ANTHROPOLOGIE • XLIII/2–3 • pp. 129–158 • 2005

ALAN BILSBOROUGH

HOMO ERECTUS REVISITED: ASPECTS OF AFFINITY AND DIVERSITY IN A PLEISTOCENE HOMININ SPECIES

ABSTRACT: Fossil material assigned to Homo erectus *is reviewed and the composition, integrity and morphological range of the species explored, to investigate its phyletic status and possible components of geographical and temporal variation. There is no convincing morphological case for differentiating early African specimens (*H. ergaster*) or "*Meganthropus*"material from* H. erectus *and claims for their specific identity seem to reflect evolutionary models and perceptions of the process rather than the characteristics of the fossil specimens themselves. Ileret and Dmanisi fossils indicate marked cranial variation in early* H. erectus*, with SK 847 a similar or closely related form. New dates and clarified stratigraphy indicate early hominin presence in Java and a correspondingly long interval between early and latest* H. erectus *there. Regional trends include some increase in brain size and cranial robusticity (Africa), dental reduction (Java and China), increased brain size and cranial gracilisation (Java). Contrasts are, however, limited and could well reflect drift rather than selection, especially in SE Asia. Variation in cranial (? and body) size apparently persisted in African* erectus *with possible behavioural and socio-ecological correlates. Similar variability is lacking among the Asian fossils, implying major differences between African and Asian populations, but much more fossil evidence is needed to resolve this. Late Lower Pleistocene African* H. erectus *populations were ancestral to more derived forms, with the species persisting in Asia until Middle-Upper Pleistocene times.* H. floresiensis *was probably derived from SE Asian* H. erectus *via a transilience event and selection for endemic dwarfing.*

KEY WORDS: H. erectus – H. ergaster – H. floresiensis – Meganthropus – *Nariokotome – Sangiran – Ngandong – Zhoukoudian – Paleodemes – Multiregional continuity*

INTRODUCTION

In numerous papers over more than three decades Jan Jelínek articulated a model of human evolution grounded in the influential "New Synthesis" paradigm that integrated Darwinian perspectives with those of evolutionary population genetics, and based upon the Old World –wide anagenetic change of *Homo erectus* populations into *Homo sapiens s1.* (to include "archaic" *H. sapiens*, as well as anatomically modern humans). The transition occurred at varying times in different regions, resulting in morphological mosaicism within each region over time, and mosaic patterning between regions at any given time prior to the final Pleistocene. As applied to later hominid evolution and the appearance of modern humans, the model is, of course, also known as Multiregional Continuity or Multiregionalism.

One corollary of such a model is that *H. erectus* and *H. sapiens* are viewed as sequential chronospecies of a single lineage, or in some versions with the former taxon subsumed within the latter, since the interface between them, wherever drawn, is an arbitrary division of what is, in reality, a continuum. Thus:

"Many paleoanthropological materials show that there is direct continuity from the Middle-Pleistocene hominids to later *H. sapiens* finds and that these finds belong to one (albeit complicated) evolutionary line. The individual morphological characters change at different rates and to different degrees.

There is no good reason, anatomical or cultural, why we should separate Middle-Pleistocene and Upper-Pleistocene hominids into two separate species, namely into *Homo erectus* and *Homo sapiens*. There is only a fluent transition from the more archaic complex of traits in older finds to a more progressive morphology, with the main change in the degree of cerebralization bound up with social and cultural developments. The quantitative and qualitative characters of this transition enter into the mosaic pattern. Therefore, some populations in which some of the characters are less developed may even be contemporary with other populations in which some of the characters are more advanced. The consequences for the interpopulation contacts in such a situation are evident and make the evolutionary process of *Homo sapiens* even more complicated and fascinating." (Jelínek 1980a)

"… the value of *H. erectus* as a species is a problematic one. In such a case it is time to replace the paleontological species with a biological one ... . The changes typical for the Mid-Pleistocene situation are characteristic not only of this important evolutionary stage. The mosaic picture differing in degree, composition of characters and tempo of their changes is typical of the whole origin and evolution of *Homo sapiens* in Middle as well as Late Pleistocene periods and probably of the whole genus *Homo* in general." (Jelínek 1980b)

"… and the author, not recognising *Homo erectus* as a reasonable taxon ..., considers taxonomically the Azych individual as a regional type of *Homo sapiens erectus*." (Jelínek 1997).

Despite continuing powerful advocacy – most notably in the debate over modern human origins – the multiregional model is no longer the dominant paradigm, and alternative interpretations, some of them highly speciose, are also influential. I long held a view of human evolution similar to Jelínek's – compare, for example, Bilsborough (1978) with Jelínek (1978), and see Tobias' commentary thereon (Tobias 1978). However, more recently I have revised my view and now consider a different model of human evolution to be a more plausible interpretation of the evidence. Whilst incorporating markedly fewer species than some other interpretations, my current views accommodate more species (and so cladogenetic events and extinctions) than I had previously countenanced. And as a corollary my view of hominin species generally, and the dynamics and pattern of human evolution, have also changed. The changed perspective results in part from a reconsideration of evidence in the interim, and from greater awareness of alternative evolutionary mechanisms and processes, and their relevance for the interpretation of human evolution.

