



17 Apples and Oranges: Morphological Versus Behavioral Transitions in the Pleistocene

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... one is not being too daring in pointing to major contrasts between archaic and modern humans.

— David Pilbeam (1986:334)

Introduction

Paleoanthropologists who seek correspondences between the fossil and archaeological records of the Pleistocene have a frustrating task. The fossil record suggests that *Homo erectus* (or possibly *H. ergaster*) migrated out of Africa by 1.8 Ma and then evolved in Africa, Europe and Asia into a group of taxa or populations—often termed collectively as “archaic *Homo*”—that are chiefly distinguished from early African *H. erectus* by larger brains and faces. While many subsequent events are unclear, archaic *Homo* populations in various parts of the Old World had different subsequent evolutionary histories: in Africa they were ancestral to modern *H. sapiens*; in Europe they evolved into the Neanderthals; and in Asia they persisted as *H. erectus* and/or archaic *Homo*.

A series of archaeological transitions, defined primarily on the basis of lithic technologies, also occurred over the same time period, but with little evident correlation to the species identified in the fossil record (Figure 17.1). We have no idea who created the earliest lithic industry, the Oldowan, that first appears approximately 2.6 Ma (Semaw et al. 2003). Moreover, the Oldowan gave rise to various chopper-chopping tool industries that persisted for almost two million years throughout much of the old world. The Acheulian industry, characterized by handaxes, first appears at about 1.7 Ma (Dominguez-Rodrigo et al. 2001), significantly after the first appearance of early *H. erectus* in East Africa and Eurasia. Acheulian industries are present in Africa, western and south Asia, and western Europe until about 250 Ka but have no more correlation to any hominid species than the contemporaneous core-chopper or core and flake industries. Likewise, the Middle Paleolithic (MP) and Middle Stone Age (MSA) industries, based on prepared core reduction techniques, are widely present by 250 Ka although they may be as old

as 500 Ka in East Africa (Deino and McBrearty 2002; McBrearty this volume). MP/MSA industries were produced by archaic and modern *Homo*; they are also correlated with the origins of *H. sapiens* in Africa (McBrearty and Brooks 2000). Finally, the Upper Paleolithic (UP) and Later Stone Age (LSA) industries, based mostly on prismatic blade core reduction techniques, first appear about 45 Ka in East Africa and the Levant, and are widely associated with modern humans. In Europe, the Chatelperronian, a blade-based lithic industry, is associated with a secondary burial of a Neanderthal at St. Cesaire (Leveque and Vandermeersch 1980) and a few isolated fragments at Arcy sur Cur (Hublin et al. 1996).

Why so little correspondence? There are three possible explanations for the poor correlations apparent between archaeological industries and hominid species. First, the taxonomies may be wrong. The most extreme example of this viewpoint is the multiregional hypothesis which proposes that the Lower, Middle and Upper Paleolithic industries are all products of a single, highly variable species, *H. sapiens*, that has been present since about 1.8 Ma (Wolpoff 1999). A second possibility is that there are correspondences, either in shared-derived cultural features (Foley and Lahr 1997), or in aspects of behavior that are subtle or difficult to discern in the archaeological record. Lieberman and Shea (1994), for example, suggested that Neanderthals and modern humans in the Levant had differences in hunting frequencies and mobility strategies. Alternatively, Klein has suggested that the Upper Paleolithic marks a cognitive, neurological shift within *H. sapiens* that is not evident from cranial remains, but which accounts for the rapid expansion of *H. sapiens* throughout the world and the corresponding demise of archaic *Homo* taxa such as the Neanderthals (Klein 1995; Klein and Edgar 2002).

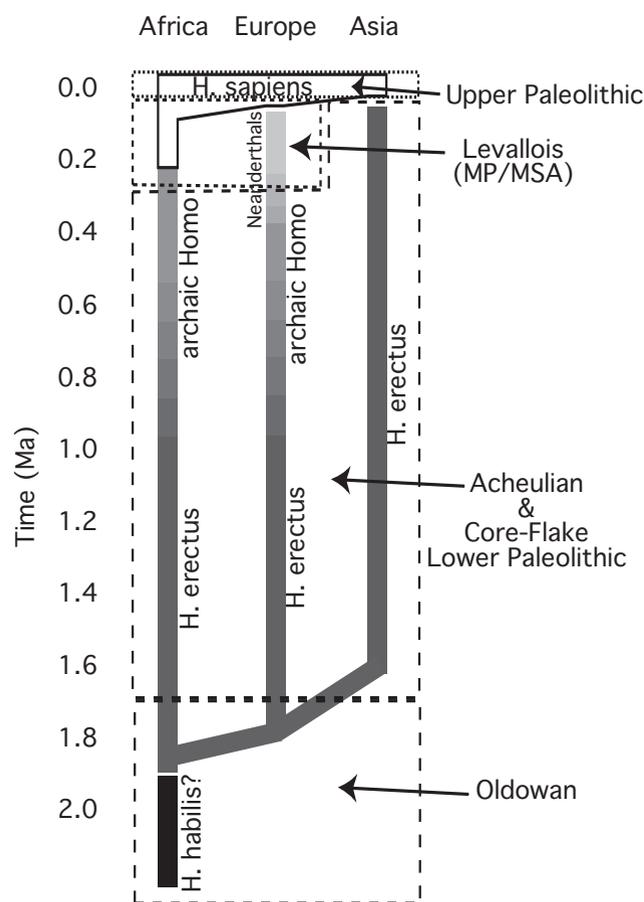


Figure 17.1 Major fossil taxonomic categories and lithic industries by region during the Pleistocene. See text for details.

A final possibility is that we shouldn't expect any relationship between the lithic and fossil records because they are fundamentally different categories of data—even more different than apples and oranges. Biological taxonomies are essentially nested hierarchies of organisms whose identities derive from evolutionary history. Species are real and discrete entities with unique ancestor-descendant relationships and whose origins are the product of diversions between lineages. Archaeological industries are also classified using a taxonomic system whose origin stems from a 19th century view of prehistory that both humans and stone artifacts are part of a natural order (Sackett 1981). But, of course, archaeological industries are nothing like species because they are the products of learned cultural and technological traditions. Thus the taxonomies we employ to categorize lithic industries are essentially groups of cultural traditions,

with no necessary relationship to the evolutionary histories of the organisms that made them. In addition, cultural traditions are additive and not necessarily divergent. Even recent humans, such as the Late Pleistocene occupants of China, sometimes produce stone tools using an essentially Oldowan technology.

We therefore reexamine here in broad perspective the major transitions within the genus *Homo* and their relationships, if any, to the archaeological record. In particular, we address two questions. First, how different in degree were the major morphological transitions from *H. erectus* to archaic *Homo* and from archaic *Homo* to *H. sapiens*? Second, is there any basis for inferring a relationship between these morphological transitions and the somewhat correlated archaeological transitions from the Lower to Middle to Upper Paleolithic? We begin first with a consideration of the paleontological evidence, before examining the archaeological record, and the relationship between the various transitions.

Morphological Transitions in *Homo*

Background

Prior to the 1980s, when better dating techniques and molecular systematics revolutionized paleoanthropology, the traditional view was that the major evolutionary transformations from *H. erectus* to *H. sapiens* occurred through a series of gradual, intermediate stages. These stages were reflected in a grade-based rather than a clade-based terminology that recognized only two species, *H. erectus* and *H. sapiens*, with the latter divided into “archaic” and “modern” stages or subspecies. Non-modern taxa such as the Neanderthals were thus classified as “archaic” *H. sapiens*, or *H. sapiens neanderthalensis*; modern humans were classified as “anatomically modern” *H. sapiens* or *H. sapiens sapiens*. The primary bases for classifying non-modern taxa into *H. sapiens* were their large brains, and the belief that modern humans evolved independently from different archaic human populations via multiregional evolution (e.g., Brace 1979; Wolpoff 1999; Wolpoff et al. 2001).

