0.91$, $p = 0.0453$) such that larger fossils scored lower than small ones.

In both analyses the aspects of cranial shape that differentiated the Indonesian (with the exception of S 2) from the Chinese specimens are the same as those described previously. These differences are illustrated in Figure 4.35 which uses the Zhoukoudian landmark set. The Chinese fossils had more posterior projection at inion and a more inferiorly situated opisthion. In the Indonesian sample, the parietal bone was relatively longer and the frontal squama was wider, with a higher position of frontotemporale. The

crania were wider across the temporal bone in the Chinese sample, and the lateral ends of the supraorbital torus were slightly more superiorly positioned. Figure 4.36 illustrates the

Figure 4.35: Geographic shape differences in the Asian Zhoukoudian data set (see Table 4.6 for details). Shape differences between the Indonesian (solid black line) and Chinese (dashed red line) average configurations are shown in lateral and superior views. The exclusion of opisthion and the temporosphenoid suture has resulted in the “floating” appearance of some landmarks inferiorly (PO, AUR, PG, EG and TM).

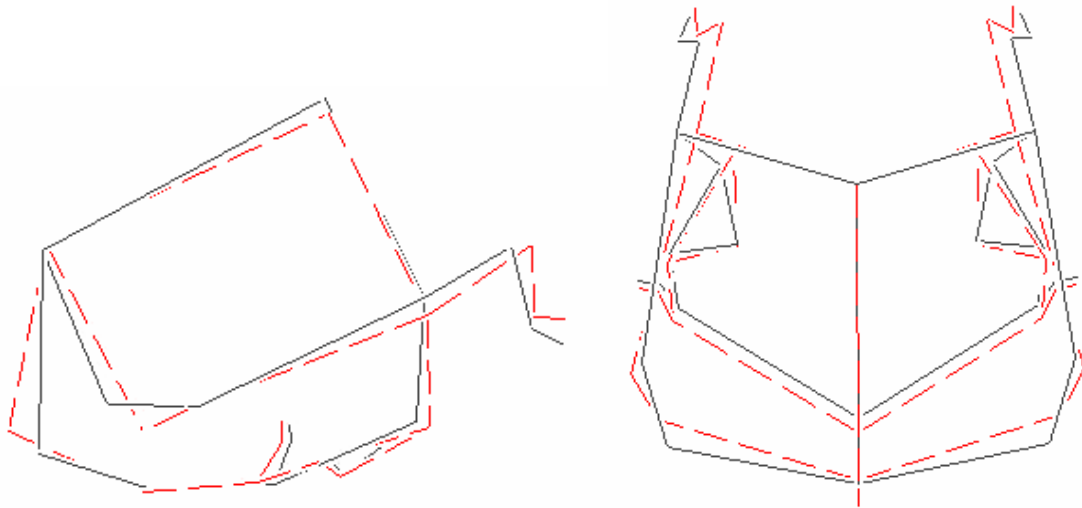


shape differences between S 2 and other Indonesian fossils using the Indonesian landmark set. S 2 differed from the other Indonesian specimens in some of the same features, including a more supero-posterior position of inion and a narrower frontal squama. The comparatively shorter parietomastoid suture, the more posterior position of porion and auriculare and more anteriorly situated frontotemporale were also unique to S 2. The temporosphenoid suture crossed onto the squama in a more anterior position and there is less width across this region, but there is greater width across the posterior vault in this specimen. The differences between Sm 3 and the Ngandong / Sangiran specimens

Table 4.13: Asian neurocranial analyses: significant results of multiple regression of PC 1 and PC 2 scores on geological age and centroid size.

Analysis	PC	% of Variance	Overall Model		Parameter Estimates (Pr > t)		
			ANOVA				
			R ²	Pr(R ²) > F	ln (geol. age)	ln(centsize)	Interaction
Indonesian	1	0.36	0.83	0.0491	0.0386	0.0476	0.0393
	2	0.19	-	N/S	-	-	-
Zhoukoudian	1	0.46	-	N/S	-	-	-
	2	0.14	-	N/S	-	-	-

Figure 4.36: Unique cranial shape of S 2 (dashed red line) compared to the average configuration of the remaining Indonesian fossils (solid black line) shown in lateral and superior views. The landmarks correspond to the Asian Indonesian neurocranial analysis (see Table 4.6 for details).



are relatively small and include the more antero-inferior position of opisthion, greater width across the temporals and supraorbital torus and the more inferior position of the midline post-toral sulcus in Sm 3.

Afro-Georgian

Three neurocranial landmark sets were used to explore variation in the Afro-Georgian *H. erectus* sample. The original landmark set was identical to that used in the original neurocranial analysis (see Table 4.7). The second analysis (using the OH 9 landmark set) also included the large OH 9 fossil. The third analysis (the subadult

landmark set) was the most inclusive, incorporating OH 9, WT 15000 and D 2700 (the latter two are both juvenile individuals).

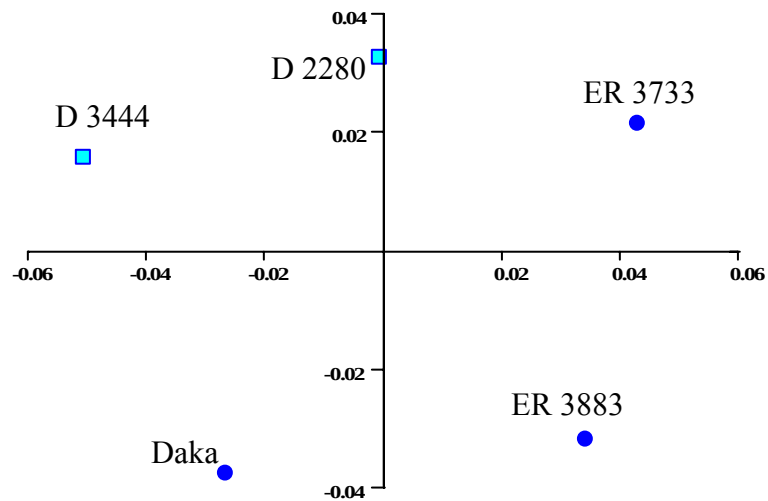
Temporal variation was the least important factor in all three analyses as described in Table 4.14. Centroid size accounted for a large proportion of the total shape variance in the original and OH 9 data sets, while both geography and size explained a high percentage of shape variance in the subadult landmark set.

In the first PCA, plotted in Figure 4.37, the East Turkana specimens scored high while Daka overlapped the two Dmanisi fossils at the negative end of the component. There was a similar pattern on PC 1 in the OH 9 analysis and OH 9 grouped with the East Turkana specimens (see Figure 4.38). As summarized in Table 4.15, nearly all variation in PC 1 scores was explained by the centroid size of the fossils in the OH 9 analysis whereas this relationship just failed to reach significance in the original analysis because Daka scored much lower than expected for its size. In the OH 9 analysis, both the addition of the large OH 9 cranium and the exclusion of lambda (a key region where Daka differs from other African specimens) resulted in a significant relationship. There was not a significant relationship between PC 1 scores and cranial capacity in either analysis. While there was a general trend for specimens with larger endocranial volumes to also have larger crania (as measured by centroid size), Daka defies this trend by having a small cranium but a larger brain size. This may be related to the thinner cranial vault bone seen in the Daka specimen (at least as measured at bregma) (Asfaw *et al.*, 2002).

The third analysis, which incorporated two juvenile specimens, WT 15000 and D 2700, showed clearer separation between the African and Georgian fossils on the first PC

as illustrated in Figure 4.39. Size variation accounted for nearly all of the variation along this component (see Table 4.15) as was the case in the OH 9 analysis. While cranial

Figure 4.37: PCA of original Afro-Georgian neurocranial data set (see Table 4.7 for details). The first two components are plotted below. The Dmanisi cranial shape differs from the East Turkana sample along PC 1 and from Daka on PC 2.



capacity was also significantly correlated with PC 1 scores, it did not explain a significant portion of the variance above and beyond centroid size.

