

## ARTICLE

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## CHRONOLOGY, VARIABILITY AND EVOLUTION IN *HOMO ERECTUS*

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**Abstract:** *Homo erectus* occupies a central position in schemes of hominid phylogeny, but views differ as to its systematic relationships, particularly with later *Homo*, the pace of its evolutionary dynamics, and the selective and other processes underlying these. This paper summarises a review of cranial diversity in East African, continental and peninsular Asian groups of *H. erectus*, and attempts to identify temporal and/or geographical components of variation. Univariate analysis of individual neurocranial dimensions together with multivariate representation of four calvarial complexes (vault, basicranium, balance, articular) scaled against Upper Pleistocene/modern comparators all indicate remarkably limited morphological variability within *H. erectus* relative to species range and duration. There are limited contrasts between African and Asian *erectus* reflecting the rather smaller endocranial capacity of the earlier group, but these are less than those exhibited by Upper Pleistocene *Homo*. Similarly, there is little, if any, evidence of significant variation between Asian *erectus* groups where, despite their extended duration (? 0.6–1.0+ my), contrasts are often comparable to those between later Pleistocene and modern *H. sapiens*. This morphological homogeneity is unexpected in the context of many reconstructions of ecology, demography and adaptation in Lower/Middle Pleistocene *Homo*. Given its limited nature, cranial variation in *H. erectus* is as consistent with founder effects and drift as with phyletic change. There is accordingly no convincing evidence in *erectus* calvaria of morphological trends corresponding to the initial stages of a ‘sapienisation’ process as argued by some proponents of the Regional Continuity model of modern human origins.

**Key words:** *Homo erectus*, cranial variability, hominid phylogeny, human evolution, regional continuity, Pleistocene Homo, Koobi Fora, Olduvai, Sangiran, Ngandong, Zhoukoudian

## Introduction

For many workers *Homo erectus* represents a distinct phyletic and adaptive shift in hominid evolution (see, for example, Wood and Collard 1999 for a recent review). Depending on definition (see below) it covers a time span of at least one million years and possibly almost twice as long; it is the first hominid species whose presence beyond Africa is well established and, again depending on definition, is arguably known from all major continental areas of the Old World. Such temporal and spatial range contrasts markedly with the more restricted distributions of earlier hominid species. Moreover, *H. erectus* is known both from the interior of continents and from their margins including, in SE Asia, what must have been the limit of hominid distribution for all but the Upper Pleistocene.

Previous studies of regional diversity in *H. erectus* have largely centred around comparisons of the African and Asian specimens in attempts to demonstrate (e.g. Andrews 1984; Stringer 1984; Wood 1984; Groves 1989) or controvert (Rightmire 1986a, 1990, 1998; Brauer and Mbau 1992; Brauer 1994) their claimed specific distinctiveness (see below). In this paper I attempt a broader treatment, with the early East African fossils as one of several regional groupings whose cranial variation is considered within the more general context of intra- and inter-population diversity in *H. erectus sensu lato*, as a widespread hominid species of extended duration.

A major problem in such studies is disentangling the spatial (i.e. polytypic) and chronological components of diversity, and I therefore summarise stratigraphic, faunal and chronometric evidence relevant to dating *H. erectus*. All the regional samples span considerable periods of time – c. 0.5 my for the East African sample; c. 0.75 my for the Javan material excluding Ngandong, and 1 my or more with the latter included, although the bulk of the SE Asian specimens included here cover a much more restricted range – perhaps 0.4 my in the former case, and 0.6 my in the latter. Similarly, the Zhoukoudian crania span around 0.4 my, with those of the present study probably confined to 0.15 my or thereabouts.

Aggregating specimens from different time zones is inevitable if one is to have even minimally satisfactory sample sizes, but such a procedure will, of course, conceal any intra-regional chronological trends. However, the East African specimens considerably pre-date, and are presumably ancestral to, the continental and peninsular Asian samples, so that inter-regional contrasts might be expected to be evident. Additionally, the Puchangan/Kabuh and Notoporo samples are treated separately (see below), so that any chronological trends within SE Asian *erectus* populations might be apparent.

### *Africa*

The Turkana basin has yielded the majority of early African *erectus* fossils, with the KNM-ER 2598 occipital at c. 1.9 mya as the oldest example of the morphology. Much more extensive evidence is provided by the KNM-ER 3733 cranium and 3883 calvaria (dated to 1.78 mya and 1.6 mya respectively), together with the KNM-ER 992 mandible (c. 1.5 mya) (Feibel et al. 1989; Wood 1991) and the wonderfully preserved KNM-WT 15 000 skeleton (c. 1.53 mya) (Walker and Leakey 1993; Brown and McDougall 1993). Wood (1991, 1992a, b, 1993), following Stringer (1984), Andrews (1984) and Wood (1984) has argued that these early African specimens represent an 'erectus-like' but more primitive and distinct hominid species, to which he assigns the name *H. ergaster*. Clarke (1990; 1994) provides a similar argument but prefers the name *H. leakeyi* for these early African specimens. Wood's viewpoint has received some support (e.g. Tattersall 1986, 1992; Groves 1989) but has more often been criticised on various grounds (eg Rightmire 1986a, 1990, 1998; Turner and Chamberlain 1989; Brauer and Mbau 1992; Brauer 1994; Harrison 1993; Kramer 1993; and see below).

In any event, there is general agreement, even among proponents of *H. ergaster* that the large, ruggedly built OH 9 cranium from Upper Bed II, Olduvai Gorge at c. 1.2 mya (Rightmire 1979, 1984, 1990), represents *H. erectus sensu stricto*. In South Africa the species is possibly represented by the 1.5–2.0 my old SK 847 cranio-facial fragment from Swartkrans Member I (Clarke and Howell 1972; Clarke 1977, 1985; Walker 1981) although Grine et al. (1993, 1996) concluded that its affinities lie with smaller, more gracile forms of *Homo* and, in contrast with both these viewpoints, Bilsborough (in press) has argued that it represents a more primitive, possibly precursor species to *erectus*, showing facial resemblances to the latter but lacking its neurocranial expansion.

### *SE Asia*

The Indonesian *H. erectus* sample is the largest and potentially most valuable of all regional collections. However, several problems attend its analysis and evaluation:

- many recently discovered specimens have yet to be described, and even some recovered three or more decades ago have yet to be provided with anything more than a preliminary description.
- Virtually all specimens were recovered by local collectors during farming or exposed through landslips following rain, rather than through controlled excavation. They therefore lack contextual association; provenance, dating and in some cases even location are problematic. Most specimens consist of calvaria, with other cranial regions poorly represented; there are few mandibular or maxillary specimens, and only one cranium (S 17) preserves the face. Postcrania, apart from Dubois' early discoveries, and the Ngandong tibiae, are virtually unknown.
- Contextual uncertainties apart, the geology of Java is complex: in the late Pliocene/basal Pleistocene parts of the present island were differentially exposed

through the effects of tectonic uplift and fluctuating sea-levels, and establishing a chronological framework for the hominid fossils is correspondingly difficult.

- There are systematic uncertainties, with several workers arguing for a second (or additional) hominid(s) on Java besides *H. erectus*. The morphological characteristics and affinities of such claimed additional species remain problematic, as does the allocation of individual specimens to them. Specimens considered to be possible representatives of other species are excluded from the following analysis.

Despite these difficulties the Javan *H. erectus* sample is important in representing a particularly interesting evolutionary phenomenon: a population close to, if not actually at, the extreme periphery of hominid distribution for most of the Quaternary and, as such, presumably subject to selection pressures associated with distinctive and possibly marginal habitats. Hominids presumably reached Java when Sundaland was exposed during a period of low sea level, and were subsequently isolated there when sea level rose during following interglacials. We might therefore expect Javan *erectus* to display distinctive features resulting from founder effect and genetic drift, as well as the local selection pressures referred to above, and which would serve to further differentiate it from continental *erectus* populations.

