ANTHROPOLOGIE • XXXVIII/2 • pp. 151–163 • 2000

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PHENETIC PATTERNING AND SPECIES SORTING IN EARLY AFRICAN *HOMO*

ABSTRACT: The morphological diversity exhibited by African hominids around the Plio-Pleistocene boundary continues to generate conflicting systematic and phyletic interpretations. At least five schemes are currently utilised to differentiate early Homo specimens, *while debate continues over whether early African* H. erectus*-like fossils represent that taxon or the claimed more primitive species* H. ergaster *and* H. leakeyi. *This paper summarises findings from regionally based morphometric analyses (face and brain case) of early* Homo *crania and the resulting patterns of affinities derived from them. It reviews the implications of such patterning for the above schemes, and for recent proposals to revise the lower boundary of the genus* Homo *and its included species.*

KEY WORDS: Homo – H. habilis – H. rudolfensis – H. erectus – H. ergaster – *SK 847 – Morphometrics*

INTRODUCTION

Despite the recent spate of significant – and in some instances (e.g. the Stw 573 skeleton (Clarke 1998)) spectacular – discoveries of hominid fossils dating between *ca* 4.5 and 2.5 million years ago (mya), the half to three-quarters of a million year span of the final Pliocene/basal Pleistocene (*ca* 2.2 +–1.5 mya) exhibits a still unparalleled range of hominid morphological diversity. Most workers recognise at least two *Paranthropus* species (*P. boisei* and *P. robustus*) with a second South African species (*P. crassidens*) sometimes identified. In East Africa *P. boisei* may date back to *ca* 2.6 mya or, more likely, the earlier fossils represent another "robust" species, *P. aethiopicus*, that extends down to around 2.2 mya or just before. Assessments of early *Homo* are even more diverse, with several interpretations current that differ in the number, composition and morphological parameters of included species, and in their systematic and taxonomic implications.

The majority of the early *Homo* specimens were recovered in the 1960s and 1970s from sites in Olduvai Gorge and the Turkana basin; this extensive sample has been augmented by discoveries elsewhere e.g. Omo L 894-1 (Boaz, Howell 1977), the UR 501 mandible from the Chiwondo Beds at Uraha Hill, Malawi (Bromage *et al.* 1995), and in South Africa, SK 847 (Clarke, Howell 1972, Clarke 1977) and Stw 53 (Tobias 1978) from the Sterkfontein Valley. Most recently, the discovery of the A.L. 666-1 maxilla from Hadar, Ethiopia pushes the origin of the genus back to > 2.3 mya (Kimbel *et al.* 1997). Over the last two decades the bulk of this fossil evidence has been extensively studied, with major, and defining, monographic descriptions of the Olduvai fossils (Tobias 1991) and Koobi Fora hominids (Wood 1991) appearing. These and other accounts have greatly increased our understanding of the morphology of these crucial specimens, but they have not resolved disputes over their systematic affinities. On the contrary: there are at least five widely known and so influential interpretations of early *Homo* diversity current in the literature. These are:

- a monospecific interpretation, in which all specimens are accommodated within a single, necessarily highly variable, species – the "broad" *Homo habilis* concept (e.g. Tobias 1991).
- A view which recognises *H. habilis* at Olduvai, and another species of *Homo* at Koobi Fora and in South Africa (e.g. Chamberlain 1987, Chamberlain, Wood 1987).

TABLE 1. Characters used to describe the hominid facial skeleton and neurocranium.

Face

1 Medial thickness of supraorbital torus
2 Supraorbital torus thickness above highest point on orbit
3 Transverse development of supraorbital torus (chord)
4 Transverse development of supraorbital torus (arc)
5 Maximum vertical height of orbit
6 Maximum horizontal breadth of orbit
7 Minimum interorbital distance
8 Maximum breadth of nasal bones
9 Bimaxillary breadth
10 Maximum breadth of nasal aperture
11 Length of nasal bones: nasion-rhinion chord
12 Height of nasal aperture: rhinion-subnasale chord
13 Premaxillary development: subnasale-alveolare chord
(14, 15 omitted)
16 Medial facial projection: Upper face. Glabella-porion chord
17 Medial facial projection: Upper face. Nasion-porion chord
18 Medial facial prognathism: Mid-face. Rhinion-porion chord
19 Medial facial prognathism: Mid-face. Subnasale-porion chord
20 Medial facial prognathism: Lower face. Alveolare-porion chord
21 Lateral facial prognathism: Upper face. Zygo-orbitale-porion chord
22 Lateral facial prognathism: Mid-face. Zygomaxillare-porion chord

Cranial vault

1 MSP Frontal development: supratoral sulcus to bregma (chord)
2 MSP Frontal development: supratoral sulcus to bregma (arc)
3 Coronal Frontal development: minimum fromtal breadth at glabella level (chord)
4 MSP Parietal development: bregma to lambda (chord)
5 MSP Parietal development: bregma to lambda (arc)
6 Parietal development above porion: tempero-parietal – inter-parietal distance (chord)
7 Parietal development above porion: tempero-parietal – inter-parietal distance (arc)
8 Temporal development:porion to tempero-parietal suture (chord)
9 Temporal development:porion to tempero-parietal suture (arc)
10 MSP Occipital development: lambda to opisthion (chord)
11 MSP Occipital development: lambda to opisthion (arc)
12 Coronal Occipital development: biasterionic diameter (chord)
13 Coronal Occipital development: biasterionic diameter (arc)
14 Biporionic diameter (chord)

- An interpretation that incorporates the Olduvai and smaller Koobi Fora specimens, and possibly some South African fossils, in *H. habilis*, with a second species, *H. rudolfensis*, represented at Koobi Fora by KNM-ER 1470, ER 3732 etc. (e.g. Wood 1991, Grine *et al.* 1993, 1996).
- Schemes which associate larger Olduvai and Koobi Fora crania (including OH 7 and KNM-ER 1470), possibly together with some smaller specimens, in *H. habilis*, leaving other smaller crania as members of a second species (e.g. Stringer 1986, Rightmire 1993).
- A polyphyletic interpretation that recognises four *Homo* species at Koobi Fora, all distinct from *H. habilis,* which is present at Olduvai and in South Africa (Groves 1989).

Concurrent with these conflicting views on species sorting and morphological parameters within the early *Homo* material has been a parallel debate as to whether early East African "*erectus* -like" forms such as KNM-ER 3733, KNM-ER 3883, and probably KNM-WT 15000 are indeed *H. erectus,* or whether they represent a more primitive, possibly precursor, species (Andrews 1984, Stringer 1984, Wood 1984, Clarke 1990, 1994). This is generally referred to *H. ergaster* (Groves, Mazák 1975, Wood 1991, 1992, 1993) but has also been called *H. leakeyi* (Clarke 1990, 1994).

In addition, the discovery of the remarkably preserved youth's skeleton (KNM -WT 15000) from Nariokotome, West Turkana (Brown *et al.* 1985, Walker, Leakey 1993a), focused attention on postcranial morphology and body proportions, and catalysed views forming in many workers' minds that the appearance of early *H. erectus/ergaster* represented an important phyletic and adaptive shift that contrasted in many ways with earlier and contemporary hominid species. Over the last decade several studies have explored the likely contrasts between early *H. erectus/ ergaster* and other hominids in such functionally critical systems as locomotor modalities, dietary ecology, central nervous system complexity, metabolic needs and their implications, thermoregulation, life history patterns etc. A further, natural, development has been a recent suggestion from Wood and Collard (1999) that the systematic implications of such multiple contrasts be formalised by excluding non-*ergaster/erectus* forms from *Homo,* and relegating them – at least *pro tem* – to *Australopithecus*.

This paper focuses on patterns of phenetic affinities displayed by early *Homo* crania in the face and neurocranium and assesses alternative systematic interpretations in light of such patterning. In the following sections I summarise results from some morphometric studies and briefly consider in turn their bearing on the above issues.