The shape differences between the two geographic regions are small. Figure 4.40 shows the average Georgian and African landmark configurations using the original landmark set. The African specimens had a relatively shorter parietal and more posterior projection at inion, which resulted in a more angled occipital bone. They were also narrower across the temporal base but had less constriction across frontotemporale. The lateral ends of the supraorbital torus were slightly more inferiorly positioned in the Georgian fossils.

Table 4.14: African neurocranial analyses: proportion of total variance explained by geography, geological age and centroid size.

Factor	Original		OH 9		Subadult	
	Variance	% of Total	Variance	% of Total	Variance	% of Total
Total	0.00388	100	0.00373	100	0.00412	100
Geography	0.00117	30.1	0.00102	27.4	0.00107	26.0
ln(geological age)	0.00075	19.3	0.00049	13.2	0.00059	14.3
ln(centroid size)	0.00141	36.2	0.00146	39.1	0.00129	31.4
Geog. & ln(geol. age)	0.00210	54.1	0.00167	44.9	0.00158	38.3
Geog. & ln(cent. size)	0.00236	60.8	0.00198	53.1	0.00172	41.7
ln(geol. age) & ln(cent. size)	0.00230	59.2	0.00196	52.6	0.00177	43.0
Geog., ln(cent. size) & ln(geol. age)	0.00304	78.4	0.00255	68.4	0.00215	52.3
Angle between ln(cent. size) & ln(geol. age)		77		71		55

Table 4.15: African neurocranial analyses: significant results of multiple regression of PC 1 and PC 2 scores on geological age and centroid size

Analysis	PC	% of Variance	Overall Model				
			ANOVA		Parameter Estimates (Pr > t)		
			R ²	Pr(R ²) > F	ln (geol. age)	ln(cent. size)	Interaction
Original	1	0.41	-	N/S	-	-	-
	2	0.27	-	N/S	-	-	-
OH 9	1	0.41	0.91	0.0034	-	0.0034	-
	2	0.19	-	N/S	-	-	-
Subadult	1	0.33	0.9	0.0003	-	0.0003	-
	2	0.23	-	N/S	-	-	-

Figure 4.38: PCA of Afro-Georgian OH 9 neurocranial data set (see Table 4.7 for details). PC 1 and 2 are shown below. The Dmanisi fossils do not differ from the African sample as a whole because of overlap with Daka. D 2280 is more similar to the East Turkana and Olduvai specimens than is D 3444.

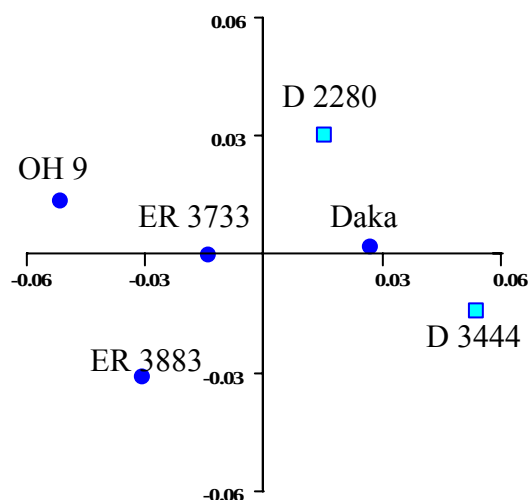
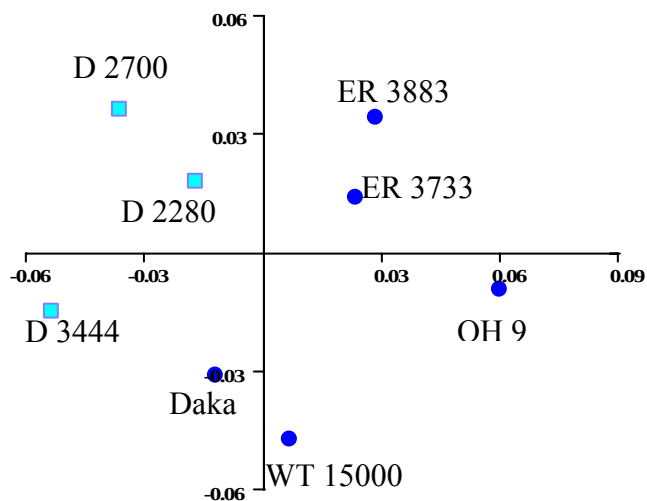


Figure 4.39: PCA of Afro-Georgian subadult neurocranial analysis (see Table 4.7 for details). The first and second components are plotted below and indicate separation of the Georgian and African samples on the first component. The two juveniles (WT 15000 and D 2700) do not share any special resemblance on these components.



The size-related shape differences are illustrated in Figure 4.41 using the OH 9 landmark set. The changes corresponding to an increase in size were a relatively longer, lower cranial profile with a narrower vault across the temporals but less constriction across frontotemporale. The frontal squama was much less steep in larger individuals, but the supraorbital torus was considerably more anteriorly projecting and the lateral corners were more superiorly situated. Both inion and opisthion occupied more superior positions in larger individuals as well. Smaller individuals were broader across the parietal notches than at asterion while the opposite was true in larger ones. In smaller individuals there was greater antero-posterior distance between the mandibular fossa and the temporosphenoid suture.

It was also possible to examine the shape differences associated with being a subadult using two subadult fossils, WT 15000 and D 2700. Figure 4.42 illustrates these differences using the subadult landmark configuration. The shape changes associated with development are shown in Figure 4.42; the biggest differences between the subadult and adult cranial morphology were in the occipital bone – there was less height at lambda and inion was not as projecting. The subadult specimens were also distinct in the more lateral and inferior positioning of the entoglenoid. With only two subadult specimens, however, it is unclear whether these ontogenetic shape changes can be extrapolated to *H. erectus* as a whole.

Figure 4.40: Differences between Georgian (solid black line) and African (dashed red line) cranial shapes shown in lateral and superior views. The landmarks used correspond to the Afro-Georgian original analysis (Table 4.7).

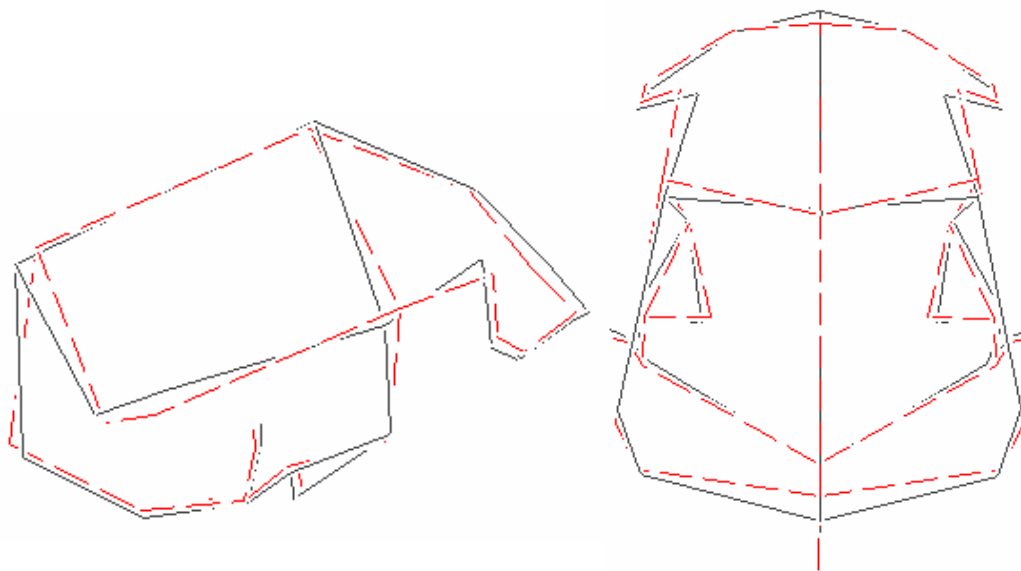


Figure 4.41: Size-related shape variation in the Afro-Georgian OH 9 analysis (Table 4.7). The shape associated with smaller individuals is shown by the solid black line and the shape of larger individuals is shown by the dashed red line.