Most fossils are from the Sangiran area of central Java, with other localities (Sambungmachan, Trinil, Ngandong) along the Solo river to the east. Jacob (1980) provides a schematic spatial distribution of the Sangiran finds. As noted, geological interpretation is difficult; the following general account is based on several sources, principally those of Itihara et al. (1994) and Howell (1994). At Sangiran, erosion has exposed beds within a volcanic dome, the oldest towards the centre. Above the marine Puren or Kalibeng Formation are > 110 m of deposits of the Sangiran or Puchangan Formation (formerly Djertis beds), consisting mainly of 'Black' Clay (in reality often blue-grey) and considered early Middle or Lower Pleistocene, or even late Pliocene, in date. Tuff layers within the Black Clay provide markers and dates: tuffs T5, T6 and T11 have been fission track dated to 1.51±0.25 mya, 1.49±0.32, and 1.16±0.24 mya respectively. The lower Puchangan Formation reflects brackish or estuary/bay conditions while the upper part is lacustrine, indicating a shift from coastal or marine to freshwater deposition.

Nearer the Sangiran dome's rim is the mainly fluvial Middle Pleistocene Bapang or Kabuh Formation, also exposed at Trinil, with a conglomeritic marker of chalky sands and gravels, the Grenzbank, at the base. Higher up, the Lower, Middle and Upper Tuff layers subdivide the Kabuh deposits, and overlying them are the late Middle or Upper Pleistocene Pohjajar (Notopuro) beds. These are almost 50 m thick and divided by the Upper and Uppermost Lahars, and the Upper Pumice Bed. The Notopuro formation is also exposed at Ngandong, about 25 km downstream from Trinil. A palaeomagnetic switch, identified as the Jaramillo normal subchron (0.90–1.05 mya), occurs in the uppermost part of the Puchangan Formation, between tuff T11 and the Grenzbank, while another R/N transition in the Middle Kabuh Formation below the Upper Tuff is considered to be the Matuyama – Brunhes boundary (0.78 mya).

Biostratigraphic data supplement the above framework and also throw light on the region's ecology and evolutionary dynamics (de Vos et al. 1994; Aziz et al. 1999; de Vos et al. 1999; Sondaar et al. 1999). The lower Puchangan beds (c. 1.5 mya) yield the indigenous and isolated Satir fauna, lacking large carnivores and reflecting swampy habitats. Following faunal turnover around 1.2 mya and the appearance of continental forms such as *Stegodon* and *Panthera*, the Ci Saat fauna indicates drier, more open conditions. The lower part of the Kabuh Formation (including the Grenzbank) at Sangiran and at Trinil contains a more advanced fauna (Trinil HK) with further taxa. Estimated to be c 1 my old, this also points to relatively dry, open woodland conditions, and is more balanced than earlier faunas; most genera are of continental origin, indicating a land-bridge linking Java with mainland Asia. Rather younger, (c. 0.8 mya), is the Kedung Brubus fauna, containing many Trinil H.K. forms with additional continental species including hyaena, tapir and true elephants. Again, its overall composition indicates a dry, open woodland habitat and maximal connection with mainland Asia via an exposed Sunda Shelf and reduced tropical forest.

The Ngandong fauna, collected from and named after the hominid site, is evidently younger than the above faunas but has not been studied in such detail. It suggests an open woodland habitat, but one not as dry as that indicated by Kedung Brubus. The main evolutionary and adaptive contrasts are clearly between the Satir fauna and the remainder which are sometimes grouped together as the '*Stegodon* – *Homo erectus*' fauna, reflecting the continuity of these forms as faunal indicators.

Most Sangiran specimens whose provenance is known (including S 3, 10, 12, 17 and possibly S 2) are from the mid – upper part of the Kabuh beds well above the Grenzbank, associated with the Kedung Brubus fauna, and probably between 0.5 and 0.8 my in age. A few specimens are from towards the base of the Kabuh formation, and one or two, including the S 4 cranium and some mandibular remains, and possibly also including S 2, appear to be from the Grenzbank or the uppermost Puchangan beds. The Grenzbank finds are linked to Trinil HK faunas, as is the Trinil calotte itself, while Puchangan fossils are associated with either Ci Saat or Trinil HK faunas. The bulk of the evidence therefore suggests an age of c 1.0–1.2 my is not unreasonable for these earlier Javan specimens. However, in recent years this estimate has been contested by dispute over the dating of the infant cranium from Modjokerto (Perning), some 180 km east of Sangiran.

Swisher et al. (1994) published  $^{40}\text{Ar}/^{39}\text{Ar}$  dates of  $1.81\pm 0.04$  mya and  $1.66\pm 0.04$  mya respectively for Modjokerto and the sites of 'Meganthropus' specimens S 27 and S 31 at Sangiran. They interpreted the normal polarity recorded at Modjokerto as the Olduvai event not, as previously considered, the Jaramillo. If correct, these dates point to an early colonisation of SE Asia, and an even earlier (perhaps pre-*erectus*) hominid expansion out of Africa. However, major problems attach to these figures: they may be 'real' dates but they cannot be tied securely to the hominid specimens, their localities or horizons since such data are mainly missing. For example, at Modjokerto their relevance for the *erectus* cranium depended upon the

collector recalling the locality and level at which it was found some 40 years after the event. Furthermore, the  $^{40}\text{Ar}/^{39}\text{Ar}$  dates have been criticised as conflicting with biostratigraphic, palaeomagnetic and fission track profiles from the areas, as well as for their dissociation from the hominid specimens (de Vos and Sondaar 1994), which these authors link with the Kedung Brubus fauna (i.e. around 0.8 mya) – see also Swisher (1994), and Langbroek and Roebroeks (2000).

Of the other specimens, the Sambungmachan braincase is of broadly *H. erectus* appearance with strongly marked temporals and a well developed angular torus, but with higher, more inflated frontal and expanded occipital regions reflecting an expanded endocranial volume of >1000 cm<sup>3</sup> compared with Trinil and most of the Sangiran remains. The associated fauna is of early Trinil type, with some archaic elements, considered equivalent to the lower part of the Kabuh. Palaeomagnetic samples show normal polarity (Jacob et al. 1978) implying either Jaramillo or early Brunhes age.

Sambungmachan shows undoubted similarities to the twelve Ngandong (Solo) calvaria (Weidenreich 1951; Santa Luca 1980). These are also larger than most Sangiran braincases, with capacities of c. 1,000–1,250 cm<sup>3</sup> reflected in higher, more vertical frontals and laterally expanded sides to the neurocranium. They are usually regarded as either advanced *H. erectus* (*H. erectus soloensis*) or a primitive sub-species of *Homo sapiens* (*H. sapiens soloensis*) (see below). The fossils were recovered from Notopuro deposits of broadly Upper Pleistocene age but dating is again problematic. The terrace unconformably overlies, and so is younger than, Notopuro lahars from Lawu, F/T dated to 0.250 mya. Fauna from Ngandong has been dated by U/Th to 101±10 kya while another site on the same terrace gave a figure of 165 kya. More recently, Swisher et al. (1996) reported much younger U-series and ESR dates of 27–53 kya on fauna from Ngandong, although these results have been criticised by Grun and Thorne (1997; see also Swisher et al. 1997) both in terms of the analytical model used and the lack of confirmed association between fauna and hominids. The wide-ranging age estimates assigned to the Ngandong hominids have very different implications the phyletic position of this and similar populations, and for the evolutionary dynamics of *H. erectus*, which are discussed further below.

### *China*

The largest and best known *erectus* sample from mainland Asia is that from Locality 1, Zhoukoudian (ZKD), Beijing. Most material is cranial, mainly calvaria, with remains of > 45 individuals recovered from several sites (loci D, E, L etc.) and at different levels within the 40+ metres of deposit (Liu 1985; Howell 1994). A few hominid fossils have been found in layer 11, but most come from layers 10–8 and 4–3, and with a few recovered from levels 7 and 5. A combination of fauna, pollen and the cave deposits themselves suggests a climate varying between warm to cool – temperate and cold, with colder, dryer phases at the base (beds 10 and 11) and

towards the top (4), with the intervening period more temperate, and with evidence of a warmer climate at the very top of the sequence (bed 3). The hominid levels have been dated by U series, FT, TL and ESR dating, and are widely accepted to cover from around 0.58 mya to about 0.26 mya: layers 8–9 have dates of >.40 mya (U series) and .418 mya (ESR); layer 10 between .417 and .592 mya (TL) and layer 11 .578 mya (ESR). Layers 6–7 are dated to .35–.36 mya (U series) and layers 3 and 4 .282 to .312 mya by ESR and TL methods (see Grun et al. 1997).