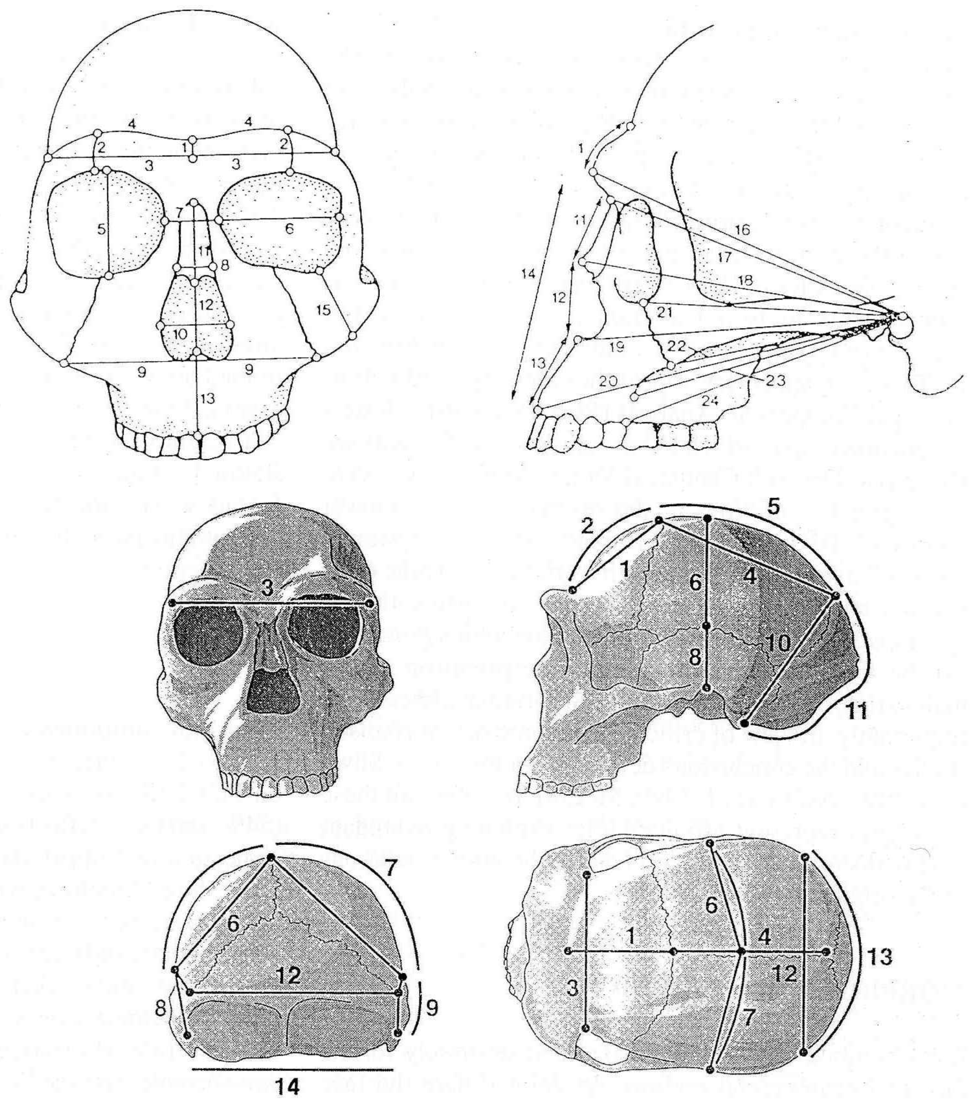
MATERIALS AND METHODS

Included hominid specimens and taxa (both definitive and putative) are listed below. Since most early hominid fossils are incomplete, only a minority could be included in both face and cranial vault analyses:

Early hominids

Australopithecus africanus: Sts 5 , Sts 25, Sts 71; MLD 1, MLD 37/38 (Broom, Schepers 1946, Broom *et al.* 1950, Robinson 1954, Tobias 1967).
Paranthropus robustus: SK 46, SK 48 (Broom, Robinson 1952, Robinson 1954, Tobias 1967).
Paranthropus boisei: OH 5, KNM-ER 406, KNM-ER 407, KNM-ER 732 (Tobias 1967, Leakey *et al.* 1978, Wood 1991).
Homo habilis: OH 7, OH 13, OH 16, OH 24; KNM-ER 1805 KNM-ER 1813 (Leakey *et al.* 1964, Leakey *et al.* 1971, Wood 1991).
Homo rudolfensis: KNM-ER 1470, KNM-ER 3732 (Leakey *et al.* 1978, Wood 1991).
Early African *Homo erectus/H. ergaster*: KNM-ER 3733, KNM-ER 3883; OH 9; KNM-WT 15000 (cast) (Walker, Leakey 1978, Rightmire 1979, Walker, Leakey 1993b). KNM-WT 15000 is relatively intact but immature, and as such not directly comparable with adult crania; it is therefore included in the PCA of individuals, but omitted from the D^2 and CVA of groups (see below).
Early *Homo sp.*
SK 847 (Clarke, Howell 1972, Clarke 1977); Stw 53 (Tobias 1978). This last specimen is widely, though informally, regarded as *H. habilis.*

FIGURE 1. Characters used to describe the hominid facial skeleton and neurocranium.



Comparators

In addition to the above, the following groupings were included for comparative purposes:

Javan *Homo erectus*: Trinil 1 (Pith I); Sangiran 2 (Pith II); Sangiran 11 (Pith IV); (Weidenreich 1945).

Chinese *Homo erectus*: Zhoukoudian (Pekin) Crania II (D), III (E), X (LI), XI (LII), XII (LIII) (all measurements from casts) (Weidenreich 1943). For the face Weidenreich and Swan's reconstruction of a female (Weidenreich 1937), and Tattersall and Sawyer's (1996) reconstruction of a male were used.

European Neanderthals (*Homo sapiens neanderthalensis/H. neanderthalensis*): Neanderthal, Spy 1, Spy 2, La Ferrassie I, La Quina, Mt. Circeo, La Chapelle-aux-Saints, Gibraltar 1 (all measurements from casts).

Upper Pleistocene *Homo sapiens*: Cro-Magnon 1, Cro-Magnon 3, Předmostí 3, Předmostí 4, Combe Capelle, Brno 1, Brno 2, Grotte des Enfants 6 (all measurements from casts).

Modern *Homo sapiens (H. s. sapiens)*: Fifty crania in the Duckworth Collection, Department of Biological Anthropology, Cambridge.

Morphometric approaches

Multivariate analysis has been used to investigate the patterns of affinity. Such approaches permit analysis of the interactions between included variables and provide measures of affinity based upon all characters within the data set in a way akin to Le Gros Clark's (1962, 1964) concept of "total morphological pattern". They thus typically comprise a mix of plesiomorphous and apomorphous traits. This is entirely legitimate since the primary aims are to model cranial diversity and identify phena, not to reconstruct evolutionary relationships *per se*. Two complementary approaches are employed below: Principal Components Analysis (PCA) to identify clusters of specimens upon which to base groups, and Generalised Distances (D^2) with Canonical Variate Analysis (CVA) to investigate the affinities of the resulting groups (Gower 1966 a, b). D^2 quantifies the between-group dispersion in terms of average within-group variability, while CVA permits an intelligible summary by collapsing the D^2 hyperspace into "real" (3-D) space within which groupings can be figured, and also allows interpretation of the multivariate dispersion in terms of the original dimensions. Importantly, in view of criticisms of some recent cladistic studies and the conclusions derived from them (e.g. Suwa *et al.* 1997, Asfaw *et al.* 1999, McCollum 1999), all these techniques represent affinities after excluding redundant (and so distorting) information due to the intercorrelations of the original variables.

MORPHOLOGICAL REGIONS

Early hominid affinities were explored separately for the face and neurocranial regions. As defined here the face extends from the supraorbital torus inferiorly to the alveolar margin of the premaxilla and maxilla, and laterally to the orbital margins and the junction of the anterior and lateral surfaces of the zygoma. The maxillary zygomatic process and the anterior face of the zygoma are therefore included within the facial region but the arch itself (which is rarely preserved intact) is not. The cranial vault extends from the sulcus above the supraorbital torus posteriorly to the rear of the skull (opisthocranion) and inferiorly to the posterior margin of the foramen magnum (opisthion). Coronal development is characterised by frontal breadth, development of the temporals and parietals above the poria, and occipital breadth. The vault thus includes the squamous frontal, but not the supraorbital torus which is best considered functionally as a component of the face (see above), nor the foramen magnum and the regions immediately lateral and anterior to it, which comprise the cranial base. *Table 1* and *Figures 1 a, b* indicate the characters used to describe face and vault proportions. Below I summarise the results of morphometric analyses for face and neurocranium separately, and then discuss their joint implications for the systematic issues noted in the Introduction.

FACE

Principal components

Figures 2 a, b present the positions of the early hominids on PCs I-III. As is usual in analyses of this kind, PC I (54% variance) reflects overall size, with median sagittal projection and upper face breadth especially influential. Large-faced hominids with prognathous and/or anteriorly positioned faces relative to the neurocranium (e.g. Neanderthals and large *A. boisei* specimens) are at one end of the array, and smaller, flat-faced modern humans at the other. Nonetheless the spread of the anatomically modern crania (late Pleistocene and modern humans) is considerable, and the PC does not separate these from the bulk of the early hominid samples. PC II (22% variance) orders on contrasts in facial proportions rather than overall size, with breadth and lateral projection of the mid-face, and prognathism and depth of the lower face, heavily weighted. Unlike PC I, it effectively sorts early hominids (i.e. Pliocene and basal Pleistocene forms) from Middle Pleistocene and later crania. Of the former group, putative *H. habilis* specimens (OH 24 and KNM-ER 1813) and especially *H. erectus/ergaster* (KNM-ER 3733) lie closest to later *Homo*, and bridge what would otherwise be two discrete clusters. Other early *Homo* crania such as SK 847 and especially KNM-ER 1470 (*H. rudolfensis*) are more distant, clustering with *Australopithecus* and *Paranthropus*.