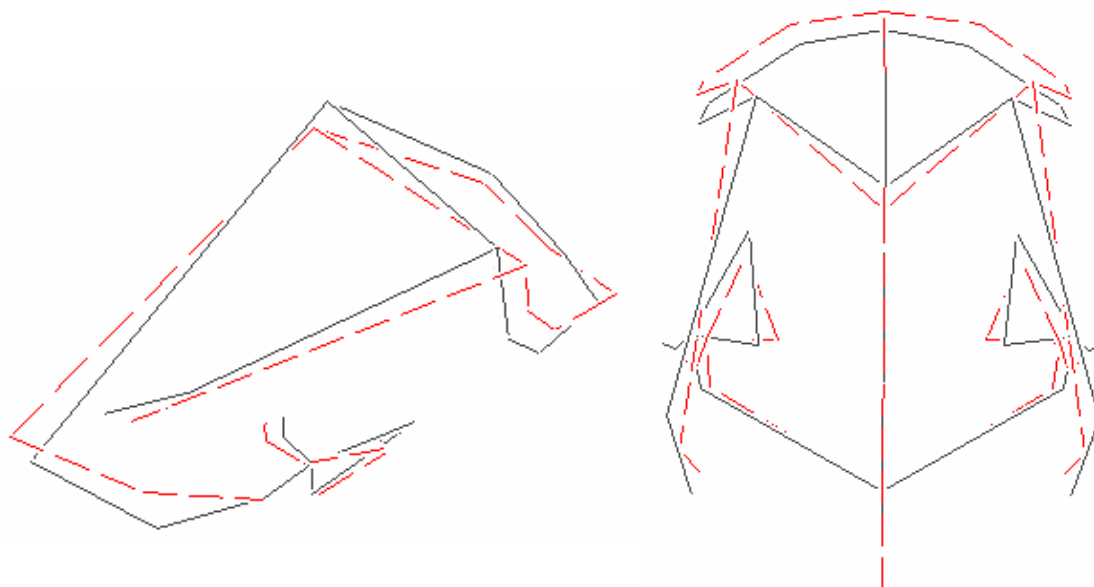
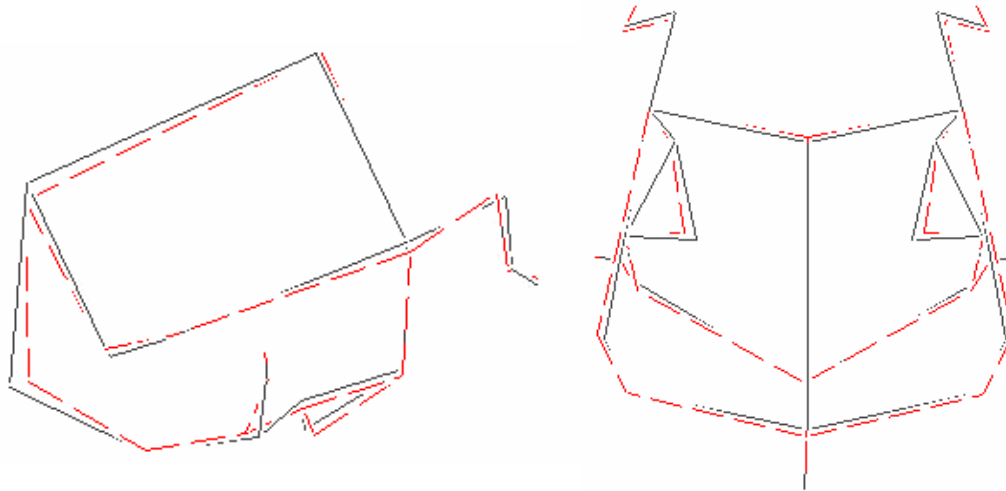


Figure 4.42: Ontogenetic shape variation in the Afro-Georgian subadult data set. The differences between the adult (solid black line) and juvenile specimens (dashed red line) are shown below. The juveniles were represented by WT 15000 and D 2700.



Discussion:

This study explored temporal, geographic and size-related patterns of intraspecific variation within *H. erectus* using the shape of both the cranium overall as well as several more restricted cranial regions (i.e., the frontal, occipital, temporal and face). I used PCA to assess affinities among specimens from East and West Turkana, Olduvai Gorge, Daka, Olorgesailie, Dmanisi, Zhoukoudian, Sangiran, Ngandong, Sambungmacan and Ngawi, and multiple regression analysis to quantify the relative influence of geographic origin, geochronological age and size to cranial shape. Visual comparison of average configurations highlighted the actual shape differences highlighted by the regression analyses.

Temporo-geographic versus size-related variation

In addition to describing variation in *H. erectus* cranial shape, a major goal of this analysis was the quantification of the effects of geographic, temporal and size variation on cranial shape. Because the relationship between age and cranial size was weak, it was possible to distinguish more easily between these factors than between geography and age which were more highly conflated. Numerous specimens were larger than expected for their age (S 17, OH 9 and Ng 6), while others were smaller than predicted (D 2280, Daka, S 2 and Sm 3). The tight correlation between the size of the frontal bone and cranial capacity yielded an estimated endocranial volume between 499 and 696 cm³ for OL 45500, which is therefore the youngest (0.9 Ma) and likely the smallest African *H. erectus* specimen. It is clear from the above analyses that the effects of geography / time are greater than the effect of size variation on cranial shape in *H. erectus*. As indicated by the proportion of total variance in both cranial shape and PC scores, temporo-geographic differences are a better predictor of shape than either cranial size or endocranial capacity. The observations from this study pertaining to the cranial shape of individual specimens and temporo-geographic samples accorded well with those made by previous workers. However, the use of 3D geometric morphometrics also highlighted more subtle shape patterns. Correspondence with previous descriptions / comparisons will be discussed in greater detail below.

While the patterns of cranial shape variance explained by geological age and by centroid size were not entirely independent, neither were they highly correlated as indicated by angles of 39-70° between their vectors. The variance explained by these

factors was more strongly correlated in the frontal bone and facial analyses, but the latter had such a small sample size that its results must be regarded with caution.

The most marked changes in cranial shape over time include an outward expansion of the frontal squama, a decrease in the constriction across frontotemporale and a narrowing of the supraorbital torus. Asterion becomes more posteriorly located and the parietal notch migrates anteriorly, increasing the length of the parietomastoid suture in this region. Also, the relative inferior projection of the entoglenoid process decreases over time. Many of these shape changes are consistent with an increase in brain size in *H. erectus*.

With the exception of an increase in cranial capacity, only a few temporal trends have been identified that apply across geographic groups of *H. erectus*. Temporal trends identified previously by Bräuer (1994) are a decrease in the length and breadth of the mandibular fossa and an increase in biauricular breadth and the bregma-asterion chord length. These results of Bräuer (1994) are not directly comparable to this study because he used a more limited sample of *H. erectus* individuals (e.g., no Ngandong individuals were used) and his variables were raw measurements with no size-correction. However, this study also found an increase in the relative bregma-asterion chord length and possibly a slight increase in the biauricular breadth through time. The African sample had a particularly wide mandibular fossa, in contrast to the Zhoukoudian sample, but relative to the rest of the cranium the fossa did not become narrower or shorter over time. Santa Luca (1980) also noted an increase in the verticality of the occipital plane through time. There was not strong support for this result in this study. Although the occipital plane was more vertical in the younger specimens in the original neurocranial analysis,

this was not the case when additional Dmanisi specimens were included. However, the results of this study are not directly comparable to Santa Luca's analysis because he did not include any of the African *H. erectus* specimens and because he positionedinion in the center of the occipital torus (rather than where the superior nuchal lines met on the midline plane).

Implications for Homo erectus evolutionary history and taxonomy

In general, the most variable aspects of cranial shape (as identified by the first PC in each PCA) did not differentiate between Africa and Asia or between Africa / Georgia and Asia. Most frequently the younger Indonesian specimens were contrasted with the East Turkana, Dmanisi and Zhoukoudian fossils in those aspects of cranial shape which were most variable. The distinct African vs. Asian patterns of temporal base and facial shape were notable exceptions to this rule, although the very small sample size in the latter analysis cautions against drawing wide-reaching conclusions regarding intraspecific variation of the facial skeleton.