Most paleoanthropologists have now rejected all or part of this scenario following the refutation of the multiregional hypothesis. Instead, there has been a trend to recognize more rather than fewer species within post-erectus *Homo*. Although a few researchers still employ

grade-based taxonomic schemes (e.g., Braüer 1992, 2001), archaic *Homo* is usually split into several species that are poorly defined. In Europe, three species of archaic *Homo* have been recognized, of which the best known are *H. heidelbergensis* and *H. neanderthalensis*. The type specimen of the former is the Mauer mandible (Scheotensack 1908), but the hypodigm is generally considered to be best represented by fossil crania dated to between roughly 600–200 Ka such as Petralona, Steinheim, Arago and the material from the Sima de los Huesos, Atapuerca (Arsuaga et al. 1997; Rightmire 2004). Most of the derived features of *H. heidelbergensis* in Europe are not particularly distinctive relative to other archaic *Homo* taxa (see below), and include a large face, an expanded cranial vault, rounder parietal and occipital contours, and large, separate ridges above the orbits (see Howell 1994).

Interestingly, some later European specimens attributed to *H. heidelbergensis* (e.g., Steinheim) have a few apparently derived features of *H. neanderthalensis* (Rosas and Bermudez de Castro 1998; Stringer 1996). *H. neanderthalensis*, which lived in Europe and Western Asia from between \approx 200–30 Ka, is the most accepted and well-documented species of archaic *Homo*. Neanderthals share many cranial features with other archaic *Homo* such as double-arched supraorbital tori, large faces, and large brains, but are widely considered a separate species on the basis of their distinct pattern of ontogeny and many unique derived features including a projecting midface around a huge nasopharynx, an occipital “bun”, a supramastoid crest, and a mandibular retromolar space (e.g., Trinkaus 1986; Lieberman 1995; Lieberman et al. 2002; Ponce de Leon and Zollikofer 2001; Harvati et al. 2004).

One other potential archaic *Homo* taxon from Europe that deserves mention is *H. antecessor*, so far attributed only to a handful of teeth and cranial fragments from Level 6 of Gran Dolina, dated to about 750 Ka (Bermudez de Castro et al. 1997). These fossils, among the oldest in Europe, are generally similar to other archaic *Homo* material, but differ from European *H. heidelbergensis* in lacking any derived Neanderthal features; they may also share have a few derived features with modern humans including a canine fossa, a non-projecting lower face, and a sharp inferior nasal margin

(Arsuaga et al. 1999). If so, then *H. antecessor* could be the last common ancestor of the human and Neanderthal lineages, but the taxon is not widely recognized because the material is quite fragmentary and all the supposedly derived human features are from a juvenile face.

The taxonomic situation in Africa is much less clear than in Europe. The earliest African fossils attributed to *H. erectus* dated to 1.9–1.5 Ma are considered by some to belong to a separate species, *H. ergaster* (Wood 1991), that may also include the contemporary material from Dmanisi, Georgia (Gabunia et al. 2000; Vekua et al. 2002). Many experts, however, do not consider *H. ergaster* to be distinct from *H. erectus*, in part because of the general similarities between classic *H. erectus* fossils from Asia and Lower Pleistocene crania from East Africa such as OH 9, OH 12, and the Daka fossil (Asfaw et al. 2002). Regardless of whether these fossils belong to *H. erectus* or *H. ergaster*, they are followed in the fossil record by a number of crania younger than 1 Ma and older than 200 Ka such as Broken Hill, Bodo, Eyasi, Elandsfontein (Hopefield) and Nduutu that are generally ascribed to archaic *Homo* and not to *H. erectus* or *H. sapiens* (for reviews, see Lahr and Foley 1998; Rightmire 1990, 1998; McBrearty and Brooks 2000; Anton 2003). Like their European counterparts, these crania tend to be quite robust with expanded cranial capacities relative to *H. erectus*, large faces, and large, double-arched brow-ridges. Some researchers (e.g., Howell 1994; Stringer 1996; Rightmire 2004) assign them to *H. heidelbergensis*. An alternative classification (based on the hypothesis that *H. heidelbergensis* is the exclusive ancestor of *H. neanderthalensis*) is to classify these African fossils in a distinct species, for which *H. rhodesiensis* Woodward, 1921 would be an appropriate name. An additional species, *H. helmei*, has also been proposed for possibly transitional fossils such as Florisbad which have a few but not all the derived features of modern *H. sapiens* (Lahr and Foley 1998, 2001; McBrearty and Brooks 2000).

Making taxonomic sense of the Asian fossil record is also difficult. It is widely agreed that *H. erectus sensu stricto* is present in Java from 1.6 Ma at Sangiran (Swisher et al. 1994) to perhaps less than 100 Ka at Ngandong (Swisher et al. 1996); and in China at sites ranging from 1.2 Ma at Gongwangling to 200 Ka at sites such as Zhoukoudian, Hexian and Nanjing (for

details see Anton 2002, 2003). So far, no fossils from Java appear to fall within the general category of archaic *Homo*, as they all retain several distinct features of *H. erectus* including an angulated occipital torus, a continuous supraorbital torus, and a low maximum breadth of the cranial vault (Anton 2003). However a number of Middle Pleistocene fossils from China (notably Dali, Jinnuishan, and possibly Xijiayao and Yunxian) are proposed to belong to archaic *Homo* and not *H. erectus* given their absence of any key derived *H. erectus* features along with large faces, expanded endocranial volumes, more rounded occipital contours, and more divided supraorbital tori (Rightmire 2004). One partial cranium from Narmada, India may also belong in this archaic *Homo* taxon (Cameron et al. 2004). At present, there is not enough information to assess the species, *H. floresiensis*, dated to between 30 Ka and possibly as young as 13 Ka from the island of Flores (Brown et al. 2004). While the species may be an insular dwarf descendent of *H. erectus*, the hypothesis has not been tested securely, and we await further evidence and analyses.

It is difficult to derive a consensus taxonomy of archaic *Homo* when one considers the African, Asian and European evidence together. However, we can make two generalizations relevant to this study. First, it is probable that several regional variants of *Homo* evolved following the initial dispersal of *H. erectus*/*H. ergaster* out of Africa. Second, the morphological differences between these regional variants are, for the most part, subtle. With the exception of *H. neanderthalensis* and some European fossils attributed to *H. heidelbergensis*, most archaic *Homo* fossils differ from *H. erectus* in just a few respects, regardless of their geographic location. The key derived features of archaic *Homo* are larger brains, more rounded occipital and parietal contours, larger faces, and more continuous supraorbital tori above the orbits. Archaic *Homo* also lack the derived features of *H. sapiens* such as facial retraction and neurocranial globularity, canine fossae, and a chin. As a consequence, many researchers now lump non-Neanderthal archaic *Homo* fossils from Africa, Asia and Europe into a single species, *H. heidelbergensis*. This species has become something of a “waste-basket” taxon for fossils not quite like *H. erectus* and not quite like either *H. sapiens* or *H. neanderthalensis*.