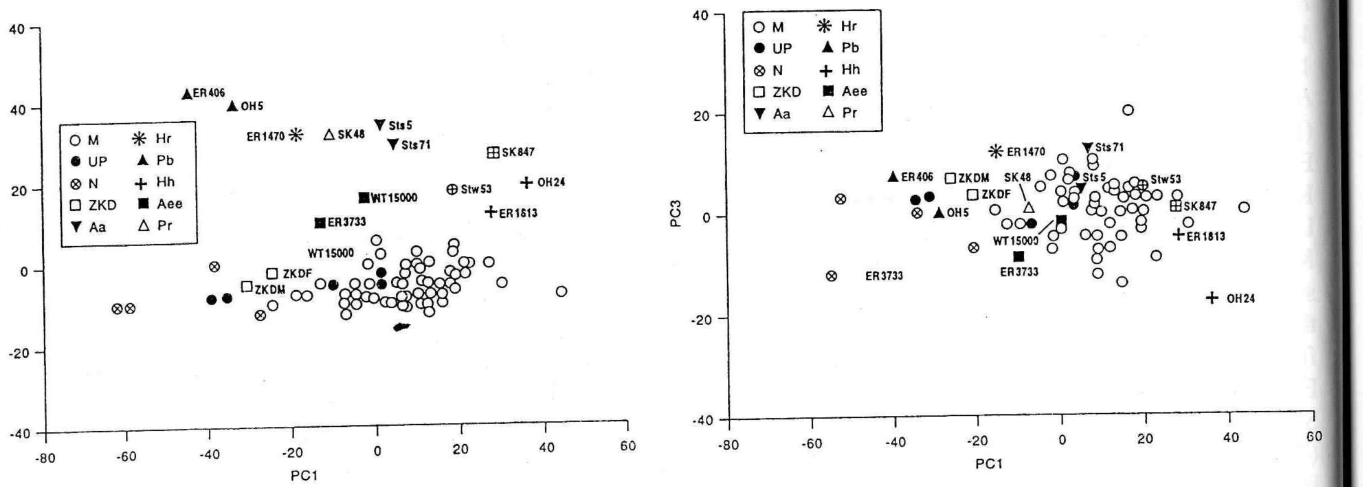


FIGURE 2. Principal Components: Face. Plots of hominid specimens on PCs I & II (2a) and I & III (2b).

TABLE 2. D^2 values between early hominid and later groups for face and neurocranium.

	Face	Cranial vault
U. Pal. *H. sapiens* – modern *H. sapiens*	4.8	3.7
Neanderthal – U. Pal *H. sapiens*	9.6	5.7
Neanderthal – modern *H. sapiens*	9.5	6.0
ZKD *H. erectus* – modern *H. sapiens*	6.7	6.6
ZKD *H. erectus* – Neanderthal	7.6	6.4
Java *H. erectus* – modern *H. sapiens*	–	8.8
Java *H. erectus* – Neanderthal	–	7.9
African *H. erectus* – modern *H. sapiens*	11.9	7.7
African *H. erectus* – Neanderthal	10.3	6.2
African *H. erectus* – ZKD *H. erectus*	9.7	5.1
African *H. erectus* – *H. rudolfensis*	12.2	6.7
African *H. erectus* – *H. habilis*	15.2	8.6
H. habilis – *H. rudolfensis*	9.5	7.0
H. habilis – *A. africanus*	7.2	6.2
H. rudolfensis – *A. africanus*	11.9	6.8
African *H. erectus* – *A. africanus*	16.7	10.3
H. rudolfensis – *P. boisei*	11.0	7.8
H. rudolfensis – *P. robustus*	10.0	–
P. boisei – *A. africanus*	13.6	7.4
P. robustus – *A. africanus*	7.1	–
P. boisei – *P. robustus*	9.8	–
A. africanus – modern *H. sapiens*	16.0	–
P. robustus – modern *H. sapiens*	17.5	–
P. boisei – modern *H. sapiens*	21.2	13.6

PC III (> 5% variance) sorts on upper facial breadth and medial and lateral projection of the mid-face. Again there is extensive overlap between early and later hominid crania, although within the former group KNM-ER 1470 is well separated from other early *Homo* fossils, clustering instead with *Paranthropus* specimens. PCs I-III overall account for > 82% of variance and produce two roughly parallel arrays of Pliocene/ basal Pleistocene hominids and mid-later Quaternary *Homo*, rather tenuously linked via *H. habilis* and *H. erectus/ergaster* respectively. *H. rudolfensis*, on the other hand, is comparatively distant from these early *Homo* crania.

Generalised distances

Relevant D^2 distances extracted from the full matrices are given in the left hand column of *Table 2*. The values reveal three broad groupings: Mid-later Quaternary forms (i.e. ZKD *erectus*, Neanderthals and *H. sapiens*) cluster together, as do gracile early hominids (*H. habilis* and *A. africanus*), with *Paranthropus* species as a third, looser, grouping. *H. rudolfensis* (KNM-ER 1470) and early *H.erectus/ergaster* both occupy comparatively isolated positions. However, their affinities clearly contrast: *H. rudolfensis* is closest to *P. robustus* and *P. boisei*, whereas KNM- ER 3733's nearest neighbours are ZKD *erectus* and the Upper Pleistocene and modern groups; Pliocene and other basal Pleistocene forms are all markedly more distant.

Canonical variate analysis

Further insights into the affinities of these groupings are provided by CVA of facial dimensions *(Figures 3 a, b)*. For this and for the vault analysis below, positions are plotted separately for Koobi Fora and Olduvai sub-samples of *H. habilis* and *H. erectus/ergaster*, as well as for the combined samples which I focus on here. CV I (68% variance) discriminates primarily upon overall projection, especially of the medial and lateral components of the mid-face, and on orbital and supraorbital breadths. CV II (15% variance) sorts mainly on breadth and projection of the

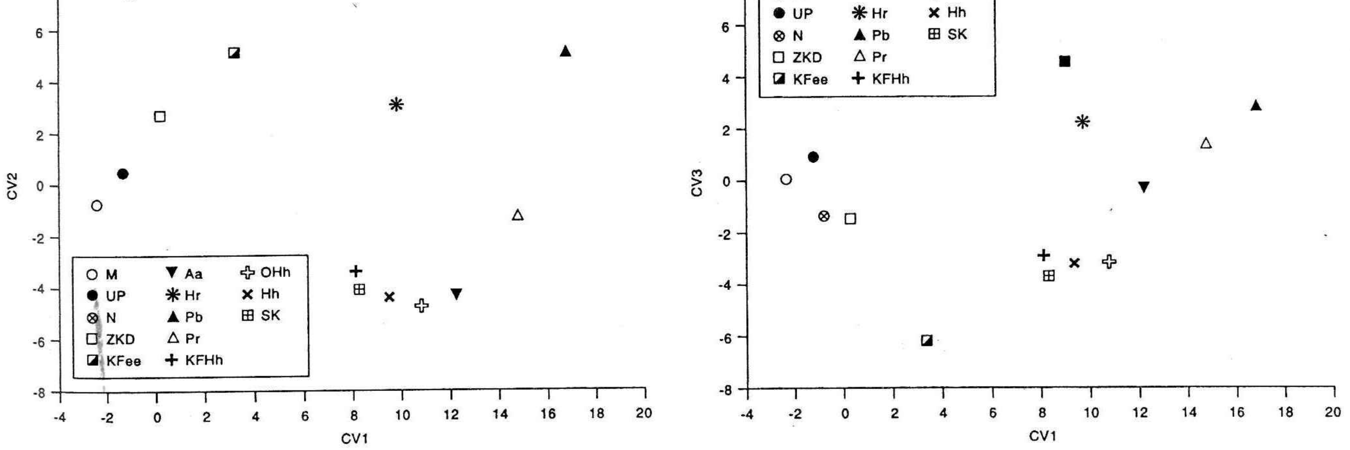


FIGURE 3. Canonical Variate Analysis: Face. Plots of hominid groups on CVs I & II (3a) and I & III (3b). M = modern H. sapiens; UP = Upper Palaeolithic H. sapiens; N = Neanderthals; ZKD = Zhoukoudian H. erectus; J = Java H. erectus; Aa = A. africanus; Hr = H. rudolfensis; Pb = P. boisei; Pr = P. robustus; SK = SK 847; KFHh = Koobi Fora H. habilis; OHh = Olduvai H. habilis; H.h = Combined H. habilis; Kfee = Koobi Fora H. erectus/ergaster; Oee = Olduvai H. erectus/ergaster; Aee = Combined African H. erectus/ergaster.

upper face, CV III (6% variance) on mid-face prognathism and lower facial length. There are obvious resonances – although not complete identity – here with the PCA weightings above. The resulting hominid array reveals two groupings: Modern humans, Neanderthals and ZKD *erectus* form one cluster, early hominids (early *Homo*, *A. africanus, P. robustus, P. boisei,*) another but broader spread, with the last two species at its limit. Within this grouping the gracile early *Homo* specimens form a compact cluster, but KNM-ER 1470 is relatively isolated, especially on CV III where it approaches *P. robustus*, due to similarities in the malar region and naso-alveolar clivus. Early African *H. erectus/ergaster* is separated from both groupings but, as in the D^2 matrix, is closer to the Middle-Upper Pleistocene and modern forms. Its isolation from other contemporary *Homo* species, especially on CV I and II is noteworthy.