Although the Indonesian specimens appeared to form a homogenous group in some neurocranial shape analyses, the addition of multiple Sangiran fossils resulted in a discontinuous distribution (e.g., Figure 4.2 vs. Figure 4.16). The Indonesian fossils were all quite similar in their frontal bone shape, but of the earlier Indonesian fossils only S 17 was complete enough to be analyzed (Figure 4.18). However, in the more inclusive occipital profile analysis, S 4 and 12 were quite different from the remaining Indonesian fossils from Sangiran, Ngandong and Sambungmacan (Figure 4.28). Even when

comparing only the Zhoukoudian and Indonesian specimens, there was not perfect separation as S 2 and Sm 3 overlapped the Zhoukoudian distribution on PCs 1 and 2, respectively (Figure 4.33). The results of this study do not confirm a single Indonesian cranial shape *Bauplan*.

This pattern is different from that reported by Antón and colleagues (Antón, 2002; Antón *et al.*, 2002b) who argued for a consistent cranial shape across time in Indonesia. While their analyses incorporated a wide range of specimens, the limited number of linear measurements (three to five) analyzed may not have been sufficient to capture the entirety of the cranial shape. The results of this study were more consistent with those of Delson *et al.* (2001) based on the midsagittal profile, and Kidder and Durband (2004) and Liu *et al.* (2005) based on linear measurements, all of whom found broad but not complete separation between the two Asian groups.

The Sangiran specimens were clearly more variable than the later sample from the same region. Antón (2003, p.144) found that the greater range of morphological variation in discrete traits observed in the earlier Indonesian sample subsumed the more limited morphological variability in the later sample. This argument did not apply to aspects of cranial shape, however, as was particularly clear in the occipital bone profile analysis. Several recent Indonesian fossils were not within the range of the earlier specimens (Figure 4.28), nor were they within the range of variation of S 2 and S 17 in terms of overall cranial shape (Figure 4.16). The fact that some Sangiran individuals resembled the Indonesian group while others share aspects of cranial shape with the African specimens could support previous suggestions of multiple early migrations to this region (Kaifu *et al.*, 2005).

The consistent homogeneity of the Ngandong, Sambungmacan and Ngawi fossils in nearly every analysis may reflect population-level similarities. This lends support to the interpretation of a similar age for these specimens despite the lack of provenance for some individual fossils. This study also confirms the interpretation of the Ngawi specimen as more similar to Ngandong and Sambungmacan than to the Sangiran sample (Widianto and Zeitoun, 2003). Despite its small size, Sm 3 plots in the general vicinity of the other young (but large) Indonesian hominins. However, Sm 3 is always at the edge of the distribution and is frequently somewhat separated from other *H. erectus* specimens, particularly the African individuals. Although S 17 is likely more than 1 Myr older than the younger Indonesian specimens, they share a similar cranial shape. This confirms earlier observations by Jacob (1975) and Sartono (1975) of a greater similarity between Ngandong / Sambungmacan and S 17 than between Ngandong / Sambungmacan and other Sangiran individuals. It was difficult to identify clear temporal trends within the Indonesian sample, in part because of the closer resemblance between S 17 and the much younger Ngandong / Sambungmacan / Ngawi samples rather than S 2 or S 12, who are more similar in age to S 17. This pattern may be related to the larger size of S 17 compared to other Sangiran fossils and highlights the influence of both geological age and size on cranial form in the Indonesian fossils. Jacob (1975) has also argued for a separate S 4 – Ngandong lineage due to similarities in the base and occipital bone. While S 4 most closely resembles Ng 12 among the Indonesian specimens in basal temporal bone anatomy, the sagittal occipital profile of S 4 is very different from that seen in Ngandong (more closely resembling the pattern seen in S 12). Therefore the evidence is ambiguous in regards to the hypothesized relationship between S 4 and Ngandong.

The frontal bone of the Indonesian fossils was distinctive in those that could be analyzed due to the lack of a supraglabellar sulcus, the postero-superior position of frontotemporale, and the very straight supraorbital torus (in anterior view) which was particularly thick at its lateral extent (corresponding to the development of a zygomatic trigone) and then angled inferolaterally to the frontozygomatic suture. The glabellar region (regardless of the presence of glabellar inflexion) was more anteriorly projecting than the lateral portions which sloped posteriorly, creating a rounded edge in *norma verticalis*. The individual elements of frontal bone shape which together differentiate the Indonesian *H. erectus* have been described previously by Weidenreich (1951), Santa Luca (1980), Rightmire (1990), Wolpoff (1999) and Antón (2002, 2003). Other general Indonesian *H. erectus* traits include a deeper lateral mandibular fossa and a narrower petrotympanic crest.

Although the Indonesian hominins as a whole were not distinct in their overall cranial shape and occipital profile, as discussed above, the recent Javanese hominins (and usually S 17) did exhibit some unique shape characteristics relative to all other *H. erectus* fossils. In particular, the recent Indonesian specimens had a relatively long frontal bone due to the well-developed supraorbital region and a more outwardly expanded frontal squama. They also had a long, vertically oriented occipital bone with a short and fairly horizontal nuchal plane and a more elongated parietomastoid suture. The more horizontal orientation of the nuchal plane results in a more superior position for opisthion. Some of these shape changes – like the superior and lateral expansion of the frontal squama and longer parietomastoid suture – reflect broader evolutionary patterns and may be linked to the increasing brain size through time that has been documented in

H. erectus by numerous workers (Wolpoff, 1984; Leigh, 1992; Antón and Swisher, 2001; Rightmire, 2004).

The Chinese sample from Zhoukoudian formed a coherent group in terms of neurocranial shape, a conclusion which was consistent with multivariate analyses of linear measurements (Antón, 2002; Antón *et al.*, 2002b; Kidder and Durband, 2004). Increasing the representation of the Zhoukoudian individuals in the PCA made this particularly apparent by creating additional separation between these specimens and the early African and Georgian samples (Figure 4.12). The addition of Zkd 5 and 3 also incorporated additional temporal and size-related variation, because Zkd 5 is the largest and youngest of the Zhoukoudian fossils, while Zkd 3 is the smallest. Previous analyses have suggested that Zkd 3 may be a subadult individual (Black, 1929, 1930, 1931; Weidenreich, 1943; Antón, 2001), but grouped with the other Chinese fossils in this analysis. The rounded midsagittal frontal bone contour and thin supraorbital torus were two features which appeared more consistent with a young adult in Antón's (2001) analysis, but Zkd 3 was within the variation of other adult Zhoukoudian fossils in its overall frontal bone shape (Figure 4.17). Although Zkd 3 did not fall outside the range of cranial shape present in the other adult Zhoukoudian fossils, other indicators of age were not considered in this study. Therefore, this analysis lent weak support to a adult status for this fossil. While the scale of differences within the Zhoukoudian sample is similar to that seen within the late Indonesian sample, the more extreme position of the youngest specimen, Zkd 5, in the PC plots suggests that this fossil expresses the Chinese morphology most strongly, which may be the result of isolation of this population as suggested by Antón (2002).

The greater breadth across the midvault (including auriculare) noted here for the Zhoukoudian fossils was consistent with previous descriptions of an absolutely narrow anterior and posterior vault relative to biauricular breadth (Antón, 2002, 2003; Kidder and Durband, 2004). However, other changes related to the projection at inion and details of the frontal bone shape were also apparent. The Chinese fossils had a relatively long frontal squama due to a more posteriorly positioned bregma and a more projection of the occipital at inion. There was a strong frontal tuberosity with an anteriorly positioned mid-toral sulcus and a narrow, straight supraorbital torus. These aspects of frontal bone shape were consistent with previous descriptions of the Zhoukoudian fossils (e.g., Weidenreich, 1951; Santa Luca, 1980; Antón, 2002, 2003). The mandibular fossa was also quite narrow, and the posterior position of the petrosal crest (the inferior border of the tympanic tube) relative to the squamotympanic fissure created a long anterior face of the tympanic bone. This may have been related to the very short and deep mandibular fossa observed by Weidenreich (1951) in Zkd 11 and particularly Zkd 5, which were also the two specimens with the shortest fossae in this study.