Of the more complete calvaria included here, ‘skulls’ II, X, XI and XII (Weidenreich 1943) are from layer 9 or its equivalents, and ‘skull’ III from layer 11, so the specimens span around 0.15 my, with a mean age of about .45 mya. The chronologies thus suggest temporal overlap between the ZKD hominids and the bulk of the Javan specimens from the mid-upper Kabuh beds. No ZKD specimen appears to be as old as the Grenzbank or upper Puchangan fossils, although continental populations of comparable age are probably represented by the Gongwangling (Lantian) L 2 skull cap. Latest Locality 1 specimens such as ‘skull’ V (H 3) from within the Upper Travertine (? equivalent to Layer 3) and other finds such as Longtandong, Hexian and Quyuanhekon, Yuxian (not included here) may approach the Sambugmachan or Ngandong crania in age, but this is uncertain.

## Materials and methods

Tables 1–2 and Figs. 1–5 present data and comparisons based on some linear dimensions of *H. erectus* specimens. In order to maximise sample sizes, analysis is confined to neurocranial (calvarial) dimensions. While maxillary and mandibular remains are known from all three geographical regions, these are fewer in number, generally incomplete and separated from other cranial material, with resulting taxonomic uncertainty. Evidence of the *erectus* facial skeleton is even more restricted: KNM–ER 3733 and S 17 are, respectively, the only mature East African and Javan specimens to preserve the face (with the latter’s reconstruction problematic), while no ZKD cranium retains that region intact.

The following analysis is divided into two parts. The first considers intra- and inter-regional variation in individual calvarial dimensions of *H. erectus*, largely taken from the literature, and attempts to identify possible temporal and/or spatial contrasts. The second part uses multivariate techniques to summarise between – group contrasts of *erectus* cranial dimensions in combination, and compares patterns of dispersion with those between Upper Pleistocene and modern human populations. This second analysis is based on original measurements, and sample sizes for Javan *H. erectus* in particular are smaller than in the preceding part. Besides overall neurocranial proportions, other aspects of calvarial morphology (articular region, basicranium and balancing complex) are also analysed in this section. The final Discussion considers the phyletic and evolutionary implications of the resultant patterning.

### *Individual calvarial dimensions*

Table 1 summarises data on individual cranial dimensions for *H. erectus* groups and specimens compiled from: Anton and Franzen 1997; Brauer 1994; Rightmire 1979, 1990, 1994; Santa Luca 1980; Walker and Leakey 1993; Weidenreich 1943, 1945, 1951; Wood 1991. Included specimens are:

Early East African *H. erectus* (EA)

KNM-ER 3733; KNM-ER 3883; OH 9; (Although relatively complete, KNM-WT 15000 is excluded because it is not fully mature).

Javan (Kabuh/Puchangan) *H. erectus* (K/P)

Trinil T 2; Sangiran: S 2; S 3; S 4; S 10; S 12; S 17; Sambungmachan S 1.

Javan (Ngandong) *H. erectus* (Ng)

Ng 1; Ng 6; Ng 7; Ng 10; Ng 11; Ng 12.

Zhoukoudian *H. erectus* (ZKD)

Ckn.D 1.PA.17 (II); Ckn.E 1.PA.16.(III); Ckn.L 1.PA.98.(X); Ckn.L 2.PA.99.(XI); Ckn.L 3.PA.100(XII).

## **Results**

The scatter diagram of separate dimensions (Fig. 1) generally shows considerable overlap of crania from different regions, with no obvious breaks in the distribution of character values. Overall, the spread of the K/P specimens is greater than for the other specimens. Some frontal and occipital dimensions are relatively variable across *erectus*, but parietal coronal lengths (both arc and chord) are restricted in range.

### *East Africa*

OH 9 is some 0.5 my younger than the two Koobi Fora crania, and has been considered by some to be specifically distinct from the latter specimens. Its metrics are therefore given separately from the Turkana fossils in Table 1, and means and standard deviations are calculated for the Turkana fossils alone, and for the combined East African sample. The two sets of statistics are similar, with no noticeably discrepant values. The most variable character (as measured by the CV) is occipital sagittal chord, reflecting major differences between the two Koobi Fora crania; inclusion of OH 9 appreciably reduces the CV. The following comparisons are therefore based on the combined East African sample. Compared with the other specimens, the East African crania have sagittally short parietals.

### *Java*

Similarly, Javan K/P values are given both excluding Sambungmachan, and incorporating it. The main differences between the two sets of figures are in the frontal, reflecting the fact that apart from Sambungmachan most of this bone's

Table 1

Cranial dimensions for *H. erectus* groups and specimens

	Koobi Fora			OH9	East Africa				Java K/P				Sa	Java K/P and Sa			
	n	$\bar{x}$	s		n	$\bar{x}$	s	v	n	$\bar{x}$	s	v		n	$\bar{x}$	s	v
Fr. S. Ch	2	102.5	2.12	–	2	102.5	2.12	2.1	3	102.7	14.2	13.8	113	4	105.8	13.12	12.4
Fr. S. A	2	118.5	.71	–	2	118.5	.71	0.6	2	103.8	4.95	4.8	–	2	103.5	4.95	4.8
Min Fr. b	2	81.5	2.12	88	3	83.7	4.04	4.8	3	86.7	8.02	9.3	102	4	90.5	10.08	11.1
Max Fr. b	2	107.5	3.54	–	2	107.5	3.54	3.3	5	103.9	9.04	8.7	117	6	106.1	9.70	9.1
Par. s: ch	2	82.5	4.95	–	2	82.5	4.95	6.0	6	92.7	3.78	4.1	97	7	93.3	3.82	4.1
Par. s: a	2	88	7.07	–	2	88.0	7.07	8.1	6	96.5	4.04	4.2	102	7	97.3	4.23	5.2
La-ast. c	2	80.0	4.24	–	2	80.0	4.24	5.3	4	78.8	3.40	4.3	79	5	78.8	2.95	8.0
La-ast. a	2	87.5	4.95	–	2	87.5	4.95	5.7	3	88.0	3.61	4.10	84	4	87.0	3.58	3.7
Max. pr.B	2	129.5	3.54	138	3	132.3	5.51	4.2	7	137.1	4.39	3.2	148	8	138.4	5.61	4.1
Oc. s. ch	2	81.5	9.19	80	3	81.0	6.56	8.1	4	85.6	9.39	11.3	–	4	85.6	9.39	14.3
Oc. s. a	2	113.5	4.95	110	3	112.3	4.04	5.6	4	113.0	12.57	11.1	–	4	113.0	12.57	11.1
Biastr. b	2	122.5	2.12	123	3	122.7	1.53	1.3	4	119.8	6.70	5.6	126	5	121.0	6.64	5.3
Biauric b	2	130.5	2.12	135	3	132.0	3.0	2.3	4	131.8	9.50	6.9	146	5	138.6	9.21	6.6
	Java: Ng				China: ZKD				Sp. Mean exc. Ng.				Sp. Mean inc. Ng.				
	n	$\bar{x}$	s	v	n	$\bar{x}$	s	v	n	$\bar{x}$	s	v	n	$\bar{x}$	s	v	
Fr.S. Ch	5	116.9	4.48	3.8	5	109.8	5.54	5.1	11	107.0	8.54	8.0	16	110.1	5.27	4.8	
Fr.S.A	5	130.8	8.17	6.2	5	122.6	5.03	4.10	9	117.4	9.64	8.2	14	122.2	10.71	8.8	
Min Fr. b	5	103.6	3.65	3.5	5	85.9	3.53	4.1	12	86.9	5.90	6.8	17	91.8	5.22	5.69	
Max Fr. b	4	118.0	3.65	3.1	5	106.7	3.24	3.0	14	106.6	6.47	6.07	18	109.3	5.83	5.33	
Par.s: ch	6	102.2	5.0	4.9	5	95.2	7.66	8.1	14	92.4	7.14	7.7	20	95.4	7.0	7.3	
Par.s: a	6	107.7	6.0	5.6	5	100.8	8.38	8.3	14	97.2	7.40	7.6	20	100.4	7.64	7.6	
L-ast. c	4	84.8	1.26	1.5	5	82.4	2.97	3.6	12	80.5	3.25	4.0	16	81.6	3.46	4.2	
L-ast. a	4	91.5	2.08	2.3	5	91.6	2.70	3.0	11	89.2	2.45	2.8	15	89.2	3.54	3.9	
Max. pr. b	6	144.0	4.34	3.0	5	136.7	3.21	2.4	16	136.8	3.51	2.6	22	138.8	4.63	3.3	
Oc. s. ch	6	85.9	4.76	5.5	3	85.3	1.16	1.4	10	83.1	8.70	10.5	16	84.2	7.02	8.3	
Oc. s. a	6	118.2	6.68	5.7	3	113.7	6.66	5.9	10	113.2	4.05	3.6	16	115.1	5.54	4.8	
Biastr. b	6	125.8	1.47	1.2	5	111.8	5.40	4.8	13	117.8	7.81	6.6	19	120.4	6.92	5.8	
Biauric b	6	145.3	7.50	5.2	4	145.5	4.44	3.1	12	139.3	7.12	5.1	18	141.3	8.27	5.9	