Overall, the clusters identified by PCA, and the D^2 and CVA analyses of the groupings derived from these, identify two basic patterns of facial morphology within the Plio-Pleistocene hominid record (Bilsborough, Wood 1988). The majority of Pliocene and basal Pleistocene hominids display a pattern in which upper faces are narrow, mid-faces broad, zygomatic processes are set well forward relative to the nasal region and their anterior faces are vertical or anteriorly inferiorly sloping. There is generally considerable overall facial prognathism, with projection especially marked in the mid-face. This pattern is seen at its fullest development in large *P. boisei* crania such as KNM-ER 406 and OH 5, but these are linked via *P. robustus* and *A. africanus* to smaller, lightly built crania such as *H. habilis,* which possess a pattern basically similar to, but more lightly constructed and less prognathous than that seen in *A. africanus.* SK 847 occupies an intermediate position, while *H. rudolfensis,* represented by KNM-ER 1470, displays a unique pattern; overall it falls within this cluster but diverges markedly from other early *Homo* specimens and in some respects mimics the *Paranthropus* arrangement.

The other pattern, first displayed by *H. erectus / ergaster* and characteristic of subsequent *Homo* specimens, is of a more orthognathic face overall, and one that is particularly flat in the mid-facial area, with projecting nasals, retracted, lightly built, shallow and posteriorly inferiorly sloping zygomatics, and modest sub-nasal prognathism. The upper face is broad relative to the mid-face, with lateral rather than medial development of the supraorbital torus. There is a distinct break between these two morphologies, with the *erectus/ergaster* specimens showing clear affinities with all the later *Homo* comparators rather than with other, broadly contemporary, early *Homo*.

CRANIAL VAULT

Principal components

Figures 4 a, b illustrate the positions of the specimens on PCs I-III. PC I (64% variance) sorts principally on sagittal expansion of the anterior and mid-vault, and on sagittal and coronal development of the occipital. PC II (*ca* 12% variance) separates on transverse/vertical development of the lower/rear vault, and sagittal expansion of the anterior-mid vault. PC III (>7% variance), orders on coronal and vertical development of the mid-rear vault. Overall, the first three PCs account for just under 83% of the total variance.

PC I sorting results in two clusters: one consists of early, small-brained hominids *(Australopithecus, Paranthropus,* Olduvai and Koobi Fora *H. habilis*); the other comprises later *Homo* (*H. erectus/ergaster* onwards). Between them, but isolated from adults of both clusters, is KNM-ER 1470; only the immature KNM-WT 15000 cranium is relatively close, while still well separated from the tightly clustered *habilis* specimens. Within the *H. erectus/ ergaster* grouping the Koobi Fora and Javan forms are set apart from later Quaternary crania while the ZKD crania and OH 9 just overlap the modern spread.

Distribution along PCs II and III is more compact, with the extremes for II represented by Upper Palaeolithic and modern neurocrania at one end with Neanderthals and Early African and Javan *H. erectus* at the other, and for III by *H. sapiens* specimens at both limits.

H. habilis ss. neurocrania cluster on PC I-III, and the analysis thus supports associating Koobi Fora specimens KNM-ER 1805 and 1813 with Olduvai hominids such as OH 24. Similarly, KNM-ER 3733, 3883 and KNM-WT 15000 regularly group with *H. erectus* on PC I-III, with the juvenile West Turkana specimen predictably as the outlier of this cluster; if these African specimens represent a separate species (*H. ergaster)* it is one that is remarkably similar to *H. erectus ss* in neurocranial size and proportions. By contrast, the position of KNM-ER 1470 is distinctive. It is generally intermediate between early, small-brained *Homo* and *H. erectus/H. ergaster* on PC I-III, and close to these, especially the latter on PC II and III, but isolated from mature individuals of both groups on PC I. Its neurocranial separation is reminiscent of, but is less extreme than, that evident in the face (see above).

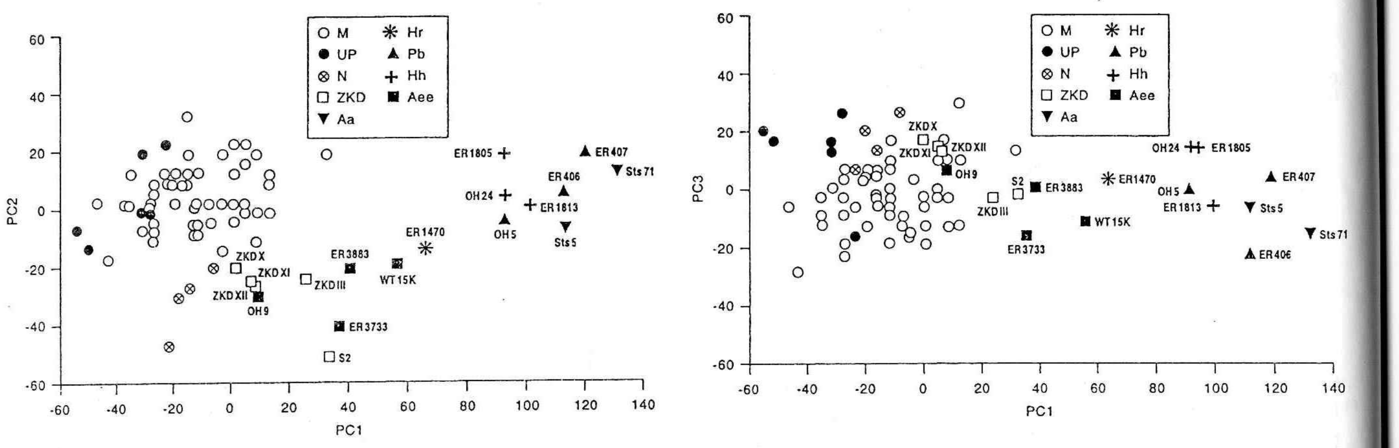


FIGURE 4. Principal Components: Cranial Vault. Plots of hominid groups on PCs I & II (4a) and I & III (4b).

Generalised distances

D^2 values are given in the right hand column of *Table 2.* Early *Homo* crania are generally closer to more recent forms than are the australopithecines, but in some cases only slightly so; the early *Homo* specimens are also consistently closer to *A. africanus* than to *P. boisei.* The *H. erectus* groups form a cluster: the ZKD sample is a little farther than Neanderthals from modern crania, with the other *H. erectus* groups slightly more distant.

Australopithecine species *(A. africanus* and *P. boisei)* and the majority of Quaternary *Homo* specimens (i.e. *H. erectus* onwards) span comparable degrees of neurocranial variation. However, when *H. habilis* and *H. rudolfensis* are taken into account, neurocranial diversity exhibited by *Homo* is *ca* 40–50% greater than that displayed by *Australopithecus* and *Paranthropus.*

H. rudolfensis is closest to, yet still comparatively isolated from, *H. erectus* groups; beyond these the nearest forms are *H. habilis* and then *A. africanus*, with *P. boisei* yet more distant – a significant ordering in view of the patterning on facial dimensions, and the affinities sometimes claimed between KNM-ER 1470 and *P. boisei* on the basis of these (Bilsborough, Wood, 1988, Grine *et al.* 1996, and see below).

Early East African *H. erectus/ergaster* is, as expected, closest to the other *H. erectus* groups, with Neanderthals and modern *H. sapiens* also relatively close. This emphasises the metrical affinities between early *H. erectus* neurocrania and later hominid groups, and the former's separation from other Pliocene/basal Pleistocene forms. The nearest of these is *H. rudolfensis*, but separation here is still of the order seen between early *H. erectus* and Neanderthals/modern *H. sapiens;* other early hominids are even further distant from *H. erectus.*

Canonical variate analysis

Figures 5a and *5b* plot the group centroids on canonical axes I-III, accounting for *ca* 88% of the total variance, and so approximating the D^2 dispersion. The relationships are again similar to those in the PCA but, predictably, with a clearer separation between the groups. The trio of small-brained hominid species are at one end of the distribution, with the Upper Pleistocene and modern humans at the other. Between them the *H. erectus* and *erectus/ergaster* groups form a tight cluster, with *H. rudolfensis* again occupying an intermediate, relatively isolated, position between these and *H. habilis.*

Most of the spread (61%) is accounted for by CV I, which produces an array broadly comparable to PC I, although, as in the face analysis, again sorting on shape rather than overall size. Transverse, vertical, and sagittal development of the mid-neurocranium, together with coronal expansion of the frontal are heavily weighted. *P. boisei* and *H. sapiens* occupy opposite ends of the variate, whilst *H. erectus* and *erectus/ergaster* crania, with high biporionic values and coronal development of frontal and parietals comparable to *H. sapiens*, but with smaller