Overall the results do not support the most common formulation of *H. ergaster* vs. *H. erectus* s.s. that was proposed by Wood (1991, 1994). According to that taxonomic scheme, *H. ergaster* would be restricted to WT 15000, several East Turkana specimens including ER 3733, 3883 and 730 and possibly SK 847 from Swartkrans, while *H. erectus* s.s. would include the Asian specimens and OH 9 (Wood, 1991, 1994). ER 730, which consisted of occipital and frontal fragments, was too incomplete to evaluate in any of these analyses. The results here highlighted variation within the East Turkana *H. erectus* sample at ~1.5 Ma in the form of ER 42700 (if this is truly *H.*

erectus) and ER 3883 but also verified the similarities in cranial morphology of ER 3733 and 3883. However, these resemblances did not extend to WT 15000, also considered to be *H. ergaster* (Wood, 1991). On the other hand, WT 15000 is not an adult specimen and it is certainly possible that further changes in cranial shape would have occurred as this individual matured (Delson, 1985; Walker and Leakey, 1993). Also, there were similarities in the shape of the facial skeleton between ER 3733 and WT 15000, although the small sample size makes this result difficult to interpret. While OH 9 is sometimes considered to be closer to the Asian morphology than the African (Wood, 1984, 1991, 1994), its cranial shape does not resemble either the Indonesian or Chinese pattern. Although OH 9 is larger than ER 3733 and 3883, it shares a similar cranial *Bauplan* with these individuals from East Turkana.

These African specimens all have a relatively low cranial vault with a wide supraorbital torus and a short parietomastoid suture. The supraorbital torus is more arched over mid-orbit and the supraglabellar depression is more posteriorly positioned compared to the Zhoukoudian specimens. The more arched supraorbital torus has been specifically noted previously for individual African fossils (Rightmire, 1990; Wood, 1991; Asfaw *et al.*, 2002) and more generally by Potts *et al.* (2004). The mandibular fossa is also longer and wider as well as deeper medially (due to a more projecting entoglenoid process). Descriptions of individual African *H. erectus* fossils have referenced the large entoglenoid process (e.g., Rightmire, 1990; Picq, 1990; Wood, 1991) and both Wolpoff (1999) and Antón (2002, 2003) characterized the mandibular fossa of the African fossils as wide. Although, Antón (2002, 2003) found that Ngawi, and possibly S 2, also have wide mandibular fossae, the size of the entoglenoid process could

not be evaluated in these specimens. In addition, the petrosal crest terminates laterally in a more posterior position, closer to the mastoid process (there is no mastoid fissure) as noted by Andrews (1984) and Antón (2002).

As suggested by Asfaw *et al.* (2002), Daka appears to be intermediate in its overall cranial shape between the African and Asian portions of the *H. erectus* hypodigm. In the Afro-Georgian analyses it groups more closely with the Dmanisi sample despite its larger size. Like the Indonesian specimens, it has more superior expansion at bregma and metopion, less inferior projection at the entoglenoid processes and a wider frontal squama. Although the frontal squama was short as in the East Turkana fossils, it shared greater frontal bossing with the Zhoukoudian sample. Daka also displayed a very deep mid-toral sulcus. The vertical orientation of the occipital plane was similar to that seen in the Indonesian specimens, but it is unique in the superior expansion at lambda. However, it does share more specific resemblances to the African sample in its frontal bone and, to a lesser extent, its temporal base anatomy, both regions which clearly separated all African fossils from the other geographic regions. For example, the supraorbital torus was much wider and less inferiorly positioned at its lateral ends, as in the East Turkana sample. The parietomastoid suture was intermediate in length between the African and Asian crania. It is possible that gene flow or migration may have resulted in its more modern cranial shape. Alternatively, a parallel increase in endocranial capacity in Africa and Asia within a similar cranial form (e.g., a long, low cranium with a wide base) may have may have resulted in similar shape changes in both regions.

The affinities of ER 42700 are particularly enigmatic (see also Chapter 3). It is very dissimilar to the East Turkana and D 2280 fossils, but is also different from the

Asian sample. Like Daka, ER 42700 exhibited greater superior expansion at bregma but its lambda was very posteriorly projecting. Despite the more superior position of opisthion, this resulted in a fundamentally higher cranial profile with a more open occipital angle in ER 42700 than that seen in other *H. erectus* crania. Also, the supraorbital torus was less projecting than other *H. erectus* and the less- developed mid-toral sulcus resembles the Indonesian morphology. Although ER 42700 was a small individual, these differences in cranial shape were inconsistent with size-related changes indicated by the other neurocranial analyses. The other juvenile *H. erectus* crania (D 2700, WT 15000 and possibly Zkd 3) also do not share any of these shape characteristics. Therefore, it seems that the unique cranial shape of ER 42700 was not attributable to either its small size or subadult status. This confirms the conclusions of Chapter 3 that ER 42700 does not fit the pattern seen throughout *H. erectus*.

Few conclusions can be drawn regarding the Dmanisi population because only D 2280 was included in multiple analyses. It is clear that D 2280 conforms to the cranial shape of *H. erectus*. Previously, similarities were noted between some of the Dmanisi and East Turkana fossils by Gabunia *et al.* (2000b) and Vekua *et al.*, (2002). Of the Dmanisi fossils examined here, D 2280 approached the East Turkana cranial shape most closely, but it also shared similarities to some of the Asian fossils. D 2700 and D 3444, on the other hand, did not approach the East Turkana pattern of cranial shape as closely. Rightmire *et al.* (2006, p. 134) concluded that the shape of D 2280 and 2700 was equally similar to both the East Turkana hominins and S 2. It has been suggested recently that the Dmanisi fossils may be closer in morphology to the basal form of *H. erectus*, while the East Turkana, Indonesian and Chinese samples were more derived (Rightmire *et al.*,

2006; Lordkipanidze *et al.*, 2006). Alternatively, the East Turkana hominins were closer to the base of the species while the Dmanisi population was intermediate between the early African and later Asian *H. erectus*. In the “Dmanisi” neurocranial analysis, the Georgian fossils were most similar to temporally intermediate fossils (Zkd 11, 12, Daka and S 17). The somewhat intermediate position of this sample does not clearly support either of these hypotheses to the exclusion of the other.

Conclusions

The lack of consensus regarding the morphological unity of *H. erectus*, particularly in the recent literature (e.g., Schwartz, 2000, 2004; de Lumley *et al.*, 2002, 2006; Asfaw *et al.*, 2002; Manzi *et al.*, 2003; Schwartz and Tattersall, 2003; Rightmire *et al.*, 2006), is partially attributable to an incomplete understanding of intraspecific variation within this species. Previous studies have demonstrated that the magnitude of variation in *H. erectus* appears to be within the range of a single, neontological species (Bilsborough and Wood, 1986; Kramer, 1993; Bilsborough, 2000; Kidder and Durband, 2004; Villmoare, 2005; Chapter 2 above). This suggests that geographically far-flung and temporally distant members of this species all exhibit a similar cranial shape, but with geographic and temporal variations present. This impression was confirmed by detailed comparison of *H. erectus* to other species of *Homo*; there was a distinct pattern of neurocranial, frontal and occipital shape observed across the entirety of the *H. erectus* species. Together, these results support the interpretation of a morphologically unified *H. erectus* species (Le Gros Clark, 1955, 1964; Howell, 1978; Howells, 1980; Rightmire,

1984, 1990, 1998a; Turner and Chamberlain, 1989; Delson *et al.*, 2001; Antón, 2003).