Data from: Anton and Franzen 1997; Brauer 1994; Rightmire 1979, 1990, 1994; Santa Luca 1980; Walker and Leakey 1993; Weidenreich 1943, 1945, 1951; Wood 1991

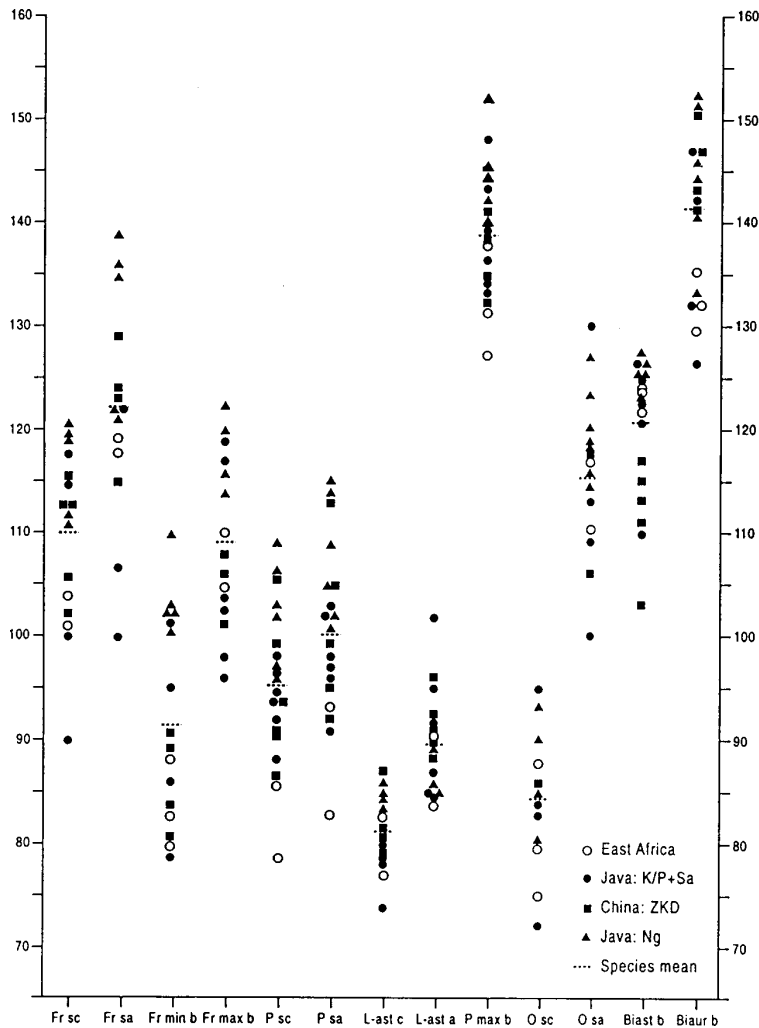


Fig. 1. Scatter diagram of *H. erectus* specimens for thirteen calvarial dimensions. Horizontal bars indicate overall species means

dimensions are known only from smaller specimens (eg T2; S2), and in biauricular breadth. In fact, there is considerable size variation among the other Javan crania, with Sambungmachan 1 resembling larger Kabuh specimens such as S17, and the former's inclusion does not result in excessively large CV values. Again, subsequent comparisons are therefore based on the combined K/P sample, including Sambungmachan 1.

The Ngandong crania are remarkably similar (Weidenreich 1951; Santa Luca 1980; Rightmire 1990), and CV values, especially for the frontal and occipital, are noticeably lower than for the preceding K/P sample. Contrasts between the Javan

samples in mean frontal dimensions are especially marked, again reflecting the mainly small K/P crania in which this region is preserved. While the Ngandong crania generally lie within the upper part of the species range for all characters, there is no obvious hiatus separating them from other specimens, but instead extensive overlap with larger K/P crania such as S 12, S 17 and Sambungmachan.

### *China*

The ZKD sample is also relatively homogeneous, and similarly contrasts with the Javan K/P sample in its sagittally larger frontal. This apart, ZKD crania have values comparable to the Javan specimens for most dimensions, but biasterionic diameter (occipital breadth) is narrower for all the Chinese fossils, although their frontal, biparietal and biauricular breadths are comparable to specimens from elsewhere.

Several points are readily apparent from comparisons of the regional samples and the species overall (Table 1 and Figs. 2–3):

- Although individual samples are often small, numbers for the species overall (even with Ngandong omitted) are in double figures, and so relatively large for hominid studies. While regional values may be disturbed by sampling effects, reasonable confidence can therefore be attached to the overall species values.
- Most variability is in the anterior and mid-neurocranium; sagittal and coronal dimensions of the rear vault are strikingly constant across *erectus* groups.
- The various regional samples resemble each other in their neurocranial proportions: in fact, given their spatial and chronological range, they are remarkably similar. East African crania have relatively short parietals, and the ZKD sample relatively narrow occipitals compared with the others, but otherwise values are very close. Even the Ngandong sample closely resembles the others, being a rather larger variant anteriorly of the same cranial pattern. The Solo crania are most distinctive in frontal size and parietal length; their remaining dimensions are closely matched by other *erectus* crania.

The relative homogeneity of *H. erectus* world-wide can also be seen by comparing the regional patterns with that for the species as a whole (Figs. 2 and 3). Limits of 1 SD either side of the species mean (calculated conservatively by excluding Ngandong) generally encompass the individual sample means save for some anterior cranial characters of the Ngandong group. Even the latter is usually only slightly beyond the 1 SD envelope, with several specimen values falling within that envelope. For example, Ng 7 and 12 fall within the + 1 SD range for Frontal and Parietal sagittal chords and arcs, as does the latter specimen for Maximum Frontal Breadth. Only in Minimum Frontal Breadth is there no overlap in specimen values and so marked separation in means between Ngandong and other *erectus*. In all other respects craniometric values that characterise the Solo sample would not be exceptional in a population of ‘classic’ *erectus* individuals, and for many posterior vault (i.e. rear parietal and occipital) dimensions would actually typify such a population. There are obvious evolutionary implications here (see below).

*Multiple calvarial dimensions*

So while the Ngandong specimens are consistently among the larger *erectus* crania, the samples generally exhibit considerable overlap in calvarial dimensions, and their values do not readily differentiate African, continental and peninsular Asian *erectus* from each other. However, even though individual dimensions show extensive overlap, it is possible that their covariation might display distinctive regional patterning and allow for group differentiation. Such patterning typifies diversity in and between populations of modern *Homo sapiens*, and many studies – among the more recent, most notably those of Howells (1973, 1989, 1995) – have demonstrated the power of multivariate approaches for sorting and characterising extant human populations. I therefore provide comparable measures of diversity between the various *H. erectus* groups.