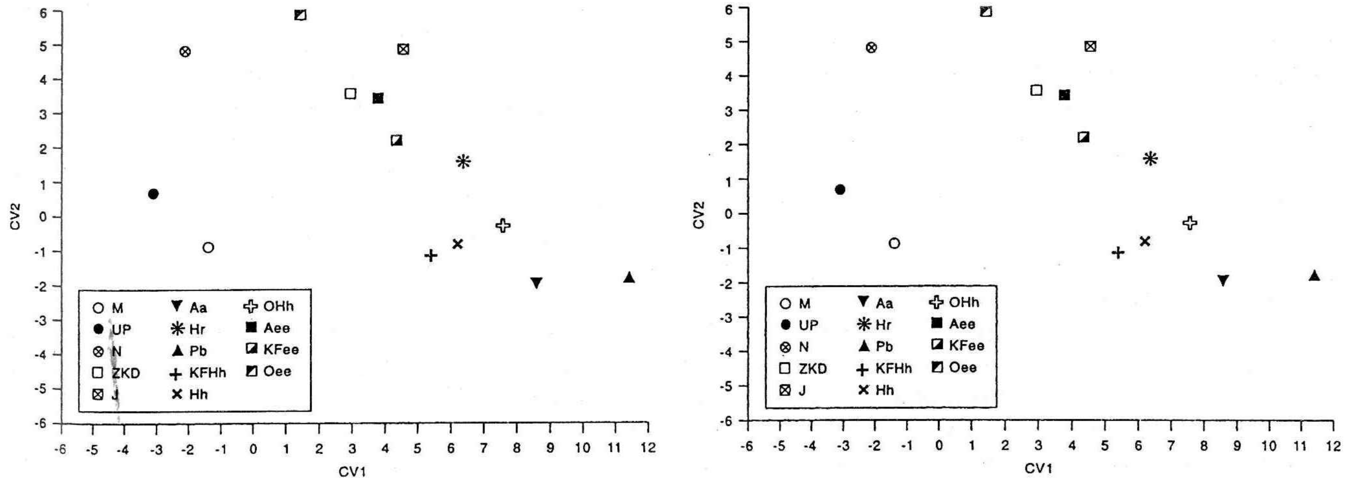


FIGURE 5. Canonical Variate Analysis: Cranial Vault. Plots of hominid groups on CVs I & II (5a) and I & III (5b).). M = modern H. sapiens; UP = Upper Palaeolithic H. sapiens; N = Neanderthals; ZKD = Zhoukoudian H. erectus; J = Java H. erectus; Aa = A. africanus; Hr = H. rudolfensis; Pb=P. boisei; KFHh = Koobi Fora H. habilis; OHh = Olduvai H. habilis; H.h = Combined H. habilis; Kfee = Koobi Fora H. erectus/ergaster; Oee = Olduvai H. erectus/ergaster; Aee = Combined African H. erectus/ergaster.

temporals and sagittally smaller parietals, occupy the mid-range. *H. rudolfensis* is again relatively well separated from *erectus*, but in contrast to PC I is practically coincident with *H. habilis*.

Axes II and III both sort principally upon aspects of fronto-parietal expansion. CV II (20% variance) orders mainly on parietal development and frontal breadth, so that early hominid crania are generally towards one end of the spread, and *H. erectus* (Java and Olduvai) and Neanderthals towards the other, and with *A. africanus,* and *P. boisei,* defining the lower limit. *H. habilis* and *H. rudolfensis* are well-separated on CV II, reflecting the latter's more expanded parietal region, although it is also well-separated from *H. erectus* groups (other than the Koobi Fora sub-sample) because of its generally smaller dimensions and narrower frontal.

CV III (7% variance) discriminates principally upon frontal development and coronal expansion of the mid-neurocranium. Forms with narrow frontals relative to transverse expansion of the mid-vault are towards one end of the spread, gracile forms in which the frontal is broader relative to biporionic diameter, occupy the opposite pole. KNM-ER 1470 is again well separated from *H. habilis* and within the *H. erectus* cluster on this axis, reflecting approximately *H. erectus*-like values for these traits.

In summary, CVs I-III encompass > 88% of variance, and identify three morphometric clines in neurocranial form: CV I sorts principally on coronal expansion of the neurocranium overall and development of the mid-cranial region; CV II on parietal expansion/curvature and frontal breadth; and CV III on frontal development and parietal breadth.

ABSOLUTE AND RELATIVE CRANIAL DIVERSITY

With some notable exceptions (see below) the D^2 values indicate that the relative orderings of affinities for many groups are broadly similar for the two cranial regions. However, absolute dispersion varies both taxonomically and regionally. *Homo*, as currently understood, encompasses significantly more cranial diversity – about 50% more – than that within or between the early hominid genera *Paranthropus* and *Australopithecus*. Although Grine *et al.* (1996) have argued that there need be no correspondence in morphometric differentiation between different pairs of hominid species, there is a strong case for the opposite viewpoint. Exact equivalence is both improbable and unnecessary, but at the very least we need to be aware whether or not taxonomic categories of equivalent rank – in this case genera – refer to broadly comparable entities in their morphological range. This is especially the case given that generalisations about the patterning, tempo and mode of hominid evolution (as of other groups) are frequently based upon numbers and duration of taxa.

Whilst in both analyses *P. boisei* defines one pole of the dispersion and later Quaternary forms the other (modern humans for the face and Neanderthals for the vault), absolute dispersion on the basis of facial dimensions is > 50% greater than that of the neurocranium. Within the earlier *Homo* material the most striking separation in the face is that between early *H. erectus/ergaster* and other hominids from around the Plio-Pleistocene boundary; despite their near contemporaneity, specimens such as OH 24 and ER 1813 are more isolated from KNM-ER 3733 etc. than the later *Homo* groups some 1.5–1.8 million years younger than *H. erectus/ergaster*. In its facial morphology, *H. rudolfensis* is relatively isolated, being well-separated from *H. habilis* and other hominids by distances appreciably greater than those of the vault. It is also widely separated from later *Homo* on face proportions, but in the neurocranial analysis occupies an intermediate position between the smaller-brained hominid cluster and the early African *H. erectus/ergaster* – later *Homo* grouping.

Absolutely greater separation and some contrasting patterns of affinities in face and vault are not unexpected. The face and jaws are directly influenced by functional requirements for feeding and food processing, and are therefore likely to display marked differentiation in response to selection pressures associated with particular dietary niches. Neurocranial form on the other hand, largely determined by brain proportions, is less likely to be closely tied to a given niche. Expanded brain size, driven by selection pressures favouring improved cognitive processing and greater behavioural complexity and flexibility, is likely to be generally advantageous and not niche specific to the degree expected in face and masticatory apparatus, so minimising interspecies contrasts in neurocranial parameters. There is evidence for independent cerebral expansion in the *Paranthropus* and early *Homo* radiations, and very possibly within the latter (Lieberman *et al.* 1996). Such parallel developments would reduce still further interspecific differences in neurocranial affinities.

DIVERSITY IN EARLY *HOMO*

The above results provide no support for the idea of a single species of early *Homo* – the broad *H. habilis* concept – encompassing all the non *erectus/ergaster* forms. In the two important functional complexes of face and neurocranium early *Homo* specimens display marked diversity, and the separation between them is often greater than that between some of those specimens and modern humans. To argue for a single basal Pleistocene *Homo* species is accordingly to argue that the internal morphological variability of the species exceeds that of the entire hominid fossil record of the last million years or more – i.e. from the later Lower Pleistocene onwards – a record that itself comprises several species. While the monospecific interpretation originated as a laudable attempt to accommodate the concept of intra-specific variation into early *Homo* systematics, it has also been influenced by a tendency on the part of some to view *H. habilis* as a dumping ground for specimens not easily assigned to the well established polarities of *A. boisei* and *H. erectus*, so grouping them on negative rather than positive criteria.

Several studies, some explicitly modelling early *Homo* diversity against a range of fossil and modern comparators, reinforce this conclusion. See, for example, Wood (1985) and Lieberman *et al.* (1988), who compared multiple dimensions of KNM-ER 1470 and 1813 and concluded that the monospecific interpretation required for *habilis* a greater degree of sexual dimorphism than that of the modern gorilla. Similarly, Kramer *et al.* (1995) employed randomisation methods to test whether cranial variation in early *Homo* could be matched in large-bodied living higher primates, concluding that if *H. habilis* were indeed a single species then it displayed a pattern of craniofacial shape unlike that observed in their comparator groups. A similar conclusion had been reached by Wood (1991, 1993) using multivariate methods to compare shape differences within early *Homo* to the pattern and degree of intraspecific differences in higher primates.

Using cladistic methods Lieberman *et al.* (1996) explored character state distributions within early *Homo*, and concluded that the different synapomorphies supported division of "broad" *H. habilis* into two groups with contrasting cladistic affinities. Finally, Grine *et al.* (1996), analysing mainly facial characters in early *Homo*, concluded that their results were incompatible with a single inclusive species, and supported the separation of the smaller early *Homo* specimens, OH 24 and KNM-ER 1813, from KNM-ER 1470.