However, analyses of discrete character data often support the presence of multiple species (e.g., Andrews, 1984; Wood, 1984, 1991; Villmoare, 2005), and it is possible that *H. erectus s.l.* actually samples two very similar but taxonomically distinct species (Stringer, 1984). To address such a possibility, this study quantified variation within *H. erectus s.l.* and correlated it with geographic differences, geochronological time and size.

Although the early specimens from East Turkana often group together at the edge of the *H. erectus* distribution, the Asian fossils do not form a homogenous group, and OH 9 does not bear a greater resemblance to the Asian portion of the hypodigm (in fact, the opposite pattern was observed), as would be expected if the *H. ergaster* – *H. erectus s.s.* division was correct. The distinctiveness of the East Turkana hominins may be due to their greater antiquity (as a result of temporal changes in later populations). However, the Dmanisi hominins do not consistently group with the early East Turkana fossils but rather show similarities in cranial shape to both the African and Asian samples, in agreement with Rightmire *et al.* (2006). If the Dmanisi hominins were close to the stem of *H. erectus*, then the morphology of the both the Asian and the East Turkana hominins is derived. Comparative analysis (Chapter 3 above) suggested that the Asian specimens exhibited autapomorphic cranial shape characteristics relative to later species of *Homo* more than did the African fossils (similar to findings based on discrete characters, Andrews, 1984; Stringer, 1984; Wood, 1984; and Villmoare, 2005; but see Hublin, 1986; Bräuer, 1990; Kennedy, 1991; and Bräuer and Mbua, 1992 for alternative views). However, only a strictly cladistic approach to systematics would require the recognition of two separate species. Alternatively, a single lineage containing both ancestral and

terminal populations can be viewed as a single species if the populations are clearly unified morphologically and therefore genetically, as I would argue is the case here. Such a species can then be defined using a unique combination of primitive, derived and unique traits (e.g., Rightmire, 1984, 1990; Turner and Chamberlain, 1989; Kimbel and Rak, 1993, Baab, Chapter 3). This analysis, therefore, confirms the results of chapters 2 and 3 that *H. erectus* is best viewed as a single species with consistent temporogeographic and size-related variations present across its range.

Quantification of intraspecific variation has bearing not only on taxonomy, but on past evolutionary events in the history of *H. erectus*. As my comparative analysis suggested, *H. erectus* s.l. exhibited variation in terms of overall neurocranial shape as well as frontal, occipital, facial and temporal base shape. Much of this variation was correlated with geographic, temporal and size-related differences among members of *H. erectus*, as observed by many previous workers (e.g., Weidenreich, 1943, 1951; Le Gros Clark, 1964; Jacob, 1975; Santa Luca, 1980; Rightmire, 1990; Wolpoff, 1999; Antón, 2002, 2003; Antón *et al.*, 2002b; Kidder and Durband, 2004; Liu *et al.*, 2005; Villmoare, 2005), while inter-individual differences also accounted for some of the observed shape variation. The use of geometric morphometrics was an improvement over past studies, because it allowed shape to be quantified and statistically analyzed. Geography consistently accounted for a greater proportion of cranial shape variation than did geological age of the fossils, thus confirming the influence of microevolutionary forces (genetic drift, local adaptation) in shaping cranial morphology within *H. erectus*. At the same time, it was difficult to separate geographic from temporal variation because of the rarity of Asian crania in the earlier time bands and African fossils in the younger time

bands, and it is likely that geographic differences correspond more closely to temporogeographically circumscribed populations. Careful investigation of the affinities of younger African and older Indonesian fossils provided tantalizing hints of more wide-scale evolutionary processes. There was limited evidence that some evolutionary changes in cranial shape were linked to brain size increase, while isolation may explain the more extreme morphology of Zkd 5, the youngest of the Zhoukoudian fossils. A complex pattern of migration, gene flow and isolation appear to have characterized the evolutionary history of *H. erectus* across its range. Multiple migrations could have resulted in the great variation within the Sangiran fossils and, thus, these individuals should not be treated as a single population. Gene flow, migration or parallel evolution in Africa and Asia may explain the more "Asian" aspects of cranial shape exhibited by Daka, whereas the unique morphology of ER 42700 should probably be interpreted as further taxonomic diversity in Africa around 1.5 Ma. An interesting finding of this study was that while the Zhoukdoudian fossils formed a very homogenous group in terms of their cranial shape, the Indonesian fossils did not group together as consistently. However, the later samples of Indonesian fossils from Ngandong, Sambungmacan and Ngawi were more coherent with respect to cranial shape. This further supports the notion that differences are due to both geography and time, as some but not all earlier Indonesian fossils from the Sangiran dome resembled the later hominins from Java. The distinct nature of the cranial shape of the youngest Indonesian *H. erectus* populations may have been the result of isolation during the later part of the Pleistocene epoch.

Chapter 5: Synthesis of Results and Conclusions

Results

This dissertation addressed the taxonomy and phylogeny of *H. erectus* using 3D cranial shape data. While both discrete character and cranial shape data have been used to describe *H. erectus* in the past, non-metric traits have played a bigger role in the debate over whether one or more species were present within the *H. erectus* hypodigm. Also, because discrete characters were used to determine phylogenetic relationships among species of hominins, shape change across evolutionary transitions has not been well-characterized. By using geometric morphometric techniques to analyze 3D shape coordinates, this dissertation provides a quantitative evaluation of data that has been underutilized in the past. In addition, shape data is also capable of capturing variation in the neurocranium - the region of the skull most often preserved in *H. erectus* - which contains a limited number of the discrete characters traditionally used to elucidate hominin relationships.

The broad questions addressed in this study were:

- 1) Is more than one species of hominin represented by the *H. erectus* s.l. hypodigm?
- 2) What were the relative influences of geographic, temporal and allometric / sexual variation in shaping *H. erectus* cranial morphology?
- 3) Can *H. erectus* be diagnosed relative to other *Homo* species on the basis of its cranial shape?

- 4) Which aspects of cranial shape in *H. erectus* are plesiomorphic, synapomorphic or autapomorphic?
- 5) What was the evolutionary fate of *H. erectus* populations across the Old World?

Chapter one reviewed the historical treatment of *H. erectus* from the initial fossil discoveries by Eugène Dubois on Java in the 1890's through the most recent finds in Africa, Asia and the Caucasus. The core *H. erectus* sample, including fossils from Trinil, the Sangiran dome, Zhoukoudian and Olduvai Gorge were also introduced. Additional specimens from the sites such as Ngandong, Sambungmacan, Hexian, Nanjing, Bouri and the Turkana Basin that are often assigned to this species are discussed as well. This first chapter introduced the major unresolved questions concerning *H. erectus*. Are those traits that have been identified as *H. erectus* autapomorphies restricted to the Asian portion of the hypodigm or more broadly distributed outside of this species? If these autapomorphies were only present in the Asian *H. erectus* populations, then do the less derived African fossils, particularly from East and West Turkana, represent the separate species *H. ergaster*? There are also ambiguities surrounding the phylogenetic position of Asian *H. erectus*. Specifically, their relationship to later *Homo* species, including *H. sapiens* (particularly from Southeast Asia / Australia) and *H. floresiensis* remains unclear.

Chapter two examined the level of intra-taxic variation in *H. erectus s.l.* neurocrania relative to those of numerous human and non-human primate populations, subspecies, species and genera. Variation within *H. erectus* was quantified by the summed pairwise Procrustes distances among a representative sample of 13 individuals from Java, China, Georgia and East Africa. Bootstrapping methods were employed to

compare the magnitude of intraspecific variation in *H. erectus* to that seen at varying taxonomic levels in modern humans, the great apes and several papionin monkeys, including the extinct species *Theropithecus oswaldi*. In the results of this analysis, intra-taxic variation in *H. erectus* was greater than what was calculated for a diverse sample of modern humans as well as the values for most single species and subspecies of chimpanzees (with the exception of *P.t. troglodytes*). Variation in *H. erectus* was comparable to that determined for the genus *Pan*. However, the variation in the *H. erectus* sample was less than that calculated for species and even subspecies of the larger apes, *Gorilla* and *Pongo*. Subspecies of baboons and species of macaques generally exhibited similar levels of intra-taxic variability as *H. erectus*, although a few subspecies of *P. hamadryas* were less variable than *H. erectus*. Of the two *P. hamadryas* subspecies which were less variable than *H. erectus*, *P.h. papio* was represented by a fairly small sample size (n=17) which may have influenced this outcome. Variation in *H. erectus* also fell within the range of variation seen for the *M. fascicularis* species group as well as the entire *P. hamadryas* species, but fell at the low end of the range. The fossil species *T. oswaldi*, which spans a time range similar to that of *H. erectus* was more variable than the hominin sample. Taken together, these results do not unambiguously support either a single or multiple species model for *H. erectus*. However, the observation that a similar cranial shape was maintained over both a long time span and a wide geographic range tipped the scales towards a single species interpretation.