An obvious issue in fossil hominid studies is the interpretation of results, bearing in mind the restricted sample sizes, and the likelihood of a chronological and/or spatial component to the observed variation. Many analyses, including those of Howells noted above, provide extensive information on patterns of modern human variation, but these are unlikely to serve as appropriate metrics for interpreting

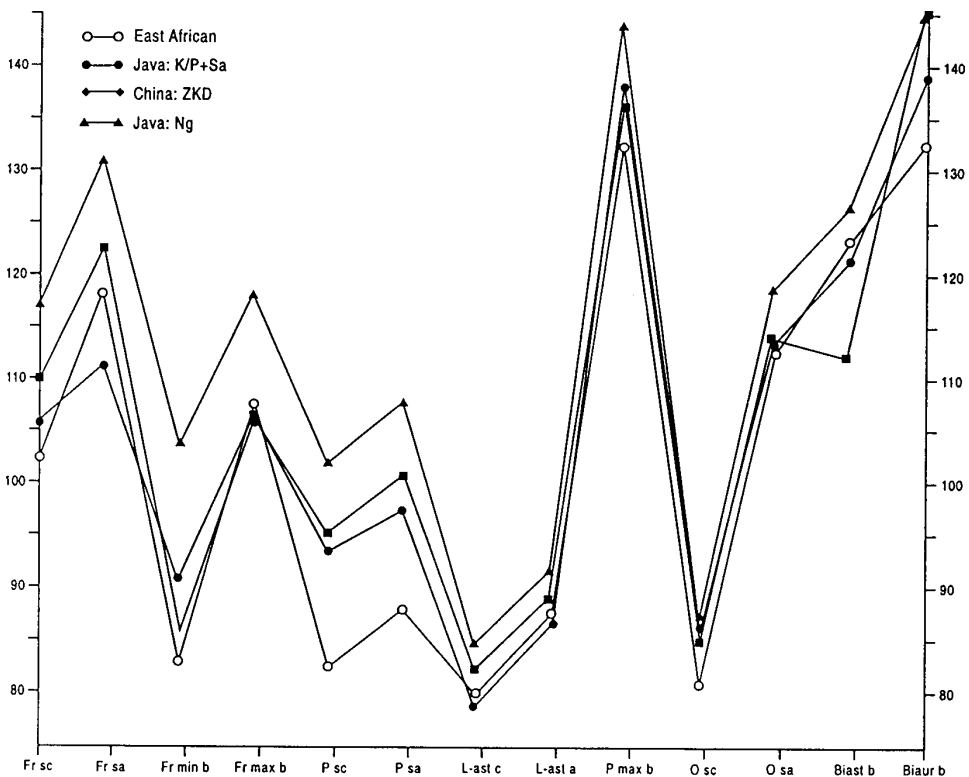


Fig. 2. *H. erectus* regional sample means for thirteen calvarial dimensions

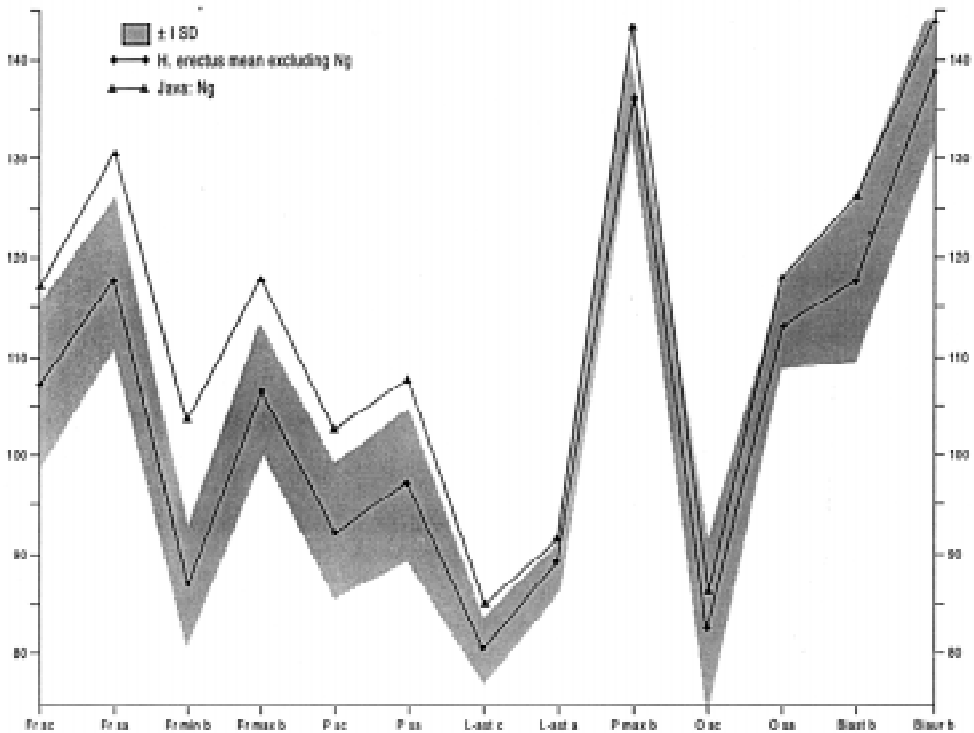


Fig. 3. Ngandong sample means compared with means and + 1 SD ranges calculated from other *H. erectus* specimens (i.e. excluding Ngandong) for thirteen calvarial dimensions

Lower and Middle Pleistocene hominid diversity for several reasons. They include: the recent rapid expansion of population numbers, the comparatively recent presence of modern humans in some parts of the world, and the likely differing adaptive bases, given what we know about contrasts in ecological, especially subsistence, patterns between earlier and contemporary hominids. Such contrasts are reflected in the rugged construction, large face and jaws and modest endocranial volume of the one compared with the lightly built, weak, orthognathic face and jaws and expanded neurocranium of the other. Moreover, Howells' and others' studies of modern humans have found most differentiation to occur in facial features, whereas *erectus* is predominantly represented by calvaria: facial remains are notable for their rarity (see above).

An alternative, indirect approach to evaluating diversity in *erectus* is to compare the separation of the regional groups with that evidenced by other fossil hominids. Sample sizes for Upper Pleistocene hominids are larger (and so more representative) than for preceding taxa. It is also generally accepted that later Quaternary *Homo* forms are both phylogenetically and adaptively closer than Pliocene hominids to *H. erectus*, and so provide more plausible models with which to explore diversity in the latter

species. The multivariate measures of *erectus* variability that follow are accordingly scaled on two standards:

- An infra-specific standard represented by the separation between a sample of European Upper Palaeolithic *H. sapiens* (UP) and a sample of modern humans (M).
- An inter-specific standard represented by the separation between Upper Palaeolithic *H. sapiens* and a sample of European Neanderthals (EN).S

Although there is still argument over the issue, there is growing acceptance that Neanderthals were effectively reproductively isolated from early moderns and that specific distinction is therefore warranted. Evidence from the Middle East for extended temporal overlap between the two distinct morphologies but without convincing intermediates certainly supports such a view. Neanderthal – Upper Palaeolithic *H. sapiens* separation is accordingly taken as an appropriate measure of inter-specific divergence in hominids. (EN–UP divergence is taken in preference to the EN–M figure since the two Upper Pleistocene groups are chronologically, adaptively and morphologically closer to each other and to *erectus* than are modern humans. They thus provide more appropriate standards than modern humans for scaling Middle Pleistocene hominid diversity). The scales are approximate measures only: strict correspondence in phenetic differentiation between Lower/Middle and Upper Pleistocene hominids is not to be expected. However, it is reasonable to aim for some consistency of patterning in species held to be close in evolutionary and adaptive terms if our taxonomic and phyletic schemes are to have any meaning.