Given such consistent findings, the case for at least two early *Homo* species is accordingly a strong one, but there still remain issues of identification, sorting and species demarcation. However, the findings of this and other studies that argue against a monospecific interpretation necessarily also militate *a fortiori* against schemes that divide the material but incorporate large (e.g. KNM-ER 1470) and small crania (e.g. KNM-ER 1813 or OH 24) within the same species. Examples of these include Stringer (1986), Chamberlain (1987) and Chamberlain and Wood (1987). Moreover, these last authors confine *H. habilis* to Olduvai, although the KNM-ER 3735 partial skeleton provides independent, non-cranial, evidence of its presence in the Turkana basin.

Groves' (1989) polyphyletic scheme also excluded *habilis* from Turkana, whilst identifying a species (*H. aethiopicus*) largely based upon material otherwise regarded as part of the East African robust clade. Additionally, most researchers consider that his species *H. ergaster*, based on the KNM-ER 992 mandible (and which he associates with crania KNM-ER 1805 and 1813) has not been adequately differentiated from *H. erectus*.

By contrast, virtually all workers agree in linking KNM-ER 1470, 1590 and 3732 as a natural group; the main issue is whether the Olduvai *habilis* hypodigm represents a distinct phenon or whether some specimens should be associated with the large-brained Turkana cluster, as in Stringer's (1986) and Rightmire's (1993) schemes. Stringer's grouping has already been criticised for linking OH 24 with KNM-ER 1470, 3732 etc.; Rightmire associates mixed sub-sets of Olduvai and Turkana specimens together into larger (e.g. OH 7, KNM-ER 1470 etc.) and smaller (OH 13, 24; KNM-ER 1813 etc.) morphs. The latter cluster is convincing, but the limited evidence available (the larger Olduvai specimens are particularly fragmentary) suggests that his KNM-ER 1470 / OH 7 etc. group is heterogeneous. OH 7 – the type of *H. habilis* – has an estimated endocranial volume appreciably smaller than that of KNM-ER 1470 and a narrower mid / rear vault, whilst its mandible and lower dentition contrast with the KNM-ER 1801/1802 mandibles associated by Wood and others with the Koobi Fora cranium. Moreover, Tobias (1991) has set out a detailed case for the integrity of the Olduvai *habilis* sample, a view accepted by the great majority of workers.

For all these reasons, the most plausible sorting of the East African specimens is Wood's (1991) scheme, retaining the entire early *Homo* sample from Olduvai as *H. habilis* while recognising its presence (as shown by crania KNM-ER 1805, ER 1813 as well as the KNM-ER 3735 postcranium) at Koobi Fora. In addition, the larger brained species *H. rudolfensis,* represented by the ER 1470, 1590, 3732 cluster, is also present in the Turkana basin. The present study's results, incorporating the more complete of the above specimens, strongly support such an ordering: smaller Olduvai and Koobi Fora specimens referred to *H. habilis* cluster closely in both face and neurocranial analyses, whilst KNM-ER 1470, the type of *H. rudolfensis,* is notably distant from them.

HOMO ERGASTER OR *HOMO ERECTUS*?

This analysis of neurocranial form offers no support for differentiating *H. ergaster* (*sensu* Wood 1991, 1992) from *H. erectus*. The early African forms cluster closely with Javan and Chinese *H. erectus* and the claimed apomorphies of Asian *erectus* have been shown by Brauer and Mbau (1992) and others to be both variable within Asian *erectus* and variably present in early African specimens such as KNM-ER 3733 and 3883. In addition, facial form in early African *erectus* resembles that of the reconstructed ZKD crania rather than other early *Homo*. It was not possible to incorporate original data on the face of SE Asian *H. erectus* in this study, but Rightmire (1998) has recently provided a comprehensive review, arguing – convincingly in my view – for specific identity of African and Asian specimens on the basis of facial morphology. The claimed distinctiveness of *H. ergaster* has also been criticised on metrical grounds (Kramer 1993, Brauer 1994), on the basis of likely speciation mechanisms (Turner, Chamberlain 1989) and on cladistic principles (Harrison 1993), while further support for the specific identity of the African and Asian specimens is provided by OH 9, which even staunch proponents of *H. ergaster* concede is a convincing example of *H. erectus*.

Morphological and morphometric studies thus provide solid grounds for recognising three broadly contemporary species of early *Homo* – *H. habilis*, *H. rudolfensis* and early *H. erectus* – in the East African final Pliocene. There remain the (currently unresolved) issues of their systematic and phyletic relationships.

Several studies based on different approaches and data sets – phenetic and cladistic, dental, cranial and postcranial – indicate *H. habilis* to be morphologically the most primitive of the trio. In addition, the AL 666 maxilla – at 2.33 mya the earliest well-dated *Homo* specimen – most closely resembles the *H. habilis* maxilla (Kimbel *et al.* 1997).

Less extensive evidence suggests that *H. rudolfensis*, known from about 1.9 mya in the Turkana basin, is in many respects the most derived of these early *Homo* species. Unfortunately we have no postcrania definitely associated with identifying cranial material, and so little idea of body size and proportions or locomotor pattern in *rudolfensis*. Assessments of its systematic affinities are therefore necessarily based entirely upon cranio-dental data. Evidence for *rudolfensis* beyond Koobi Fora is particularly scant, but the species is possibly represented by the UR 501 mandible from Chiwondo, Malawi (Bromage *et al.* 1995). This may date from 2.3–2.5 mya, but the estimate depends upon long range faunal correlation and so is insecure.

H. erectus is well known at Koobi Fora at just under 1.8 mya and by more fragmentary evidence > 0.1 mya before. The earliest specimen in the region appears to be the KNM-ER 2598 occipital fragment at *ca* 1.9 mya (Wood 1991), pushing the species' origin back to 2 mya or more. Examples of early *erectus* crania (KNM-ER 3733) combine a distinctive and relatively lightly built facial structure with a large (>800 cm^3) neurocranium that is surprisingly rugged in its construction. Neurocranial thickness and buttressing may be in large part an allometric consequence of increased body size. While some cranial surrogates of body size and its intra-specific patterning have been identified (Aiello, Wood 1994, Wood *et al.* 1991), more securely identified postcrania of *habilis* and especially *rudolfensis* are needed before it will be possible to determine accurately the influence of body size differences on cranial form in early *Homo*.

The evolution of the *erectus* morphology is poorly known, but is possibly represented by the SK 847 specimen from Swartkrans, South Africa. The systematic affinities of SK 847, identified as hominine and described by R. J. Clarke, are controversial. It is widely regarded as a southern African *erectus* (Clarke 1977, 1985, Walker 1981) or the closely related *H. leakeyi* (Clarke 1990, 1994), but it does not closely resemble *erectus* in overall facial proportions, and Grine *et al.* (1993, 1996) have argued that it shows similarities to Stw 53, and that both specimens represent *H. habilis*, or a *habilis*-like species in southern Africa. My own view is that SK 847 is *not* similar to Stw 53. Instead, the Swartkrans fossil shows undoubted similarities to *H. erectus* in the mid-lower face, but combines these with a narrow upper face (and so narrow supra-and post-orbital frontal regions), and a remarkable degree of upper- and mid-face prognathism pointing to a sagitally restricted anterior neurocranium. In other words, the admittedly limited evidence available points to an *erectus*-like mid-lower face combined with a small (i.e. sub-*erectus*) neurocranium in SK 847, which Thackery and Monteith (1997) have estimated to have a volume of the order of 550 cm^3, well below the *erectus* minimum.

SK 847's overall facial dimensions – and in particular the multiple measures of facial projection (in which it contrasts with *erectus*) and their weightings – mean that in these analyses the Swartkrans fossil is not particularly close to the latter species, clustering instead with *H. habilis* (Bilsborough, Wood 1988, Grine *et al.* 1996). However, analysis of mid-lower face morphology and proportions (Bilsborough, in print), demonstrates the similarities between SK 847 and early *H. erectus* identified by Clarke, Walker and others. If SK 847 does represent a proto-*erectus* form with the latter's characteristic lower face but before neurocranial expansion, then with an estimated age of 1.8–1.5 mya it must also represent a relict population, persisting in southern Africa after *erectus* had differentiated from earlier populations of the species, perhaps in East Africa.

The proximity of ER 1470 and WT 15000 in the neurocranial analysis suggests that they share a common pattern of neurocranial growth that was extended and/or accelerated in *erectus*. This closeness is not just a function of size, for specimens with smaller endocranial volumes than WT 15000 are further way from 1470. Rather the proximity reflects a similarity of neurocranial proportions, especially in the posterior parietal and occipital regions. WT 15000 had not much additional brain growth left, but had the youth lived to maturity the vault bones would have thickened and the nuchal torus developed in response to the appreciable facial growth that still remained. Whether similar growth patterns in the mid – and rear vault of *erectus* and *rudolfensis* reflect a common phyletic origin or parallel developments is a moot point: as noted, ER 1470 is derived in many respects and Lieberman *et al.* (1996) have drawn attention to apomorphies that distinguish *rudolfensis* from *habilis* and early *erectus*, and which raise the possibility that brain enlargement occurred more than once in early *Homo*. If the growth patterns in the vault do have a common phyletic origin it is likely to be a comparatively remote one, since contrasting apomorphic traits suggest that *rudolfensis* and *erectus* are not sister species.