Comparing the Morphological Transitions

As noted above, our goal is to compare the major transitions within and between the archaeological and fossil records of *Homo*. Regardless of how many species exist within archaic *Homo*, the recognition of taxa such as *H. heidelbergensis* that are somehow intermediate between *H. erectus* and *H. sapiens* raises the question of how different are these various taxa. Most importantly, are the differences between *H. erectus* and archaic *Homo* as substantial as those between archaic *Homo* and *H. sapiens*? Phrased as taxonomic hypotheses, the fossils attributed to *H. heidelbergensis* and/or other taxa of archaic *Homo* can be either: 1) real species with unique derived characteristics; 2) derived regional variants of *H. erectus* with bigger brains and larger faces; or 3) primitive variants of *H. sapiens*. Keeping aside for the moment the question of how these hypotheses relate to the archaeological record, each has different phylogenetic implications. The first hypothesis suggests that the evolution of *Homo* following the initial dispersal of *H. erectus* and/or *H. ergaster* was speciose with multiple regional variants (e.g., Tattersall 1986). The second hypothesis suggests that there was considerable convergence and/or gene-flow, mostly related to increases in brain size, in post-*erectus* evolution prior to the evolution of *H. sapiens* (e.g., Brauer 1992). The final hypothesis is consistent with the predictions of the multiregional theory of human evolution (e.g., Wolpoff et al. 2001).

There is no simple way to test the hypothesis that the transition between *H. erectus* and archaic *Homo* was substantially different in nature from that of archaic *Homo* to *H. sapiens*. Most researchers have addressed the question using either qualitative or quantitative comparisons of particular characters such as cranial size or browridge shape. Rightmire (2004), for example, recently argued that the greater absolute and relative endocranial volume in archaic *Homo* than *H. erectus* (about 230 cc) is evidence of a speciation event. As noted above, Rightmire (2004) and other researchers such as Schwartz and Tattersall (2003) also separate these taxa on the species-level based on a few other derived features of archaic *Homo* including a supraorbital torus comprised of separate arches over the orbits, thicker cranial vault bones, a larger face, a rounder occipital contour, and expanded parietals. There are, however, several problems

with these diagnoses. First, the characters upon which they are based are considerably variable within each taxon and overlap substantially between taxa. There is no significant difference in endocranial volume between *H. sapiens* and archaic *Homo*, but Rightmire (2004) found a significant and positive slope between time and brain size within archaic *Homo* and *H. erectus*. Moreover, thicker cranial vaults (also a very variable, highly epigenetic character) are shared derived features between archaic *Homo* and *H. erectus* (Lieberman 1996). A second problem is that many if not most of the characters used to distinguish Pleistocene *Homo* taxa are not independent. Brain size is probably the dominant cause of covariation. As the brain grows and expands within the neurocranium, it stimulates growth in the sutures of the vault (see Enlow 1990; Lieberman et al. 2000b). Thus it is well established that increases in brain size are strongly related to the shape of the occipital contour, parietal expansion, and some aspects of browridge shape (see Lieberman 2000; Lieberman et al. 2000a, 2002). Face size may also generate substantial covariation in many aspects of craniofacial shape (Lieberman et al. 2004).

One useful, complementary approach that avoids the problems of character covariation and scaling effects is to use landmark-based geometric morphometrics (GM) to compare differences between the fossils ascribed to *H. erectus*, AH and *H. sapiens*. GM analyses differ from more traditional qualitative and/or caliper-based quantitative studies by comparing the spatial distribution of three-dimensional landmark coordinates between individuals standardized to the same multidimensional shape space (Bookstein 1991). The disadvantages of GM are the same as those of any other quantitative method based on landmarks: the observations are only as good as the landmarks used, and thus do not take into account more subtle aspects of morphology. GM, however, has several advantages, particularly for comparisons of complex objects such as *Homo* crania that differ in size. First, GM comparisons are size-independent. Second, GM analyses quantify size-independent aspects of shape covariation without any *a priori* model using principal components analysis (PCA). Principal components analysis is a data reduction technique that rotates the size-corrected landmark configurations (actual-

ly their variance/covariance matrices) in multidimensional space to identify independent (uncorrelated) linear combinations of geometric landmark shifts (warps) that are ordered by reducing variability (see Zelditch et al. 2004).

An additional advantage of PCA analyses of GM-based data is the ability to test quantitatively hypotheses about relationships between size and shape, as illustrated in Figure 17.2. If the morphological differences between *H. erectus*, archaic *Homo*, and *H. sapiens* are unrelated to any scaling effects of size, then covarying aspects of shape (quantified as principal components) of these taxa should differ independently of size. In contrast, if the taxa differ in shape because of scaling effects, then one or more principal components of shape that separate crania attributed to these taxa should scale to some extent with overall size. Note that not all PCs that describe covariation in cranial shape are expected to be size related.

Sample

To test the above hypotheses about the transitions between *H. erectus*, archaic *Homo* and *H. sapiens* we measured three-dimensional landmark coordinates on a sample of 33 crania (mostly casts) attributed to *H. erectus*, archaic *Homo* and *H. sapiens*. The sample (summarized in Table 17.1) has two major deficiencies. First, a few important fossils were not included because casts were unavailable (e.g. Dali, Jinnuishan, Ceprano, Atapuerca). Second, most crania attributed to *H. erectus* and archaic *Homo* preserve just the upper face and the cranial vault, and almost all of the more complete crania have damaged cranial bases and many are missing parts of the palate. It is therefore difficult to test hypotheses about aspects of shape that result from interactions between the size and position of the face, neurocranium and basicranium (see Lieberman et al. 2000a for discussion). We therefore include two analyses: a smaller, more complete study using crania that include vault and facial landmarks (mostly from the orbits and midfacial regions), and a larger less complete study using crania that include just features of the vault and upper face (see Table 17.1).

Landmarks

The landmarks used (listed and defined in Table 17.2, and illustrated in Figure 17.3) were chosen to maximize comparisons within each sample. Landmarks were categorized

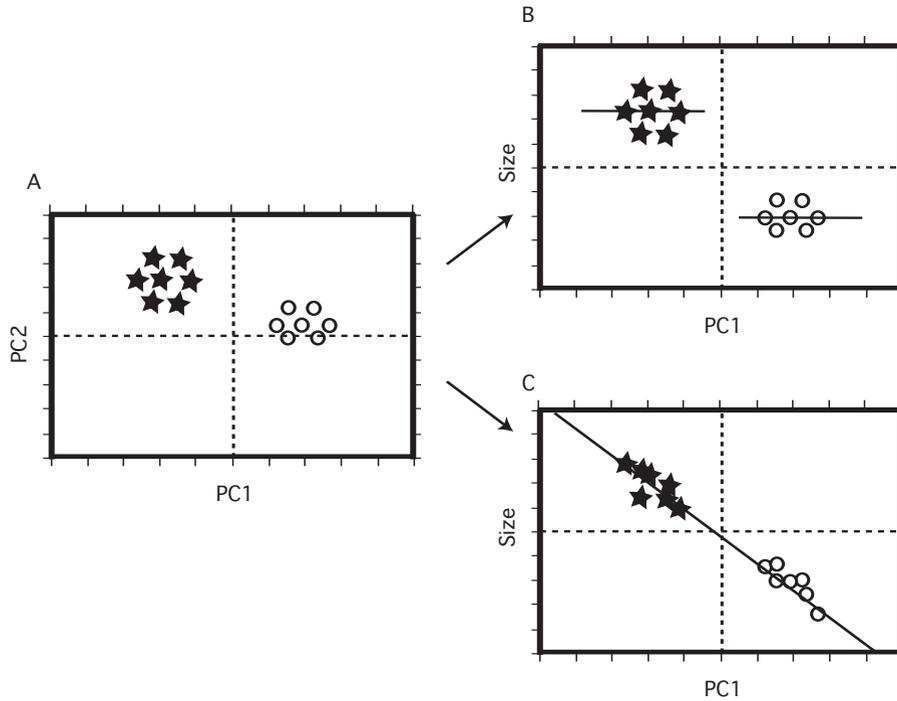


Figure 17.2 Geometric model of differences in cranial shape versus size in two species (stars and circles) that are different in size: a) idealized shape differences between the two species expressed as the first two principal components (PC1 and PC2); b) Size versus the first principal component (PC1) when there are no scaling effects within species between size and PC1. For this component of shape, the larger species is not a scaled version of the smaller species; and c) Size versus the first principal component (PC1) when there are scaling effects within species between size and PC1. For this component of shape, the larger species is an allometrically scaled version of the smaller species.