Generalised Distances ( $D^2$ ) were calculated between the *H. erectus* and other hominid groups, with canonical variate analysis (CVA) used to summarise the dispersion in 3-D space, and to assess the contributions of the original characters to the separation (Gower 1966a, 1966b). In all cases CVs I–III encompassed > 83% of total variance. For these analyses it was not possible to obtain data on all the specimens considered in the univariate section. In particular, the K/P *erectus* sample is based on measurements from T2, S2, and S4, supplemented by a cranial reconstruction based on this last specimen. Similarly, the Ngandong sample is represented by Ng 1, Ng 5, Ng 6 and Ng 7.

Of the comparators, the European Neanderthal sample consists of: Neanderthal, Spy 1, Spy 2, La Ferrassie I, La Quina, Mt. Circeo, La Chapelle-aux-Saints and Gibraltar 1. The Upper Pleistocene *H. sapiens* sample consists of: Cro-Magnon 1, Cro-Magnon 3, Predmost 3, Predmost 4, Combe Capelle, Brno 1, Brno 2 and Grotte des Enfants 6. The modern *H. sapiens* (*H. s. sapiens*) sample is based on fifty crania in the Duckworth Collection, Department of Biological Anthropology, Cambridge.

Fig. 4 indicates functional complexes of the hominid skull and their delineation. Attention here is confined to the following calvarial complexes:

Cranial Vault (Fig. 4 No. 8)

14 chord and arc dimensions describing overall proportions of the vault. Many of these correspond to the individual dimensions considered above whilst others provide alternative, comparable measures.

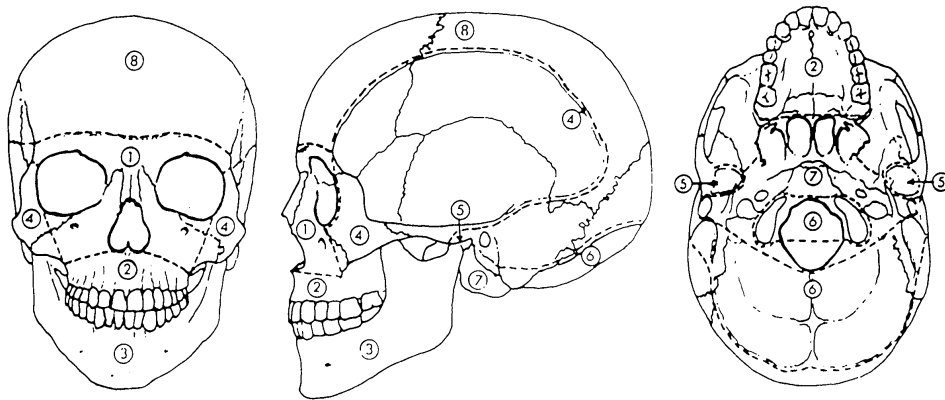


Fig. 4. Hominid cranial regions referred to in this study  
Cranial Vault (8); Basicranium (7); Balance (6); Articular region (5)

Transverse, vertical and sagittal development of the mid-neurocranium and frontal expansion, especially coronally, are the main discriminants influencing the separation.

Basicranium (Fig. 4 No. 7)

5 characters describing the sagittal and lateral extent of the basicranium and the size and proportions of the foramen magnum. Lateral expansion of the basicranium, as measured by biporionic and biglenoid diameters and foramen magnum breadth, is the main discriminant.

Balance (Fig. 4 No. 6)

6 dimensions describing the lateral, sagittal and vertical development of the nuchal musculature, proportions of the pre- and post-condylar head lever segments (estimated where missing), and size of the mastoid processes. Head lever proportions and mastoid size are more influential than nuchal extent in determining separation.

Articular (Fig. 4 No. 5)

7 dimensions describing the size and proportions of the articular fossa and associated structures (articular eminence, postglenoid tubercle, entoglenoid process). The fossa's transverse and sagittal diameters, and the vertical development of surrounding structures from the fossa floor are the main variables influencing separation.

## Results

Table 2 and Fig. 5 summarise the Generalised Distances for the above complexes, both 'raw' and scaled by the corresponding values between UP–M *H. sapiens*, and between UP *sapiens* and Neanderthals. UP–EN separation ranges between 1.5 to > twice the corresponding inter-*sapiens* distance. Several other points are also apparent:

Cranial vault and balancing complexes exhibit greater diversity among *H. erectus* and the more recent hominids groups than the basicranial and articular regions. In general, the various *erectus* groups are broadly equidistant from each other, but with a slight tendency for the African – ZKD and African – Ng pairings to be a little further apart than the others, and for ZKD – Ng to be rather closer. As with many

Table 2

Separation between *H. erectus* and comparator groups for Cranial Vault, Basicranium, Balance and Articular regions

	Cranial Vault			Basicranium			Balance			Articular		
	1	2	3	1	2	3	1	2	3	1	2	3
<b>Comparators</b>												
U. Pal. <i>sapiens</i> – modern <i>sapiens</i>	3.7	1	.65	1.3	1	.48	2.2	1	.51	1.0	1	.59
U. Pal. <i>sapiens</i> – Neanderthals	5.7	1.54	1	2.4	2.07	1	4.3	1.97	1	1.7	1.69	1
Modern <i>sapiens</i> – Neanderthals	6.0	1.62	1.05	3.0	2.33	1.13	5.4	2.45	1.24	1.9	1.85	1.89
<b><i>Homo erectus</i></b>												
Early African – Java K/P	5.2	1.40	.91	1.65	1.27	.61	3.2	1.46	.74	1.3	1.29	.76
Early African – ZKD	5.1	1.38	.90	1.8	1.38	.67	3.8	1.72	.87	1.5	1.49	.88
Early African – Java Ng	5.4	1.46	.95	1.7	1.32	.64	3.5	1.39	.81	1.55	1.53	.91
Java K/P – ZKD	5.0	1.35	.88	1.5	1.15	.55	2.8	1.27	.65	2.15	1.4	.82
Java K/P – Java Ng	4.0	1.08	.70	1.3	1.03	.50	3.0	1.36	.69	1.39	1.38	.81
ZKD – Java Ng	3.2	.86	.56	1.2	.95	.46	3.2	1.45	.74	1.16	1.15	.68

For each region: Generalised Distances (column 1); scaled by Upper Palaeolithic – modern *H. sapiens* separation (column 2); scaled by Upper Palaeolithic *sapiens* – Neanderthal separation (column 3)

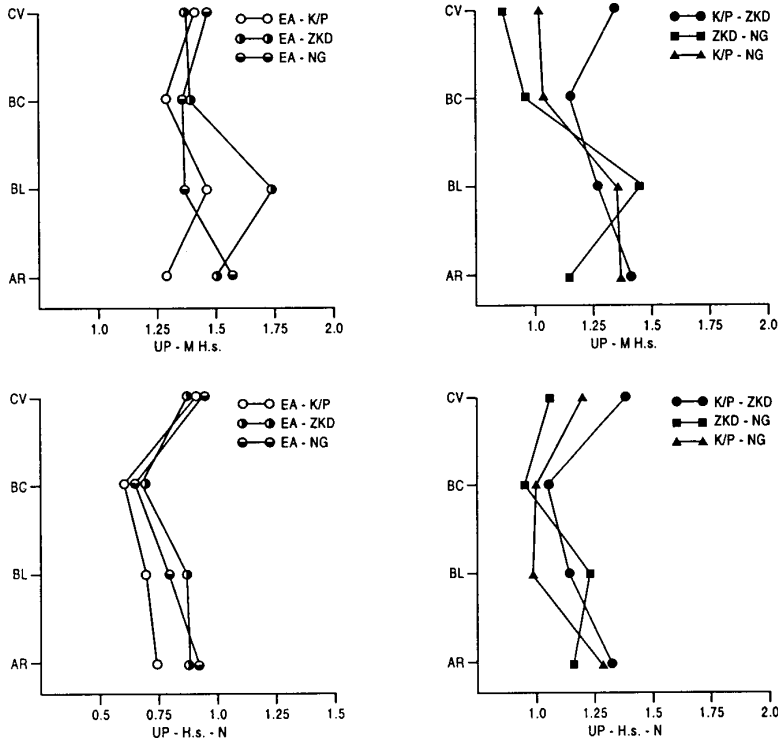


Fig. 5. Inter-*erectus* distances for Vault, Basicranial, Balance and Articular regions scaled by Upper Palaeolithic – modern *H. sapiens* separation (upper) and Upper Palaeolithic *sapiens* – Neanderthal separation (lower). For further discussion see text

hominid studies, the combined vault characters differentiate the groups more effectively than they do individually. However, the smaller samples available for the multivariate analyses – in particular the omission of larger crania S 12, S 17 and Sambangmachan from the K/P group – need to be borne in mind when assessing separation.