THE GENUS *HOMO*

Wood and Collard have recently reviewed approaches to defining the genus as a taxonomic category, and have argued that for inclusion within *Homo* a fossil species must fulfil several criteria: be more closely related to *H. sapiens* than to australopithecines; have an estimated mass and bodily proportions, and teeth and jaws more like *H. sapiens* than australopithecines; display postcranial adaptations to modern obligate bipedalism; and show evidence for extended ontogenetic development. After reviewing fossil hominid species against these criteria they redraw the lower boundary of *Homo* at *H. erectus/ergaster*, and transfer *habilis* and *rudolfensis* to *Australopithecus* (Wood, Collard 1999).

Interestingly, cranial characteristics, which are used to define most hominid species, feature only minimally in their direct criteria, but it can be argued that their judgements about phyletic relationships are based primarily upon such data. Their first criterion presupposes that these relationships are known with a fair degree of confidence, which is currently far from the case. That said, the results reported here – which are based upon the specimen clusters which (part) comprise fossil species rather than the species definitions themselves and which, as phenetic indicators, are a necessary pre-requisite to any phyletic evaluation – are compatible with Wood and Collard's proposal. The point has already been made that *Homo* and its constituent species as currently understood incorporates a far greater degree of cranial diversity than other hominid genera. In these analyses, and others, early African *erectus* specimens consistently display closer affinities with later hominids, including modern humans, than they do with earlier hominids or with their contemporaries. By contrast, the other, smaller-brained *Homo* (*habilis* and *rudolfensis)* show varying patterns of affinities, being often widely separated from *erectus* and usually closer to *Australopithecus* and *Paranthropus* species than to *Homo sapiens*.

Removing the species *habilis* and *rudolfensis* from *Homo* in accordance with Wood and Collard's argument has the effect of reducing intra-generic diversity to a rather modest extent in the neurocranium (from 12 to <10 D^2 units) but appreciably in the face (from 19 to 12 D^2 units). Allocation of the species to *Australopithecus*, as suggested by Wood and Collard, still leaves that genus with markedly less neurocranial variability and an equivalent degree of facial diversity as the revised and restricted *Homo* (7 compared with 12, and 10 & 10 D^2 units respectively). Even re-allocation of the "robusts" to *Australopithecus* (i.e. sinking *Paranthropus*) together with *habilis* and *rudolfensis*, so producing a much broader and more diverse genus than envisaged by Wood and Collard, still results in facial variability only moderately in excess (4 D^2 units), and neurocranial variation comparable to that displayed by *Homo* as narrowly defined by them.

Whether one accepts Wood and Collard's proposal or not is largely a matter of personal taste. Provided the essential minimum of clarity of communication is achieved, and there is recognition of the morphological comparability or otherwise of equivalent Linnean categories (see above), disagreements over the merits or failings of alternative taxonomic arrangements are subsidiary to issues of phena identification, species sorting and demarcation, and the reconstruction of systematic relationships. Taxonomic judgements are both subjective and complex: they invariably involve weighting of multiple kinds of information, and are often driven by extraneous considerations.

For example, alternative schemes, founded upon very different views of evolutionary mechanisms and systematic relationships, are provided by Tattersall (1992) and Wolpoff *et al.* (1994). The results reported here are also compatible with these, as are – so far as I can judge – Wood and Collard's own analyses, although the resulting taxonomies are very different.

These morphological and phyletic studies do not compel taxonomic revision, but they do suggest that if one is going to engage in the highly contentious and almost invariably unpopular practice of redrawing the generic boundary, then *H. erectus* seems an appropriate threshold for demarcation.

CONCLUSIONS

The morphometric analyses of cranial form summarised here indicate *H. habilis* (Olduvai and smaller Koobi Fora specimens), *H. rudolfensis* and *H. erectus* to be recognisably distinct phena that, as such, provide the basis for good species. They do not support recognition of *H. ergaster* as distinct from *H. erectus*. Moreover, early African *H. erectus* is sharply differentiated from penecontemporaneous hominids and has distinctly closer affinities with later human groups. Other studies of the fossil evidence, both cranial and postcranial, point to a similar conclusion, as do the archaeological and contextual records. It is accordingly difficult to resist the conclusion that *H. erectus* represents a new adaptive grade in hominid evolution. However, the origins of the clade, the timing, tempo and pattern of expansion beyond Africa, and the relationships of that continent's and extra-African populations, all remain to be worked out in detail. These results are compatible with a recent proposal to revise *Homo*, resulting in a morphologically and phyletically more restricted genus than at present, but do not compel such revision.

ACKNOWLEDGEMENTS

I thank R. E. F. Leakey and the National Museum of Kenya, the late M. D. Leakey and the Government of the Republic of Tanzania, C. K. Brain, E. S. Vrba and J. F. Thackery, Transvaal Museum, and P. V. Tobias and the late Alun Hughes, University of the Witwatersrand, for permission to examine original specimens in their care, and for facilities to do so. An earlier draft of this paper was presented at the IVth Aleš Hrdlička Congress, Prague and Humpolec, 1999. I am grateful to the Organising Committee, and especially Drs. V. Vančata and V. Přívratský, for the invitation to participate.

REFERENCES

AIELLO L. C., WOOD B. A., 1994: Cranial variables as predictors of hominine body mass. *Amer. J. of Phys. Anthrop.* 95: 409–426.

ANDREWS P., 1984: An alternative interpretation of the characters used to define *Homo erectus. Cour. Forsch. Inst. Senckenberg.* 69: 167–175.

ASFAW B., WHITE T., LOVEJOY O., LATIMER B., SIMPSON S., SUWA G., 1999: *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Science* 284: 629–634.

BILSBOROUGH A., WOOD B. A., 1988: Cranial morphometry of early hominids I: Facial region. *Amer. J. of Phys. Anthrop.* 76: 61–86.

BILSBOROUGH, A., in print: Craniofacial diversity in early *Homo* and the affinities of the Sterkfontein Valley specimens. *Hum. Evol.*

BOAZ N., HOWELL F. C., 1977: A gracile hominid cranium from Upper Member G of the Shungura Formation, Ethiopia. *Amer. J. of Phys. Anthrop.* 46: 93–108.

BRÄUER G., 1994: How different are Asian and African *Homo erectus*? In: J. Franzen (Ed.): 100 years of *Pithecanthropus:* The *Homo erectus* problem. *Cour. Forsch. Inst. Seneckenberg* 171: 301–318.

BRÄUER G., MBUA E., 1992: *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *J. of Hum. Evol.* 22: 79–108.

BROMAGE T. G., SCHRENK F., ZONNEVELD F. W., 1995: Paleoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. *J. of Hum. Evol.* 28: 71–108.

BROOM R., ROBINSON J. T., 1952: Swartkrans Ape-Man, *Paranthropus crassidens. Trans. Mus. Mem.* 6: 1–123.

BROOM R., ROBINSON J. T., SCHEPERS G. W. H., 1950: Sterkfontein ape man, *Plesianthropus. Trans. Mus. Mem.* 4: 1–117.

BROOM R., SCHEPERS G. W. H., 1946: The South African fossil Ape-Men – the Australopithecinae. *Trans. Mus. Mem.* 2: 1–153.

BROWN F., HARRIS J., LEAKEY R., WALKER A., 1985: Early *Homo erectus* from west Lake Turkana, Kenya. *Nature* 316: 788–792.

CHAMBERLAIN A. T., 1987: *A taxonomic review and phylogenetic analysis of Homo habilis.* Ph.D. Thesis. Univ. of Liverpool.

CHAMBERLAIN A. T., WOOD B. A., 1987: Early hominid phylogeny. *J. of Hum. Evol.* 16: 119–133.

CLARKE R. J., 1977: *The cranium of the Swartkrans hominid SK 847 and its relevance to human origins.* Ph.D. Thesis. Univ. of the Witwatersrand.

CLARKE R. J., 1985: *Australopithecus* and early *Homo* in southern Africa. In: E. Delson (Ed.): *Ancestors: The hard evidence*. Pp. 171–177. Liss, New York.

CLARKE R. J., 1990: The Ndutu cranium and the origin of *Homo sapiens. J. of Hum. Evol.* 19: 699–736.

CLARKE R. J., 1994: The significance of the Swartkrans *Homo* to the *Homo erectus* problem. In: J. Franzen (Ed.): 100 years of *Pithecanthropus:* The *Homo erectus* problem. *Cour. Forsch. Inst. Senckenberg* 171: 185–193.