The third chapter established a shape-based species definition for *H. erectus* relative to modern humans, Neanderthals, *H. heidelbergensis* and species of early *Homo*. This shape-based definition is an important contribution, as up to now discrete characters have

provided the only objective basis for diagnoses and definitions of this species, even though cranial shape is the most distinctive characteristic of *H. erectus*. Furthermore, questions about the definition, relevance, and taxonomic distribution of non-metric features said to differentiate *H. erectus* have not been satisfactorily answered (Hublin, 1986; Bräuer, 1990; Kennedy, 1991; Bräuer and Mbua, 1992; Villmoare, 2005); cranial shape provided an alternative source of data that was used to address the relative uniqueness of *H. erectus*. The results of these analyses are compatible with previous studies of both discrete and shape-related cranial characters. Principal components and comparative analyses of the mean species landmark configurations indicate that *H. erectus* can be defined using a unique combination of autapomorphic, plesiomorphic and synapomorphic characters. The only feature which consistently differentiated *H. erectus* from all other *Homo* species was the great relative width at the occipital bone. The combination definition for *H. erectus* incorporates both primitive features such as the low mid-line cranial contour with a receding frontal bone and a fairly inferiorly projecting entoglenoid process and more derived traits including a long frontal squama with a prominent supraorbital torus and a wide cranial vault. The frontal squama of *H. erectus* was flattened in the coronal plane and exhibited marked constriction behind the supraorbital torus. The torus was relatively straight in anterior and superior views with minimal posterior torsion of the anterior surface. In lateral view the occipital bone was angled in the mid-sagittal plane (a trait also seen in *H. heidelbergensis*). It should be noted that there was geographic, temporal and allometric variation in many of these characters (as discussed in Chapter 4), but despite these differences, *H. erectus* was distinct from other closely related species in its neurocranial shape.

Ceprano, ER 42700 and Salé have cranial shapes that are outside of the range of *H. erectus* and should not be included within this species. Although Ceprano shares a low cranial profile with members of *H. erectus*, its frontal bone shape is most similar to Kabwe, Dali and Petralona, fossils which represent a species (or more than one species) which is more advanced than *H. erectus*. ER 42700 differs from the *H. erectus* norm in its tall neurocranium and its high lambda – inion – opisthion angle. Like ES 11693 and LH 18, the cranial base of Salé was more reminiscent of modern humans than *H. erectus*, including African *H. erectus*. In contrast, other recent additions to the *H. erectus* hypodigm, such as Dmanisi, Ngawi and Daka, do fit the *H. erectus* pattern of cranial shape defined in this thesis. While Daka was at the edge of the *H. erectus* distribution in terms of its overall cranial shape, it differed from other African *H. erectus* in having a more expanded neurocranium. However, OL 45500 from Olororgesailie, which was approximately the same age as Daka (0.9 Ma vs. 1.0 Ma), presented a frontal bone shape that was particularly distinct from later species of *Homo*. Therefore, the temporal trend of increasing modernity suggested by the Daka cranium apparently did not include the population represented by OL 45500.

Chapter three also used cranial shape to evaluate the multiregional model of modern human origins in Australasia. Early modern humans from this region (WLH-50, KS 17 and Wajak 1) do not share any unique features of cranial shape with the Ngandong hominins. The flat frontal squama and robust supraorbital region of WLH-50 and Wajak 1, in combination with a more expanded midsagittal profile and less projecting occipital bone, align them with early modern humans from the Levant and North Africa rather than late Indonesian *H. erectus*. While these results may reflect a complex evolutionary

history for the earliest humans in Australasia, they do not support an *in situ* evolution from late-surviving *H. erectus* in this region (i.e., Ngandong). On the other hand, Indonesian *H. erectus* may have been ancestral to another Australasian population of hominins (from Flores) that went extinct only ~12 ka. The initial description of LB1, the holotype of *H. floresiensis*, suggested that it could be the result of endemic dwarfing of *H. erectus* or another species of early *Homo* on the island of Flores. The specimen shared an overall neurocranial shape pattern with early *H. erectus* specimens, and this shape was within the predicted interval for an equivalently small *H. erectus*.

The fourth chapter examined the relative influences of geographic, temporal and allometric variation on intra-specific variation in *H. erectus*. Although these different factors were conflated to a large degree, in that the smallest and oldest specimens were generally from the western portion of its range and the larger and younger fossils were from the eastern half, the results indicated that geographic differences accounted for the largest proportion of cranial shape variation in this species. However, the pattern was more complex than a simple African – Asian dichotomy and was discordant with the proposed *H. erectus* s.s. vs. *H. ergaster* taxonomic division (*sensu* Wood, 1991).

Although many Indonesian specimens share a similar cranial shape, they encompass greater variation than has been previously recognized, particularly among the Sangiran individuals. The lack of homogeneity within the earlier Sangiran sample could support Kaifu *et al.*'s (2005) hypothesis of multiple migrations into Java during this time period, but may also reflect other sources of intraspecific variation, such as sexual variation. The most recent populations of Indonesian *H. erectus* exhibited a fairly homogeneous cranial shape which differs in some details from earlier populations. General temporal trends are

likely related in part to endocranial expansion due to the well-documented anagenetic increase in brain size in *H. erectus* (Wolpoff, 1984; Leigh, 1992; Antón and Swisher, 2001; Rightmire, 2004). However, while allometric patterning in shape often resembled temporal changes, it did not explain the observed distribution of cranial shape variation as well as did geological age. This pattern suggests that both time and size influenced the cranial form of Indonesian hominins. Analysis of intraspecific variation confirmed the results of chapter three that ER 42700 is an outlier and should probably be excluded from this species whereas Daka, the Dmanisi fossils and Ngawi were all within the *H. erectus* distribution. Although OL 45500 from Olorgesailie fell at the edge of the *H. erectus* distribution, its frontal bone shape clearly matches the African *erectus* pattern. The small size of this specimen, especially at ~800 ka, is indicative of the great variation in absolute size compared to cranial shape in this species.

Synthesis

The major conclusions of this dissertation are compatible with previous studies based on standard morphometric data and discrete character traits. Both the magnitude of neurocranial shape variation and the pattern of cranial shape variation within the hypodigm, although not unambiguous, support a single species interpretation for *H. erectus*. This first conclusion is compatible with studies based on morphometric data (Bilsborough and Wood, 1986; Kramer, 1993; Bilsborough, 2000; Kidder and Durband, 2000, 2004; Villmoare, 2005) and some based on broader examinations of cranial anatomy (Rightmire, 1984, 1990; Antón, 2003). Although the results presented here

show a strong geographic signal within this species, it corresponds neither to Wood's (1991) *H. erectus* s.s. – *H. ergaster* division nor to Clarke's (1990) *H. erectus* s.s. – *H. leakeyi* division, as OH 9 clearly fits the African pattern in most aspects of cranial shape.