Table 17.1

Crania Used in Maximum (MLS) and Vault (VLS) Landmark Set Analyses

Fossil	Taxon	Analysis	Fossil	Taxon	Analysis
Amud 1	archaic <i>Homo</i>	MLS, VLS	La Chapelle aux Saints	archaic <i>Homo</i>	MLS, VLS
Brno 3	<i>H. sapiens</i>	MLS, VLS	La Ferrassie 1	archaic <i>Homo</i>	MLS, VLS
Broken Hill	archaic <i>Homo</i>	MLS, VLS	Ngaloba	archaic <i>Homo</i>	VLS
Cro Magnon1	<i>H. sapiens</i>	MLS, VLS	Ngandong V	<i>H. erectus</i>	VLS
Dmanisi D2280	<i>H. erectus</i>	VLS	Ngandong VI	<i>H. erectus</i>	VLS
Dolni Vestonice 3	<i>H. sapiens</i>	MLS, VLS	Omo 1	<i>H. sapiens</i>	MLS, VLS
Eliye Springs	archaic <i>Homo</i>	VLS	Predmosti 3	<i>H. sapiens</i>	MLS, VLS
Eyasi	archaic <i>Homo</i>	VLS	Qafzeh 9	<i>H. sapiens</i>	MLS, VLS
Grimaldi 6	<i>H. sapiens</i>	MLS, VLS	Sangiran 17	<i>H. erectus</i>	MLS, VLS
Italy 6456	<i>H. sapiens</i>	MLS, VLS	Skhul 5	<i>H. sapiens</i>	MLS, VLS
Italy 6460	<i>H. sapiens</i>	MLS, VLS	KNM-WT 15000	<i>H. erectus</i>	MLS, VLS
Italy 6461	<i>H. sapiens</i>	MLS, VLS	Zhoukoudian 101	<i>H. sapiens</i>	MLS, VLS
Jebel Irhoud 1	<i>H. sapiens</i>	MLS, VLS	Zhoukoudian XII	<i>H. erectus</i>	VLS
Jebel Irhoud 2	<i>H. sapiens</i>	VLS	Zhoukoudian II	<i>H. erectus</i>	VLS
KNM-ER 1813	<i>H. habilis</i>	MLS, VLS	Zhoukoudian III	<i>H. erectus</i>	VLS
KNM-ER 3733	<i>H. erectus</i>	MLS, VLS	Zhoukoudian		
KNM-ER 3883	<i>H. erectus</i>	VLS	reconstruction	<i>H. erectus</i>	MLS

Table 17.2

Landmarks Used in Maximum (MLS) and Vault (VLS) Landmark Set Analyses

Landmark	Definition	Type	Analysis
Nasion	Midline intersection of nasal and frontal bones	I	MLS,VLS
Glabella	Most anterior midline point on the frontal bone at the level of the supraorbital	II	MLS,VLS
Frontex	Most inferoposterior midline point on frontal squama above glabella	II	MLS,VLS
Metopion	Ectocranial midline point on frontal at its greatest elevation relative to the chord from nasion to bregma	II	MLS,VLS
Bregma	Ectocranial midline point at intersection of coronal and sagittal sutures	I	MLS,VLS
Parietale	Ectocranial midline point on frontal at its greatest elevation relative to the chord from bregma to lambda	II	MLS,VLS
Lambda	Ectocranial midline point of actual or projected intersection of sagittal and lambdoidal sutures	I	MLS,VLS
Opisthocranium	Midline ectocranial point at the farthest chord length from the glabella	III	MLS,VLS
Mid nuchal point	Midline point between opisthocranium and opisthion	III	MLS
Frontomaxillotemporale (FMT)	Intersection of frontozygomatic suture and temporal line on outer orbital rim	I	MLS
Zygoorbitale	Intersection of zygomaxillary suture and orbital rim	I	MLS
Zygomaxillare	Most inferior and lateral point on the zygomaxillary suture	I	MLS
Orbitale inferior	Most inferior point on the orbital margin	II	MLS
Orbitale superior	Most superior point on the orbital margin	II	MLS
Ectoconchion	Most lateral point on orbital margin	I	MLS
Dacryon	Intersection of lacrimomaxillary suture and frontal bone	I	MLS
Euryon	Point of maximum curvature of parietals	II	MLS,VLS
Auriculare	Point vertically above external auditory meatus at root of zygomatic process	I	MLS,VLS

according to Bookstein (1991): type I landmarks include points where three structures meet or sites of local unusual histology; type II landmarks are points whose homology is supported by geometric criteria (e.g., maxima of curvature); type III landmarks are extremal points whose definitions refer to information from diverse, finitely separated locations (e.g., endpoints, points farthest other points, chords, and diameters). As noted above, a few important landmarks on the cranial base (e.g., basion) and the lower palate (e.g., prosthion, maxillary tuberosities) were excluded in order to maximize sample size. Landmarks coordinates were quantified using a Microscribe digitizer (Immersion Corp, San Jose) from casts in the Peabody Museum collections. Non mid-sagittal plane landmarks were taken from just one side (the least distorted) of each cranium. Error was analyzed by digitizing one skull on five separate occasions. The average standard deviation of landmark coordinates in the x , y , and z planes was between 0.43 and 0.53 mm, indicating that landmark locations can be determined consistently and with little error.

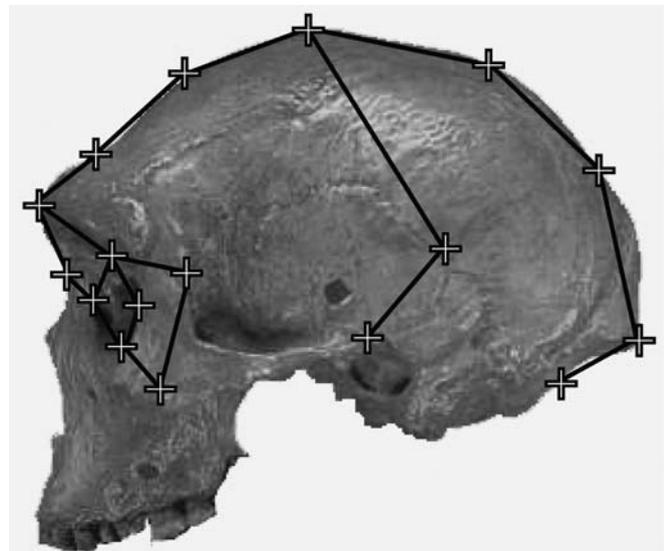


Figure 17.3 Landmarks used in analysis (superimposed on lateral view of Broken Hill).