CLARKE R. J., 1998: First ever discovery of a well preserved skull and associated skeleton of *Australopithecus. South Afr. J. of Science* 94: 460–463.

CLARKE R. J., HOWELL F. C., 1972: Affinities of the Swartkrans hominid cranium. *Amer. J. of Phys. Anthrop.* 37: 319–336.

GOWER J. C., 1966a: Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53: 325–338.

GOWER J. C., 1966b: A Q-technique for the calculation of canonical variates. *Biometrika* 53: 588–590.

GRINE F. E., DEMES B., JUNGERS W. L., COLE T. M., 1993: Taxonomic affinity of the early *Homo* cranium from Swartkrans, South Africa. *Amer. J. of Phys. Anthrop.* 92: 411–426.

GRINE F. E., JUNGERS W. L., SCHULTZ J., 1996: Phenetic affinities among early *Homo* crania from East and South Africa. *J. of Hum. Evol.* 30: 189–225.

GROVES C. P., 1989: *A theory of human and primate evolution.* Clarendon Press, Oxford. 375 pp.

GROVES C. P., MAZÁK V., 1975: An approach to the taxonomy of the Hominidae: Gracile Villafranchian hominids of Africa. *Cas. Miner. Geol.* 20: 225–247.

HARRISON T., 1993: Cladistic concepts and the species problem in hominoid evolution. In: W. H. Kimbel, L. B. Martin (Eds.): *Species, species concepts and primate evolution*. Pp. 345–371. Plenum, New York.

KIMBEL W. H., JOHANSON D. C., RAK Y., 1997: Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *Amer. J. of Phys. Anthrop*. 103: 235–262.

KRAMER A., 1993: Human taxonomic diversity in the Pleistocene: Does *Homo erectus* represent multiple hominid species? *Amer. J. of Phys. Anthrop*. 91: 161–171.

KRAMER A., DONNELLY S. M., KIDDER J. H., OUSLEY S. D., OLAH S. M., 1995: Craniometric variation in large-bodied hominoids: Testing the single-species hypothesis of *Homo habilis. J. of Hum. Evol.* 29: 443–462.

LE GROS CLARK W. E., 1962: *The antecedents of Man.* 2nd Ed. Edinburgh Univ. Press, Edinburgh. 388 pp.

LE GROS CLARK W. E., 1964: *The fossil evidence for human evolution: An introduction to the study of palaeoanthropology.* 2nd Ed. University of Chicago Press, Chicago. 201 pp.

LEAKEY L. S. B., TOBIAS P. V., NAPIER, J. R., 1964: A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202: 7–9.

LEAKEY M. D., CLARKE R. J., LEAKEY L. S. B., 1971: New hominid skull from Bed I, Olduvai Gorge, Tanzania. *Nature.* 232: 308–312.

LEAKEY R. E. F., LEAKEY M. G., BEHRENSMEYER A. K., 1978: The hominid catalogue. In: M. G. Leakey, R. E. F. Leakey (Eds.): *Koobi Fora research project. Vol. 1.* Pp. 86–182. Clarendon Press, Oxford.

LIEBERMAN D. E., PILBEAM D. R., WOOD B. A., 1988: A probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: A comparison of KNM-ER 1470 and KNM-ER 1813. *J. of Hum. Evol.* 17: 503–511.

LIEBERMAN D. E., WOOD B. A., PILBEAM D. R., 1996: Homoplasy and early *Homo*: an analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis. J. of Hum. Evol.* 30: 97–120.

McCOLLUM M. A., 1999: The robust australopithecine face: a morphogenetic perspective. *Science* 284: 301–305

RICHTSMEIER J. T., WALKER A., 1993: A morphometric study of facial growth. In: A. Walker, R. Leakey (Eds.): *The Nariokotome Homo erectus skeleton.* Pp. 391–410. Harvard Univ. Press, Cambridge, Mass.

RIGHTMIRE G. P., 1979: Cranial remains of *Homo erectus* from Beds II and IV, Olduvai Gorge, Tanzania. *Amer. J. of Phys. Anthrop*. 51: 99–116.

RIGHTMIRE G. P., 1993: Variation among early *Homo* crania from Olduvai Gorge and the Koobi Fora region. *Amer. J. of Phys. Anthrop*. 90:1–33.

RIGHTMIRE G. P., 1998: Evidence from facial morphology for similarity of Asian and African representatives of *Homo erectus. Amer. J. of Phys. Anthrop.* 106: 61– 86.

ROBINSON J. T., 1954: The genera and species of the Australopithecinae. *Amer. J. of Phys. Anthrop.* 12: 181–200.

STRINGER C. B., 1984: The definition of *Homo erectus* and the existence of the species in Africa and Europe. *Cour. Forsch. Inst. Seneckenberg* 69: 131–143.

STRINGER C. B., 1986: The credibility of *Homo habilis.* In: B. A. Wood, L. Martin, P. Andrews (Eds.): *Major topics in primate and human evolution.* Pp. 266–294. Cambridge University Press, Cambridge.

SUWA G., ASFAW B., BEYENE Y., WHITE T. D., KATOH S., NAGAOKA S., NAKAYA H., UZAWA K., RENNE P., WOLDEGABRIEL G., 1997: The first skull of *Australopithecus boisei. Nature* 389: 489–492

TATTERSALL I., 1992: Species concepts and species identification in human evolution. *J. of Hum. Evol.* 22: 341–349.

TATTERSALL I., SAWYER, G. J., 1996: The skull of „Sinanthropus“ from Zhoukoudian, China: a new reconstruction. *J. of Hum. Evol*. 31: 311–314.

THACKERAY J. F., MONTEITH B. D., 1997: Relationships between cranial capacity and prognathism in Plio-Pleistocene hominids. *South Afr. J. of Sci.* 93: 289–291.

TOBIAS P. V., 1967: *Olduvai Gorge, Vol. 2. The cranium and maxillary dentition of Australopithecus* (*Zinjanthropus*) *boisei.* Cambridge University Press, Cambridge. 264 pp.

TOBIAS P. V., 1978: The earliest Transvaal members of the genus *Homo* with another look at some problems of hominid taxonomy and systematics. *Zeitschrift fur Morphologie und Anthropologie* 69: 225–265.

TOBIAS P. V., 1991: *Olduvai Gorge, Vol. 4. The skulls, endocasts and teeth of Homo habilis*. Cambridge University Press, Cambridge. 921 pp.

TURNER A., CHAMBERLAIN A. T., 1989: Speciation, morphological change and the status of African *Homo erectus. J. of Hum. Evol.* 18: 115–130.

WALKER A., 1981: The Koobi Fora hominids and their bearing on the origins of the genus *Homo*. In: B. A. Sigmon, J. S. Cybulski (Eds.): *Homo erectus: papers in honor of Davidson Black.* Pp. 193–215. University of Toronto Press, Toronto.

WALKER A, LEAKEY R. (Eds.), 1993a: *The Nariokotome Homo erectus skeleton.* Harvard Univ. Press, Cambridge, Mass. 457 pp.

WALKER A., LEAKEY, R. E. F., 1993b: The skull. In: A. Walker, R. Leakey (Eds.): *The Nariokotome Homo erectus skeleton.* Pp. 63–94. Harvard Univ. Press, Cambridge, Mass.

WEIDENREICH F., 1937: Reconstruction of the entire skull of an adult female individual of *Sinanthropus pekinensis. Nature* 140: 1010–1011.

WEIDENREICH F., 1943: The skull of *Sinanthropus pekinensis*: a comparative study of a hominid skull. *Palaeont. Sinica,* Series D 10:1–484.

WEIDENREICH F., 1945: Giant early man from Java and South China. *Anth. Papers Am. Mus. Nat. His*. 40: 1–134.

WOLPOFF M. H., THORNE A. G., JELÍNEK J., ZHANG Y., 1994: The case for sinking *Homo erectus*: 100 years of *Pithecanthropus* is enough. In: J. Franzen (Ed.): 100 years of *Pithecanthropus:* The *Homo erectus* problem. *Cour. Forsch. Inst. Senckenberg* 171: 341–361.

WOOD B. A., 1984: The origin of *Homo erectus*. *Cour. Forsch. Inst. Senckenberg* 69: 99–111.

WOOD B. A., 1985: Early *Homo* in Kenya, and its systematic relationships. In: E. Delson (Ed.): *Ancestors: the hard evidence*. Pp. 206–214. Liss, New York.

WOOD B. A., 1991: *Koobi Fora research project. Vol. 4. Hominid cranial remains.* Clarendon Press, Oxford. 466 pp.

WOOD B. A., 1992: Origin and evolution of the genus *Homo*. *Nature* 355: 783–790.

WOOD B. A., 1993: Early *Homo*: How many species? In: W. H. Kimbel, L. B. Martin (Eds.): *Species, species concepts and primate evolution.* Pp. 485–522. Plenum, New York.

WOOD B. A., COLLARD M. C., 1999: The human genus. *Science* 284: 65–71.

WOOD B. A., YU L., WILLOUGHBY C., 1991: Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record. *J. of Anatomy* 174: 185–205.

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