The narrow frontal and occipital bones of the Zhoukoudian fossils made them the most distinct temporogeographic group in the traditional morphometric analyses of both Antón (2002) and Kidder and Durband (2004). Although a similar cranial shape pattern was noted here for the Zhoukoudian specimens, the recent Indonesian populations are at least as distinctive from the remaining temporogeographic samples of *H. erectus*. Antón (2003) also noted a greater range of morphology in the earlier Indonesian specimens than the later ones, a finding confirmed here. Geometric morphometrics techniques were able to uncover subtle patterns of shape variation such as the variation within the apparently homogenous Indonesian sample. For example, the Indonesian specimens as a whole do not always form a cohesive group which is distinct from the African and Chinese groups (e.g., the mid-line occipital profile). The younger Indonesian populations (i.e., Ngandong, Sambungmacan and Ngawi) exhibit some unique shape characteristics in the current analysis, which may reflect isolation of these populations on Java (Antón, 2003).

It was possible to discern a unique pattern of cranial shape in *H. erectus*, although it shares many aspects of this shape with later species of *Homo*. The combination of a wide neurocranium with a low sagittal profile, a flat frontal squama, a straight supraorbital torus and a wide and angled occipital bone was not found outside of *H. erectus*. The particularly wide occipital bone was the most autapomorphic aspect of cranial shape identified in this study. This shape-based diagnosis of *H. erectus* is equivalent to other “combination” definitions offered by Wood (1984, 1994), Rightmire

(1988), Turner and Chamberlain (1989) and Kimbel and Rak (1993), based on unique combinations of plesiomorphic and synapomorphic discrete characters. It is clear that a common and distinct cranial shape, as well as several non-metric traits like sagittal keeling, a transverse occipital torus and an angular torus, were common throughout the species and persisted across thousands of miles and over 1.7 myr. Small deviations from the basic *Bauplan* correspond to geographic, temporal and size variation within *H. erectus*.

Concerns that recent additions to the *H. erectus* hypodigm extend the range of variation beyond what is expected for a single species appear to be warranted in some cases but not in others. Many specimens, including those from Dmanisi, Ngawi and Bouri fit comfortably within the range of variation encompassed by *H. erectus* while others, such as Salé, Ceprano and ER 42700, do not. The exclusion of Salé and Ceprano from *H. erectus* restricts the known range of the species to East and possibly South Africa (unless the Tighenif fossils are *H. erectus*), the Far East and the Caucasus.

ER 1813 (*H. habilis*) is an outlier relative to other *Homo* specimens because many of the cranial shape features that characterize later species of *Homo* appeared first in *H. erectus*. It is possible that different selective pressures associated with the major adaptive shift from early *Homo* (*H. habilis* and *H. rudolfensis*) to *H. erectus* (Wood and Collard, 1999) were responsible for the transition to a more modern cranial form. However, these differences were also exaggerated by the very superoanterior position of lambda, which was the result of the many sutures and accessory ossicles in the lambdoid region of ER 1813.

In some respects the Asian populations appear more autapomorphic in their cranial shape than the African populations (e.g., the very straight supraorbital tori and short, narrow temporomandibular joint with a long anterior face of the tympanic tube). At the same time, they share an expanded sagittal profile and a long, narrow face with *H. sapiens*. Removing the Asian populations from the direct lineage leading to *H. sapiens* (e.g., Andrews, 1984; Stringer, 1984; Wood, 1984, 1994; Rightmire, 1990; Foley, 2002; Lahr and Foley, 2004) leads to the conclusion that these shared traits were parallel developments along both evolutionary branches. Alternatively, if the Asian populations are not excluded from *H. sapiens* ancestry (Hublin, 1986; Lieberman, 2001), then the autapomorphic aspects of cranial shape seen in Asian *H. erectus* must have reverted to a more ancestral condition. Andrews (1984) came to a similar determination using discrete characters, concluding as I do, that the former explanation is more likely. However, it is worth noting that the most extreme expression of these autapomorphies was in the recent Indonesian populations that may well post-date the first appearance of modern humans in Africa (100 Ka, Bartstra *et al.*, 1988; 53-27 Ka, Swisher *et al.*, 1996). If gene flow among earlier populations of *H. erectus* across the Old World is invoked to explain the similarity between some Sangiran fossils and African *H. erectus* or between Daka and Indonesian *H. erectus* (as discussed below), then the Asian hominins may ultimately have contributed to the gene pool of later, more derived species of *Homo*, including *H. sapiens*.

The appearance at ~1 Ma of Daka, with a cranial shape which is intermediate between the African and Asian pattern, may signal the presence of gene flow between east and west, although alternative interpretations are also feasible. For example,

endocranial expansion in both Africa and Asia, within the constraints of a similar cranial form, may have resulted in convergent shape changes. The closer affinities of Daka (vs. ER 3733 and 3883) with later *Homo* specimens may also be consistent with a temporal trend in (some) African populations toward a more modern cranial shape. The less expanded neurocranial profiles of S 2 and 17, which are at least as old as Daka, suggest that this trend was not apparent in Indonesia at this time.

There are indications that the later evolutionary history of *H. erectus* was complex, and may also have involved genetic / geographic isolation and speciation. Although the late-surviving populations of *H. erectus* underwent significant endocranial expansion, they still maintained the fundamental *H. erectus* cranial shape. The retention of this pattern across the large geographic and temporal span of *H. erectus* contrasts with the more modern shape seen in some Middle Pleistocene specimens (broadly termed *H. heidelbergensis*), and may be the result of genetic isolation of later *H. erectus* populations during the mid and late Pleistocene. A separate episode of isolation on the island of Flores may have resulted in the establishment of a dwarfed lineage, *H. floresiensis*, which persisted until ~12 ka (Morwood *et al.*, 2005). It does not appear, however, that late-surviving populations of Indonesian *H. erectus* were directly ancestral to modern humans in Australasia.

The scenario which best accounts for the pattern of cranial shape within *H. erectus* and among Pleistocene species of *Homo* is that *H. erectus* first appeared around the Plio-Pleistocene boundary. If ER 1813 (*H. habilis*) was the ancestor of *H. erectus*, then this speciation event most likely occurred in Africa as ER 3733 and 3883 resemble ER 1813 more closely than do the Dmanisi specimens. Populations of *H. erectus* spread

rapidly to the Caucasus region, appearing in both African and Georgia nearly simultaneously. The Dmanisi specimens overlap both the early African and Asian fossils in terms of cranial shape, and may therefore be similar morphologically to the earliest *H. erectus* migrants to Asia. Within Africa, some groups of *H. erectus* developed a more modern morphology (e.g., Daka) and likely gave rise to further species of *Homo*, while others became more autapomorphic (e.g., OL 45500). It is unclear whether one or more waves of migration were responsible for the establishment of *H. erectus* in China and Indonesia, but there is evidence of their presence in Indonesia before 1.5 Ma (e.g., Swisher, 1997; Larick *et al.*, 2001) and in China by the Middle Pleistocene (as reviewed by Wu and Poirer, 1995; Etler, 1996; Brown, 2001) or early Pleistocene (Li and Wang, 1982; Zhu *et al.*, 2001, 2004), if the oldest archaeological sites in China were the result of *H. erectus* activity. The less expanded midline profile of the Zhoukoudian and Sangiran fossils supports a migration prior to 1 Ma, before a more expanded midline neurocranial outline is evident in Africa (e.g., Daka). The taller neurocranium seen in younger specimens from Java, such as those from Ngandong, Sambungmacan and Ngawi, is probably the result of brain expansion within the Indonesian lineage, as these specimens do not resemble Middle Pleistocene *Homo* fossils from elsewhere in the world.

In addition to the contributions made to understanding the taxonomy and evolutionary history of *H. erectus*, this dissertation also has important implications for the use of 3D shape data in exploring variation and change in the hominin cranium. While the number of discrete traits available for analysis in *H. erectus* is limited due to a lack of preservation of the face and base, the shape of the neurocranium and lateral temporal base effectively captured both interspecific and intraspecific variation. Cranial shape is

not easily broken down into independent characters because the form of the cranium is an integrated whole, both in terms of evolution and ontogeny. One of the greatest advantages of geometric morphometric techniques is that all regions of the cranium can be analyzed simultaneously. While more focused regional analyses were important for including less complete specimens and for identifying more localized morphological changes, they were interpreted within a framework of the entire cranium because changes in relative size and orientation within the skull were not always apparent when a smaller region was analyzed in isolation.

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