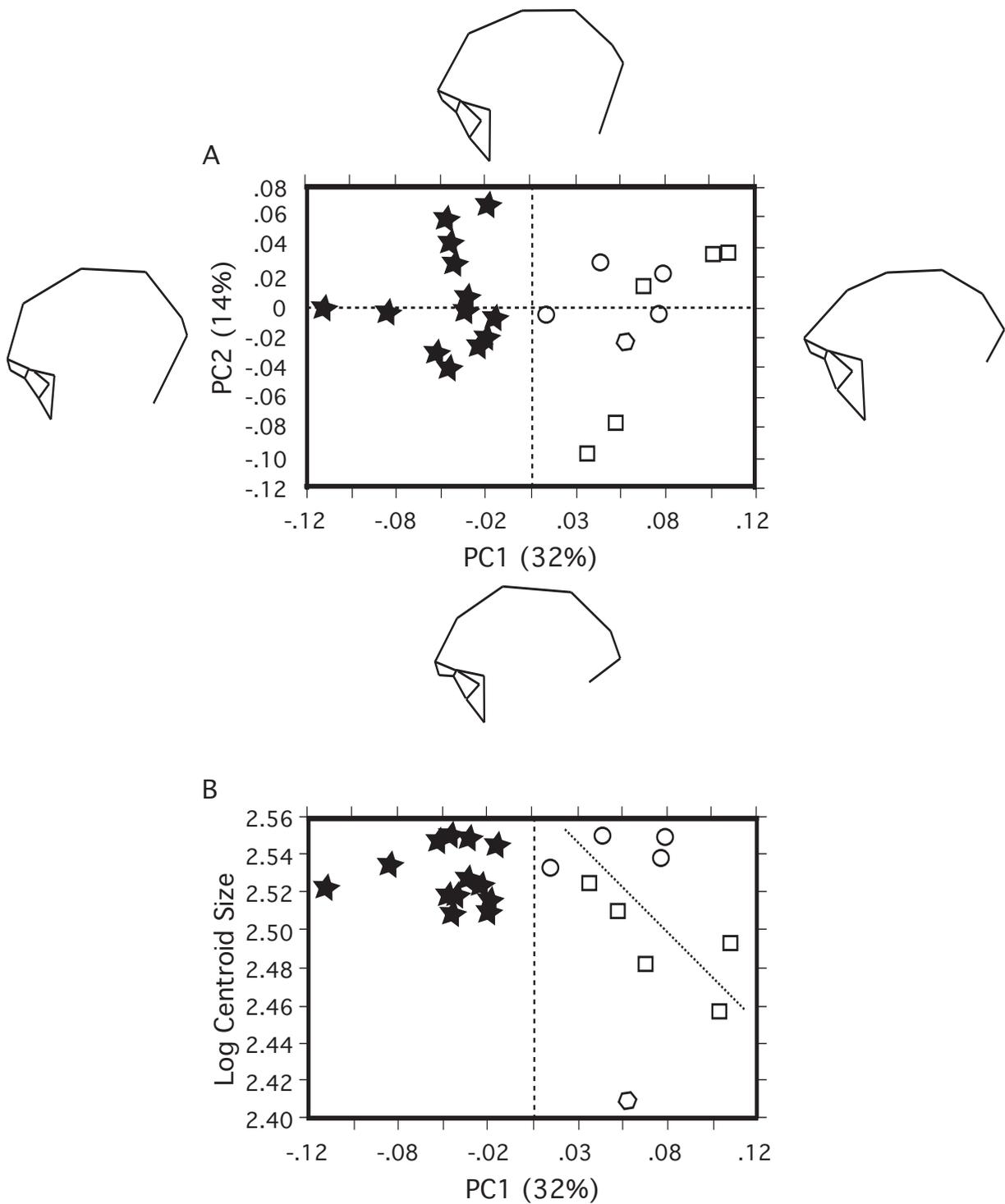


Figure 17.4 Maximum landmark set (MLS) analysis results: stars, *H. sapiens*; circles, archaic *Homo*; squares, *H. erectus*; hexagon, *H. habilis*; a) principal component 1 (PC1) versus principal component 2 (PC2). Wireframes indicate cranial shapes indicated by extremes of PC1 and PC2 (see Figure 17.3); and b) centroid size versus PC1; dashed line indicates regression between size and PC1 for combined archaic *Homo* and *H. erectus* sample. See text for details.

Analysis

Landmarks were analyzed using Morphologika software (www.york.ac.uk/res/fme/resources/software.htm) in two separate studies: a maximum landmark set (MLS), which includes both vault and facial landmarks present in 22 crania; and a smaller set of just vault landmarks (VLS) on a larger sample of 33 crania (see Tables 17.1 and 17.2). Landmarks were superimposed using a generalized least squares regression (Rohlf and Slice 1990), with reflection around the midsagittal plane. Morphologika was also used to calculate and graph the principal components of shape variation using the variance-covariance matrix of the Procrustes residuals, and to calculate centroid sizes of each individual (the square root of the sum of the squared deviations of landmarks from a centroid point). Statistical analysis of the results were tested using Statview by calculating best-fit regression lines for each taxon.

Results

Analysis of the maximum landmark set (MLS) that includes vault and facial landmarks results in six principal components that each account for more than 5% of the sample variation (see Figure 17.4a, Table 17.3). Of these, PC1 (32%) appears to be the most biologically informative, distinctly separating *H. sapiens* from *H. erectus* and archaic *Homo*. As Figure 17.4a illustrates, crania with low PC1 scores (*H. sapiens*) have relatively shorter more globular cranial vaults, relatively shorter (superoinferiorly) orbits, and less projecting faces. More detailed analyses that incorporate cranial base landmarks have shown these factors to covary with variations in cranial base angle and facial size (Lieberman et al. 2002, 2004). PC2 (14%) describes the relative superior position and roundness of landmarks on the posterior cranial vault, and primarily separates two *H. erectus* crania with faces (Sangiran 17 and the Zhoukoudian composite reconstruction)

Table 17.3

Principal Components Analysis Results

Component	Whole Skull (MLS) % Variance	Vault (VLS) % Variance
1	32	33
2	14	17
3	9	13
4	8	8
5	6	7
6	5	5

that have notably protruding and angular occipital tori. Other components (not illustrated) quantify more isolated variations in particular landmark positions. PC3 describes the relative position of metopion along with variations in orbit width; PC4 describes malar height (the position of zygomaxillare relative to other facial landmarks); PC5 describes glabellar height, and PC6 describes the relative position of parietale in the sagittal plane.

Plotting PC1 against centroid size (Figure 17.4b) reveals that this first component of variation scales moderately and significantly ($r = 0.56$, $p < 0.05$) with overall cranial size within the combined archaic *Homo* and *H. erectus* sample. In this sample, archaic *Homo* crania (all which have large endocranial volumes) and larger *H. erectus* crania appear to be scaled variants of smaller *H. erectus* crania (e.g. KNM-ER 3733) with respect to this major component of shape variation. There is no significant relationship between centroid size and PC1 in *H. sapiens*. In addition, the one *H. habilis* skull included (KNM-ER 1813) does not fall on the archaic *Homo* regression, supporting its distinct taxonomic identity. PCs 2–6 do not scale with centroid size in any of the samples.

Analysis of the vault landmark set (Figure 17.5), which includes more specimens but fewer landmarks, yields similar results. The first component, which explains 33% of total sample variation, primarily describes well-known aspects of shape variation that distinguish modern and archaic human taxa. Individuals with low PC1 scores (all *H. sapiens*) have rounder (shorter and taller) vaults, and a higher position of maximum cranial breadth (euryon). PC2 primarily describes variation in the anteroposterior and mediolateral position of eurion. Individuals with high PC2 scores have a relatively anterior and low eurion; individuals with low PC2 scores have a relatively posterior and lateral position of eurion. PCs 3–6 (not pictured) describe other subtle variations in the positions of single landmarks: PC3 describes variations in the relative anteroposterior position of bregma; PC4 describes variations in the relative height of eurion; PC5 describes variations in the position of parietale; and PC6 describes variations in the height of opisthocranium.

As with the MLS, centroid size scales significantly relative to PC1 in the VLS among the combined archaic *Homo* and *H. erectus* sample, but not in *H. sapiens* (Figure 17.5b). Thus larger archaic crania with bigger endocranial volumes have relatively higher, rounder, and wider cranial vaults than smaller individuals ($r = 0.55$; $p < 0.05$).