The scaled distances reveal separation between the *erectus* groups to be generally greater than that between UP and M *H. sapiens* – again not unexpected, given disparities in sample sizes between the earlier and more recent groups. However, greater diversity among earlier Quaternary hominids is also to be anticipated on other grounds. Population sizes are likely to have been smaller in the Lower/ Middle Pleistocene and inter-group diversity, driven by contrasting environmental pressures, founder effects, inter-generational sampling perturbations and drift, correspondingly greater. Moreover, all the *erectus* samples, save possibly Ngandong, internally span a longer interval than the 25–30,000 years between the *sapiens* referents, while the chronological separation between *erectus* groups is markedly greater. Although it is problematic to isolate their effects from other components of variability, temporal

trends, if present, are likely to contribute appreciably more to the observed *erectus* diversity than to that between the two *sapiens* groups.

Given these considerations, it is perhaps surprising that the *erectus* diversity is not greater relative to *sapiens* than it in fact is: most values are c.1.0–1.5 times the inter-*sapiens* divergence, and the maximum is c. 1.7 (the balancing complex between EA and ZKD *erectus*). For the vault K/P – Ng and ZKD – Ng distances are, in fact, closely comparable to those between the two *sapiens* groups, while inclusion of S 12, S 17 etc would doubtless reduce the former value to below the inter-*sapiens* threshold.

Similarly, the various inter-*erectus* distances are invariably less than the corresponding EN–UP values, although for some comparisons (cranial vault and articular region between EA and other *erectus*) they begin to approach the latter. While the generally greater distances between EA and other *erectus* groups are consistent with their geographical and chronological separation, given the scale of these the morphological divergence is not particularly marked. Many of the differences in vault, basicranium and balance reflect aspects of the African fossils' rather smaller cranial capacities, while contrasts in the articular region *may* reflect differences in the size of the mandible and lower dentition. Again, for intra-Asian comparisons, the omission of larger Kabuh Bed specimens needs to be borne in mind, and their inclusion would probably reduce the ZKD–K/P and K/P–Ng distances relative to the EN–UP separation.

## Discussion

Overall the results confirm the general similarity in form of *erectus* crania: there is extensive overlap of the several samples in individual dimensions coupled with somewhat clearer – but still comparatively modest – differentiation in combination. In one sense this is not unexpected: the widespread assignment of all this material to *H. erectus* is a reflection of its essential morphological similarity. However, 'widespread' is not synonymous with 'universal': the conspecificity of the early African and Asian forms has been contested (see above), as has the attribution of the Ngandong hominids. The present study offers no support for specifically differentiating the early East African fossils as *H. ergaster*, as formalised by Wood (1991, 1992 a, b) and supported by Tattersall (1992, 1996). Rather, it accords with the findings of Brauer (1994), Brauer and Mbau (1992), Kramer (1993) and Rightmire (1984, 1990, 1998) whose studies both confirm the general similarity of *H. erectus sl* and show there to be extensive overlap between African and Asian specimens in the very characters claimed to differentiate them. The status of the Ngandong hominids has also fluctuated: while most workers (eg Santa Luca 1980; Rightmire 1990) include them within *erectus*, others e.g. Tobias (1991) and Wolpoff in earlier (pre-1993) publications have referred them to *H. sapiens soloensis*, reflecting perceived contrasts between these and 'classic' *erectus* (see below).

Of the above analyses, this study's approach is most akin to that of Kramer (1993), who used (different) univariate and multivariate techniques to investigate variability in 8 cranial dimensions against different comparators – a final Pliocene mixed hominid species group, and Howells' modern human data. His *erectus* sample incorporated most of the EA, K/P, Ng and ZKD specimens included here, together with OH 12 and Sale (the specific identity of which is disputed). Kramer's prime concern was to test the specific integrity of *erectus*, rather than to explore its evolutionary dynamics or their broader phyletic implications; he concluded that there was no basis for rejecting the concept of *H. erectus* as a single species.

Taxonomic issues aside, considering the temporal and spatial separation of these *erectus* groups, their morphological differentiation is surprisingly slight. It affords little evidence to support the existence of pronounced polytypic variants – still less distinct species – however strongly these might be predicted on general evolutionary and ecological grounds. In particular, given their context – geographic isolation, marginal habitats and small population size – one might expect the SE Asian hominids to provide clear evidence of morphological differentiation from both the African and mainland Asian samples (Pope 1988), and yet this is conspicuously lacking. Whilst it has been argued that such distinctiveness might be readily reflected in soft anatomical structures (Tattersall 1992), evidence of these is necessarily absent, and the available hard anatomy offers no direct support for differentiation.

The relative homogeneity of *erectus* morphology has implications that extend beyond the species itself, for evaluation of its diversity is central to debates over the most plausible interpretation of the pattern of later hominid evolution, and the processes determining this. On the one hand the similarity of the samples militates against speciose interpretations of the Lower/Middle Pleistocene *Homo* record, and phyletic models that view speciation as the main driving force in later hominid evolution. Rather, available evidence accords with the notion of *erectus* as a single, widely distributed species, probably displaying local (demic) and perhaps larger scale (regional) patterning that is, however, morphologically limited in extent. Proponents of regional continuity (e.g. Jelinek 1978, 1985; Thorne 1981; Thorne and Wolpoff 1981; Wolpoff 1989; Wolpoff et al. 1984, 1994a, b) take such a view of Middle Pleistocene diversity and combine it with arguments that *erectus* also displays clear evidence of significant anagenetic evolution in the direction of sapienisation. The most forceful statement of this position is that of Wolpoff et al. (1994a), who view all evolution within *Homo* as a monophyletic continuum, and who accordingly propose sinking *H. erectus* (including all specimens from Early African crania such as ER 2598 onwards) within *H. sapiens*. This would give the latter species a duration of c 2 my – at least twice that of the otherwise longest known hominid species.

Wolpoff et al. consider earlier and later (Ngandong) *erectus* (their 'early' and 'middle *H. sapiens*') to exhibit significant evolutionary trends presaging more modern morphology. Wolpoff (1999, pp. 570–574) lists these as a c 12% increase in average endocranial volume with particular expansion of the frontal and occipital lobes, greater neurocranial breadth, with the maximum value positioned more anteriorly and at

a higher level, and with increased cranial height and greater frontal breadth, and a general reduction in the muscular markings and bony reinforcement of the vault. While recognising a direct, ancestor-descendant relationship between the earlier Javan fossils and the Ngandong sample Wolpoff denies that the latter is *H. erectus* in the sense used by other workers, stating that arguments for its inclusion constitute ‘a classic case of confusing regional features with traits that could be taken to indicate evolutionary grade’ (Wolpoff 1999, p. 573).

But the above analysis of individual linear neurocranial dimensions – many of which can be expected to reflect Wolpoff’s list of changes other than cranial rugosity – shows close similarity between the K/P, ZKD and Ngandong samples for many characters. In combination the character sets effect rather greater differentiation, but even here the nature and scale of changes are limited. Contrasts are essentially confined to the articular and balance complexes, while still failing to match those between Neanderthals and early moderns. For vault and basicranium the K/P–Ng separation is virtually identical to that between UP and M *H. sapiens*, despite the K/P sample incorporating only smaller specimens T2, S2, S4 (of which the first two are considered by Wolpoff (1999) to be female), thereby emphasising its contrasts with the Ngandong crania.