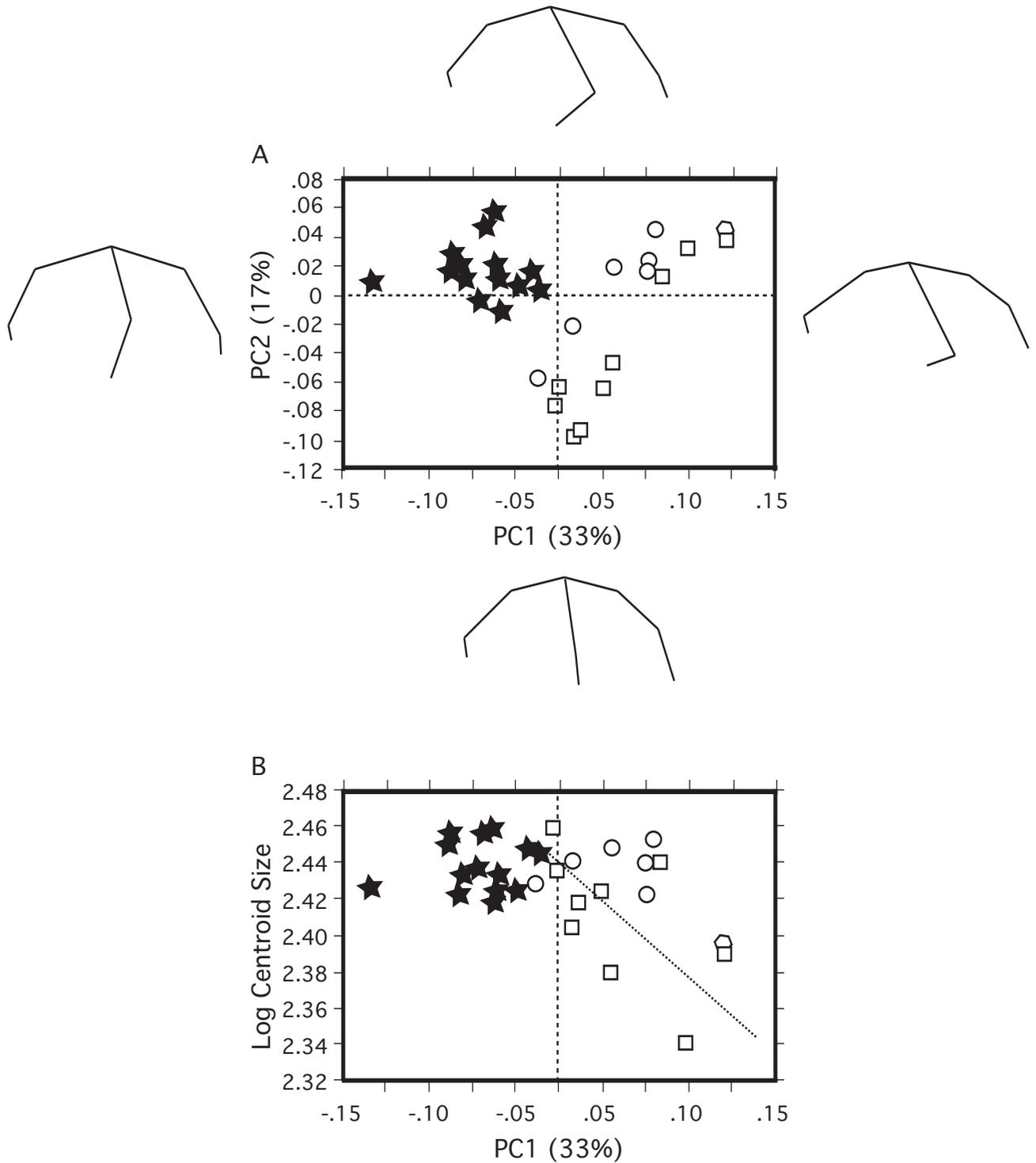


Figure 17.5 Vault landmark set (VLS) analysis results: stars, *H. sapiens*; circles, archaic *Homo*; squares, *H. erectus*; hexagon, *H. habilis*; a) principal component 1 (PC1) versus principal component 2 (PC2). Wireframes indicate cranial shapes indicated by extremes of PC1 and PC2 (see Figure 17.3); and b) centroid size versus PC1; dashed line indicates regression between size and PC1 for combined archaic *Homo* and *H. erectus* sample. See text for details.

Interpretation

The above results provide limited support for the hypotheses that the transition from archaic *Homo* to *H. sapiens* was much more different in degree than the transition from *H. erectus* to archaic *Homo*. The first principal components of cranial shape of both the MLS and VLS analyses (which account for only about 32% of the variance) primarily reflect the degree of globularity of the cranial vault and retraction of the face. As noted by Lieberman et al. (2002), these two major shape differences account for most of the co-varying measurements used by other researchers to distinguish quantitatively *H. sapiens* from archaic *Homo* (e.g., Day and Stringer 1982; Stringer et al. 1984) such as frontal angle, the ratio of the parietal to occipital chords, etc. It is important to note that shifts in cranial globularity and facial retraction are also accompanied by other changes not examined here including the presence of a chin, a distinct canine fossa, bipartite browridges (with a clear separation of the supraciliary and lateral trigonal portions), and a vertical (often posteriorly) sloping infraorbital (malar) surface (Day and Stringer 1982; Stringer et al. 1984; Lieberman 1995; Lahr 1996). These quantitative and qualitative differences reinforce the argument that “anatomically modern” *H. sapiens* belongs in a separate species from archaic *Homo* for two reasons. First, modern *H. sapiens* is distinguished by a number of derived features not shared by any archaic *Homo* fossils. Second, the basic bauplan of the skull in modern *H. sapiens* is uniquely and fundamentally different from that of archaic *Homo* (Lieberman et al. 2004).

While modern and archaic humans differ in substantial ways, the above results suggest that the transition from *H. erectus* to archaic *Homo* is much more subtle. Notably, some proportion of the differences between these taxa appears to be a function of scaling effects. The first principal components of both the MLS and VLS analyses (again, which explain just 32% of variance) scale moderately well with centroid size (note that a high correlation would be unexpected given the lack of size variation within the sample). In other words, larger *H. erectus* and archaic *Homo* crania are scaled versions of smaller *H. erectus* in terms of the first principal component of variation in skull form that mostly reflects vault globularity and facial retraction. These scaling effects,

however, are accompanied by considerable variation that is independent of size. By no means are all the differences between archaic *Homo* and *H. erectus* the result of scaling effects. Interestingly, the other principal components of shape, none of which account for much variance on their own, mostly describe variations in particular landmarks of the vault such as the relative height of euryon, opisthocranium, and the anteroposterior position of bregma. Moreover, none of these higher order principal components separates *H. erectus* and archaic *Homo*. A likely hypothesis (that needs further testing) is that these aspects of variation reflect alternative ways in which larger brains fit into a neurocranium with a relatively extended cranial base angle (see Lieberman et al. 2000a, 2000b).

While variation prevents any simplistic interpretation of the above results, it is important to emphasize that none of the fossils that fall within the *H. sapiens* shape space in Figures 17.3–17.4 can be considered scaled variants of archaic *Homo* and/or *H. erectus*. These modern-shaped crania include not only a number of fossils widely recognized as modern *H. sapiens* such as Zhoukoudian Upper Cave 101, Cro Magnon, Mladec, Brno, Predmosti, Skhul V, Qafzeh 9, and Omo I), but also a few African fossils from the late Middle Pleistocene that are not always placed within *H. sapiens*: Jebel Irhoud I, Jebel Irhoud II, Florisbad, Laetoli Hominid 18 (Nduvu), and Omo II. Whether these latter crania belong in *H. sapiens sensu stricto* is hard to assess definitively without clear criteria by which to define *H. sapiens*. Although these fossils appear to have the two major derived features of the *H. sapiens* skull (cranial vault globularity and facial retraction) they do not have all the morphological features that some researchers consider essential to inclusion within anatomically modern *H. sapiens*, particularly a bipartite browridge, and a fully developed chin (Schwartz and Tattersall 1996, 2003).

Relating Archaeological Transitions to Morphological Transitions in *Homo*

We turn now to the archaeological record. If there is any relationship between the archaeological and fossil records, then the above results raise some new predictions. First, any archaeological transitions that accompanied the origins of archaic *Homo* should be as gradual and subtle as the morphological differences (mostly associated with brain

and face size) that distinguish these taxa. In other words, there may be no reason to expect the archaeological records of archaic *Homo* and *H. erectus* to differ substantially. Second, there should be a major transition associated with origin of modern *H. sapiens* that is not present in archaic *Homo*. In both cases, the null hypothesis should be that there is no correspondence between the two types of records. In addition, an important caveat to emphasize is that even if there is a relationship between the archaeological and fossil records, we should not expect any transitions to be coincident in time. As noted above, lithic industries are learned cultural behaviors in which technological or formal innovations are often added to older traditions. So while new species may have novel cognitive or behavioral capacities that lead to the invention of new lithic industries, these inventions may occur after (but not before) speciation events and would not necessarily lead to the loss or replacement of older traditions. Recent human history provides plenty of examples: the invention of agriculture, metal technology and so on were not associated with any speciation events and did not lead to the complete loss of paleolithic technologies in many societies.

Lower to Middle Paleolithic Transition

The morphological analyses above suggest that archaic *Homo* is, in many ways, really a form of evolved *H. erectus* (one might call them “anatomically modern” *H. erectus*) and that any transitions evident in the fossil record largely reflect increases in brain and facial size that may have occurred gradually with subtle differences in various regions. If there is any correspondence with the archaeological record, then we would expect a similar degree of subtlety characterized by little fundamental change. Is this what we find?

Well, yes and no. For the most part the entire history of *H. erectus* and archaic *Homo* is associated with just two major variants of the Lower Paleolithic, the Acheulian and the core and flake industries (sometimes called the “core-chopper” industries) both of which last until about 250 Ka. In fact, the most remarkable characteristic of the LP is how little change there was. Moreover, it is impossible to associate the different variants of the LP with any taxonomic or environmental variables. This problem is well illustrated by the famous Movius Line, a

line on a map that essentially indicates the paucity of bifaces in East Asia. While it is tempting to argue that the Movius Line represents a taxonomic divide (e.g., that Asian *H. erectus* was a separate lineage), it is important to note that most of Eastern Europe was also devoid of handaxes until the Last Interglacial or the very late Middle Pleistocene. In addition, core and flake industries were common in Africa and Europe in many different types of habitats (Rolland 1998). The best known of these are the Clactonian in Britain, the Tayacian in France, and the Buda industry in Hungary. The suggestion that the Clactonian is a “facies” of the Acheulian that reflects an adaptation to closed (forest) or open (steppic) environments (Ohel 1977 with comments; Mithen 1994 with comments; White 2000) has been refuted.

A limitation on raw material availability is also an insufficient explanation for the distribution of handaxe versus non-handaxe Lower Paleolithic industries. While flint is generally rare in China and Southeast Asia, these regions abound in various metamorphic and igneous rocks that served Acheulian handaxes makers well in East Africa. In Asia, these materials were instead employed to produce mainly core-choppers, picks, and core scrapers. Indeed, core scrapers continued to be manufactured into the Neolithic in south China (Schick 1994; Leng 1998). Bifaces were manufactured in China (Yamei et al. 2000), but they were unquestionably rare. New excavations such as the late Middle Pleistocene site of Dadong cave in the south or Jinniushan did not produce any bifaces (Schepartz et al. 2000, 2003). A similar situation is true of Greece and Hungary, which also lack Acheulian industries despite concerted efforts to find them and the availability of appropriate raw materials.

In sum, there is no relationship between the distribution of environments, raw materials, hominids, and the common tool types of the Lower Paleolithic, whether biface or flake and core industries (e.g., Rolland 1998; Bar-Yosef 1998a). Detailed studies between regions indicate subtle differences in variables such as handaxe form and tool type percentages, but also stress the presence of repeated forms (e.g. ovate and pointed bifaces and cleavers in the Acheulian), probably because these tools all served the same basic purposes such as cutting, whittling, butchering and so forth. Differences between the Acheulian and the core and flake industries thus probably reflect “cultural” differences between groups and regions of *H. erectus* and archaic *Homo* populations.

While it is tempting to conclude that the enduring monotony of the LP is a reflection of evidence for gradual, subtle evolutionary change in the fossil record of *H. erectus* and archaic *Homo*, any simple correspondence between hominid taxa and lithic industries breaks down with the origins of the MP/MSA. The MP/MSA first evolves around 250 Ka. Interestingly, in spite of the paucity of research on MSA sites in sub-Saharan Africa, there is no doubt that the African MSA is best associated with early modern *Homo sapiens* such as at Klasies River Mouth and Omo (Deacon and Deacon 1999; McBrearty and Brooks 2000; McDougal et al. 2005). However, in the Levant we find one of the clear cultural boundaries in the Middle Paleolithic world. While most of the Mousterian industries and in particular the variant known as the “Tabun C type”, uncovered in Tabun, Skhul and Qafzeh caves, was associated with *H. sapiens*, often referred to as the Skhul-Qafzeh group, the later Mousterian, the “Tabun B-type”, is associated with burials of Neanderthals (e.g., the Tabun II female, Kebara, Amud, and Dederiyeh (Bar-Yosef 1992; Bar-Yosef and Callander 1999). The biogeographic distribution of *H. sapiens* and *H. neanderthalensis* differed since the Last Interglacial. The Neanderthals originated in Europe, and expanded as far west as the Caucasus, Uzbekistan, and the Zagros mountains, and only as far south as the Levant. Not only are there no Neanderthals in China, but also there is hardly any evidence for the production of Mousterian industries or the knowledge of the Levallois technique beyond Siberia and the western part of central Asia. So-called Middle Paleolithic assemblages from China fall under the category of core and flake industry and do not conform in their knapping techniques to other MP/MSA industries in Africa and western Eurasia (Clark 1993).

These data raise the question of how the MP/MSA spread. One possibility is that the MP/MSA was invented independently in different parts of the Old World. Such cultural convergence seems unlikely, particularly in light of the narrow temporal window over which the MP/MSA appears across very diverse environments. An alternative scenario—but, admittedly, one with little data to support or refute it—is that the MP/MSA was a modern human invention that originated in Africa and then spread throughout the Old World as a cultural phenomenon prior

to the migration of modern humans out of Africa and the Levant. It is hard to imagine how this spread would have occurred without some degree of population contact and/or migrations. The one aspect that unifies the MP/MSA across most of Africa and western Eurasia is the Levallois method. Detailed studies of this generalized reduction technique, involving replicating and refitting prehistoric blanks to their original cores, indicate that the Levallois is characterized by a specific chaîne opératoire (operational sequence) that tells us about the set of decisions made by the knappers (Boëda 1995). On the whole, producing flakes, blades and point by the Levallois methods requires more knowledge than making most Lower Paleolithic tools (e.g., Bordes 1961, 1980; Laville et al. 1980; Kozłowski 1990, 1998; Bar-Yosef and Meignen 1992; Kuhn 1995; Meignen 1995; Mellars 1996; Hovers 1997; Gamble 1999; Roebroeks and Gamble 1999 and papers therein; Carbonell et al. 2000; Rigaud 2000; Conard 2001 and papers therein; Golovanova and Doronitchev 2003; Boëda 1995). The various defined MP/MSA entities typically differ in the detailed aspects of the reduction sequences and or among the shaped pieces known as “tools” (e.g., Clark 1993; Hovers and Raveh 2000).