The essentially contemporary Upper Pleistocene Neanderthals and early moderns consistently display greater divergence than the *erectus* groups. Wolpoff et al., of course, also include Neanderthals within *H. sapiens* and argue for gene flow between these and early modern humans (see, for example, Wolpoff et al. 1994a, b), so that in their scheme Neanderthals merit sub-specific differentiation at best. Given that separation between the *erectus* samples is invariably less than that between the Upper Pleistocene groups, if Wolpoff et al.’s interpretation of the latter is correct, then *erectus* differentiation – and especially that between the Asian groups – must be trivial in evolutionary terms, and it is doubtful if it warrants even sub-specific rank. If Wolpoff et al. are wrong in incorporating Neanderthals within *H. sapiens* (as seems likely) the results suggest rather more pronounced but still intra-specific patterning within *H. erectus* *sl.* In particular, the similarity of Asian inter – *erectus* distances to the corresponding inter-*sapiens* standards (eg vault, basicranium) points to relatively minor differentiation in these complexes in mid – later *erectus* populations.

Neanderthal – early modern divergence probably evolved sometime within the period 80–150 kyr ago, although whether it was a comparatively rapid, episodic event followed by stabilisation of the morphology, or a longer drawn out process is unclear. At least some Neanderthal features may have evolved via founder effects, drift, or transience (Templeton 1980; Bilsborough 1999) from bottlenecking of antecedent Eurasian hominid populations in the late Middle/basal Upper Pleistocene – processes which may well have also influenced the earlier evolution of *erectus* diversity. For while there do appear to be differences between the *erectus* groups (none of the later specimens is as small as the smaller early ones, and there are corresponding shifts in mean values) their scale is such that they could easily have arisen through drift and sampling effects on small, isolated communities.

Even the most distinctive character – Minimum Frontal Breadth – can be accommodated in such a model. There is accordingly no requirement to posit directional selection favouring expanded brain size as the driving force underlying *erectus* cranial variation, and the latter cannot be cited as strong evidence of longer term evolutionary pressures associated with ‘sapienisation’, as argued by proponents of the unilinear, multiregional model. At best the multiregional case is possible but unsubstantiated. Its demonstration would depend on identifying a pulse of evolutionary change around the *erectus*/'archaic' *sapiens* interface consistent with such ‘sapienisation’ trends.

Alternatively, some workers (eg Stanley 1979, 1981; Rightmire 1981, 1985, 1986b, 1990) have argued that *H. erectus* represents a period of stasis in hominid evolution. The above analyses largely support such an interpretation, at least so far as neurocranial dimensions are concerned: there is little evidence of appreciable change over the 1 my plus between the early East African, Puchangan/Kabuh and ZKD specimens. The evidence for prolonged stasis becomes even more compelling if further investigation verifies the proposed Upper Pleistocene date of the Ngandong crania, for then its duration would extend to > 1.5 my. Dating these fossils thus becomes crucial for modelling the evolutionary processes impacting on *H. erectus* groups, but current evidence of their age is conflicting.

While the Ngandong terrace is undoubtedly <.25 mya, and absolute dates derived from faunal remains give even younger ages, (see above), the hominids may, in fact, be older. Unlike other faunal elements at the site they are worn and abraded, broken and dissociated (Santa Luca 1980). They therefore probably do not represent an *in situ* death assemblage, but rather specimens that were exposed upstream through erosion (as other Javan *erectus* specimens currently are) transported by river action, and then deposited at Ngandong and recovered by alluvium. The site's location, on a bend of the Solo river, adds support to this interpretation, and similar mechanisms have been cited to account for the different ages of the Trinil 2 (calotte) and 3 (femur). On this view the Ngandong specimens could well be of Kabuh age(s), and no prolonged phase of stasis need be posited to explain their similarities to specimens such as S 12 and S 17.

Additional, tentative support for the antiquity of the Ngandong morphology is possibly provided by the Hanoman 1 specimen – but at the cost of further muddying the chronological and phyletic pictures, and re-opening the issue of stasis. This fragmented calvaria exposed by a landslide near Bukuran in the Sangiran dome (Windianto et al. 1994) combines a narrow frontal and weak parietal sagittal keel with an evenly curved occipital and high mid-vault, comparable in profile to Sambungmachan and Ngandong crania rather than other Sangiran specimens, and implying a relatively large endocranial capacity. Despite this, it is inferred to come from a level within the Puchangan clays, not far from the Puchangan/Kabuh boundary, implying an age of around 1 mya. If confirmed, this reopens the notion of stasis in Indonesian *H. erectus* – not because the Ngandong crania are necessarily late in date, but because their morphology occurs relatively early at Hanoman.

However, the usual contextual problems (local discovery; disturbed stratigraphy) all apply, while absence of the Grenzbank in this area reinforces the need for caution. Accurate dating of the Javan sequence is thus doubly essential for obtaining a reliable view of evolutionary dynamics within *H. erectus*, and in later hominid phylogeny overall. It is possible that when a firmer chronological framework is established, the Javan fossils will be shown to broadly correspond in time to later African *erectus* finds i.e. within the c 1.0–0.5 mya interval, but the picture is currently unresolved.

Given its scale, the rather limited differentiation evident from these results is as plausibly explained by drift and sampling effects (whether of the fossil record itself, or of the small hominid populations represented by that record) as by directional selection. The generally reduced variability of the Ngandong specimens compared with the other groups is suggestive of this interpretation, whilst even their most distinctive character – Minimum Frontal Breadth – can, in my view, be accommodated within a drift/bottlenecking model. These conclusions differ from earlier views expressed by me (eg Bilborough 1976, 1978, 1983, 1992) primarily as a consequence of the larger numbers of specimens and more detailed chronological frameworks incorporated here, as well as by consideration of a wider range of evolutionary models and phyletic patterns (Bilborough 1999).

While utilising different comparators and methods, the findings in large part agree with the conclusions of Brauer (1994) and Rightmire (1990, 1994), at least so far as ‘classic’ *erectus* is concerned. Brauer does not consider the Ngandong hominids in his analysis, while Rightmire gives contrasting interpretations of their significance, suggesting (1990 pp. 196–197) that they provide evidence for cranial expansion, but subsequently (1994 p. 324) that ‘In most respects these individuals (i.e. Ngandong) are very much like the other specimens from Java’ and that ‘...they do not provide evidence for much real change within this taxon.’ The present results support this latter interpretation. Similarly, while some authors (e.g. Cronin et al. 1981; Clausen 1989) detect a trend for brain enlargement in *erectus*, in so far as their findings can be disaggregated, this conclusion appears to be mainly a consequence of the rather smaller capacities of the early African specimens rather than due to any clear intra-Asian trend.

This analysis is limited to calvarial data and it is, of course, possible that other regions – eg face, gnathic and dental evidence – provide evidence of significant evolutionary change in *H. erectus* as, for example, Wolpoff (1984, 1986) and others have argued. Indeed, there are pointers here to such changes in the rather more marked differentiation in the articular and balance complexes – both regions influenced by proportions of the face and masticatory apparatus. But facial evidence is extremely limited and in some cases its reconstruction disputed (see, for example, Brauer and Stringer 1997), while specific assignment of isolated maxillae and mandibles is often contentious. Calvaria provide by far the most extensive evidence of *H. erectus*, and their features demonstrate that neurocranial diversity in the species was remarkably limited over wide temporal and spatial spans.

## Summary and Conclusions

Univariate and multivariate analysis of calvarial dimensions in *H. erectus* describing size and proportions of the cranial vault, basicranium, balance and articular regions indicate East African, continental Asian and SE Asian specimens spanning a 1–1.5 my period to be remarkably similar, with morphological differentiation consistently less than that between geographically and temporally proximate Upper Pleistocene hominids, and in some cases comparable to that between Upper Palaeolithic and modern *H. sapiens*. Evidence for pronounced polytypism or significant evolutionary trends within the species is accordingly lacking, and what differentiation there is can be as plausibly ascribed to drift and sampling effects as to directional phyletic (anagenetic) change.

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