What variations in the MP/MSA mean remain unresolved, but the simplest explanation is cultural, in which different variants reflect the expression of the individual flint-knappers’ abilities and capacities within particular (and probably somewhat rigid) traditions of teaching. Additional factors to consider are the effects of other inter-related variables such as group mobility, flexibility in social organization, and rates of site deposition. For example, in Kebara cave, one cubic meter that was accumulated over ca. 3,000 TL years, produced over 1,000 pieces longer than 2.5 cm; the same volume at Hayonim cave contained less than 300 pieces and was deposited during ca. 10,000 TL years (Bar-Yosef 1998b). In addition, at Kebara the rare presence of microfauna indicates a more or less constant human presence and thus the almost complete absence of owls; in contrast, the abundance of microfauna in the various layers at Hayonim reflects regular occupation by owls during extended periods when humans were absent. However, in spite of the inferred differences in group mobility, settlement pattern, and demographic densities (Lieberman and Shea 1994; Stiner et al. 1999; Hovers 2001), the same chaîne

opérateur was practiced for a very long time at each site. We may therefore conclude that a rigid system of teaching and transfer of knowledge within a closed society persisted over the course of many generations among these Middle Paleolithic groups. This picture differs markedly from the Upper Paleolithic across Europe, western and northern Asia and Africa. Interestingly, basic core and flake knapping techniques continued to dominate lithic production in the early Upper Paleolithic industries of China and Southeast Asia.

Middle to Upper Paleolithic Transition

The second archaeological transition to consider is the origins of the Upper Paleolithic (UP), which first appears around 45 Ka, probably somewhere in the Nile Valley or East Africa. It is well known that elements of the UP have been claimed to first occur in Africa during the MSA (McBrearty and Brooks 2000), and similar suggestions were made about western Europe such as the Audi point in the Mousterian of Acheulian Tradition preceding the Chatelperronian points of the UP. Regardless of the ambiguities concerning the calibration of radiocarbon dates in the span of 47–38 Ka (e.g., Huguen et al. 2004), a large number of well-excavated sites indicate that there is hardly any evidence for a cultural transition from the latest Mousterian to the initial Upper Paleolithic. While this issue is being hotly debated by a few European archaeologists, most researchers now accept that the UP originated outside of Europe (partly in the Levant) and that the earliest UP industries are not the typical Aurignacian known from western Europe with its attractive mobile art objects and some early rock paintings and engravings (Kozłowski 2004; Mellars 2004, 2005).

Given the profound, grade-level morphological differences outlined above between *H. sapiens* and archaic *Homo*, the question we ask here is whether there is any evidence to associate the UP exclusively with *H. sapiens*. For many decades, the exclusive association of the UP with modern humans was unchallenged, largely based on the European record. Recently, however, the pendulum of opinion has shifted in the opposite direction thanks to several facts. First, prior to the invention of the UP, *H. sapiens* fossils are exclusively associated with MP/MSA industries that were not much different from

those made by contemporary taxa of archaic *Homo* (Bar-Yosef 1992; Bar-Yosef and Vandermeersch 1993; McBrearty and Brooks 2000). In fact, *H. sapiens* appears to have made MP/MSA industries for approximately 75% of its evolutionary history. Second, there are two examples in Western Europe of archaic *Homo* fossils associated with Chatelperronian industries in deposits dated to near the demise of the Neanderthals: St. Césaire (Leveque and Vandermeersch 1980) and Arcy sur Cure (Hublin et al. 1996). As a result, many paleoanthropologists have argued that no relationship exists between origins of modern humans and industries.

But have we thrown the baby out with the bathwater? We draw attention to two points. The first, also made above, is that there should be no reason to suppose that the origin of modern humans would have to be coincident with the origins of the UP. The UP was not a speciation event but a technological revolution on many fronts that clearly postdated the origins of our species in a manner probably somewhat analogous to the agricultural revolution (e.g., Bar-Yosef 1998c, 1998d, 2002). As such, there is no necessary reason that Neanderthals could not have adopted this new technology after they encountered it unless they lacked the cognitive ability to do so. The latter hypothesis is just speculation, and quite possibly wrong. However, regardless of whether Neanderthals and other archaic *Homo* could make UP industries, the fact is that they either didn't, or did so incredibly rarely.

A second, more speculative point (which we admit to be contentious) is that the often-touted association of Neanderthals and the UP, specifically the Chatelperronian, may have been based on field observations that do not take into account alternative interpretations. In particular, the St. Césaire Neanderthal derives from a secondary burial quite unlike the primary burials at the vast majority of other Neanderthal sites (Leveque and Vandermeersch 1980). The isolated Neanderthal remains at Arcy-sur-Cure (Grotte du Renne) are also problematic in terms of their context given the evidence for mixing between the Chatelperronian and the Aurignacian (Schmider 2002). A reasonable hypothesis that requires testing is that we may have erroneously accepted for more than two decades the notion that Neanderthals made the Chatelperronian industry.

Conclusion

Until recently, many paleoanthropologists expected and looked for correspondences between the lithic and fossil records of human origins in order to explain this complex event. Recent discoveries have largely put an end to these efforts by showing that there is no clear correlation between fossil taxa and lithic industries. However, the taxonomies we use to define lithic industries and hominid species are profoundly different. Species are units in the Linnaean hierarchy that reflect divergent lineages related by ancestry; lithic industries are cultural units based on general categories of tools that reflect common, learned methods of production. In hindsight, there is no reason we should ever expect simple correspondences between these profoundly different kinds of categories. In addition, while the general distinctions between the Lower, Middle and Upper Paleolithic have stood the test of time in terms of their explanatory power, the outdated taxonomy used to describe different species of *Homo* has confused matters enormously. Although the term “archaic *Homo*” will be hard to supplant, it incorrectly suggests (based on just one feature, brain size, and its correlated effects) that proposed taxa such as *H. neanderthalensis* and *H. heidelbergensis* share more affinities with *H. sapiens* than *H. erectus*. However, as suggested by Pilbeam (1986), a better view of the record is that archaic *Homo* is more appropriately considered a bigger-brained, larger-faced version of *H. erectus*. In contrast, the analyses presented here support the hypothesis that the transition between archaic *Homo* and *H. sapiens* appears to have been a punctuated speciation event that involved profound reorganization of the skull as a whole (Lieberman et al. 2002, 2004).

As we expected, reexamining the relationship between lithic industries and this new interpretation of *Homo*, does not lead to a simple correspondence between the fossil and archaeological records. But, in some ways, the correspondence may not be as uncorrelated as sometimes claimed. The Lower Paleolithic has several variants, but the Acheulian and core flake industries may reflect nothing more than different cultural traditions among the early *H. erectus* populations/taxa that first evolved in Africa and then migrated into various parts of the Old World, giving rise to taxa of archaic *Homo*. The monotonous persistence of the LP for

approximately two million years matches the lack of major morphological shifts within these lineages other than an increase in brain and facial size. In addition, there is increasing evidence that modern *H. sapiens* may have invented both the MP/MSA and the UP. In the case of the MP/MSA, the new chaîne opératoire spread like other technologies to both modern human and archaic *Homo* populations throughout the Old World via means that have not been documented. In contrast, the UP appears to have spread almost exclusively within modern humans. Further evidence, including a careful reexamination of the context of Neanderthals in the Chatelperronian, is needed to test this hypothesis.

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