This conceptual shift provides part of the context for what follows; other, more significant influences are the much augmented pan-continental fossil record, new chronological and environmental frameworks, and the methods, findings and interpretations of other workers. These developments have inevitably led to a wider reconsideration and recasting of views on *H. erectus* as a hominin species. Below I consider some current issues surrounding *H. erectus*, focusing particularly on the following aspects:

- The relevance of recent discoveries for the composition and geographical, temporal and morphological limits of the *H. erectus* hypodigm.
- Whether the species as usually defined represents a phyletically meaningful entity, or an adaptive grade subsuming multiple hominin species.
- Whether there is evidence for significant geographical variability and/or distinct temporal trends within the material commonly assigned to *H. erectus.*
- The likely phyletic status of *H. erectus* and its relationships to other hominin species.

I also summarise a possible model of Pleistocene hominin evolutionary diversity as an alternative to that of multiregional anagenesis noted above.

Any assessment of these and other issues will clearly depend upon the nature of the material referred to the species. It is therefore pertinent to summarise the characteristics and distribution of *H. erectus* specimens, with a particular focus on discoveries over the last decade or so, before considering their implications for the above issues. The following summary is broadly geographically based with some additional temporal groupings. Howell (1996, 1999) has explicated the value for evolutionary studies of forming analytical or operational units by aggregating specimens into clusters based on morphology but bounded in space and time. Such clusters are samples of past local populations (demes), and so units of evolutionary change; they may individually (if isolates), or as aggregates, correspond to sub-species. From them it may be possible to identify more securely species clades, and to explore patterns of intra- and inter-population diversity and the dynamics of morphological change. For these reasons in what follows I consider some aspects of paleodemes (p-demes) within *H. erectus*, as well as aspects of the species overall, although the local groupings below do not necessarily correspond to the p-demes identified by Howell.

SUB-SAHARAN AFRICA

The oldest securely dated *H. erectus* fossils continue (just) to be those from the Turkana Basin, with the earliest example (*ca* 1.9 mya), the part occipital KNM-ER 2598. More complete material dating from 1.5–1.8 mya, includes the KNM-ER 3733 cranium and 3883 calvarium (1.78 mya and 1.6 mya), the KNM-ER 992 mandible (*ca* 1.5 mya)

(Leakey *et al.* 1978, Feibel *et al.* 1989, Wood 1991, 1992a, 1992b), and the KNM-WT 15000 skeleton (*ca* 1.53 mya) (Brown *et al.* 1985, Walker, Leakey 1993a, 1993b, Brown, McDougall 1993), with isolated postcrania (e.g. KNM-ER 1481 femur, KNM-ER 3228 hip bone). An important recent discovery is the KNM ER 42700 cranium from Ileret (Leakey *et al.* 2003, Gibbons 2003) – see below. All this points to a well-established presence in East Africa, and possibly also Southern Africa (e.g. SK 847) by *ca* 1.75 mya.

Later African *H. erectus* fossils include the large mandible from Konso-Gardula, Ethiopia (Asfaw *et al.* 1992) and the OH 9 calvarium from Upper Bed II Olduvai Gorge, Tanzania (Rightmire 1979, 1984, 1990, Schwartz, Tattersall 2003), both dating around 1.4 mya. Finds from Olduvai Bed IV (cranium OH 12, mandibles OH 22 and OH 51, a femoral shaft and part innominate OH 28) probably date ≥1.0 mya, with the OH 23 mandible fragment from the Masek Beds (0.7–1.0 mya?). Vault fragments, a part mandible and distal humerus from Gombore II, Garba III and IV localities at Melka Kunture, Ethiopia are of about the same age (Schwartz, Tattersall 2002).

Much more complete, and also dating around 1 mya, are the BOU-VP-2/66 cranium from the Dakanihylo or Daka member at Bouri, Middle Awash, Ethiopia (Asfaw *et al.* 2002), and the remains (cranium, two incisors, pelvic fragments) from Buia, Eritrea (Abbate *et al.* 1998). Both OH 9 and BOU-VP 2/66 are around 1,000 cm^3 internal capacity, but the Bouri specimen is shorter. It is largely complete, includes the base, and is only slightly distorted by skewing. The Buia cranium (UA 31) including vault and much of the left face but largely lacking the base, is relatively long and narrow, but of comparatively small capacity (750–800 cm^3). See Anton (2003) for a dissenting view on the affinities of the Bouri and Buia specimens. There is also a remarkably small part cranium (KNM-OL 45500) from Olorgesailie, Kenya, consisting of most of the frontal with supraorbital torus, squamous and mastoid parts of the left temporal and some vault fragments) and dated to 0.90–0.97 mya (Potts *et al.* 2004).

Possibly of comparable age to this East African material is the Swartkrans SK 15 mandible. The Sub-Saharan *H. erectus* record peters out sometime after 0.7–1.0 mya, with later material usually being referred to *H. rhodesiensis* or *H. heidelbergesis*.

Howell (1996, 1999) identifies an earlier Nariokotome p-deme, and a later, more derived, Olduvai/LLK-II p-deme based on much of the above material.

NORTH AFRICA

The North African record is more limited, with the oldest Tighenif or Ternifine (Algeria) specimens of basal Middle Pleistocene age (0.7–0.8 mya), and so no older than the youngest East African material. There are three mandibles differing markedly in size, a vault fragment (an immature parietal) and isolated teeth, usually referred to *H. erectus*. There are rather younger finds from adjacent Moroccan sites: a large mandible from the Littorina Cave, Sidi Abderrahman, and from the Thomas Quarries at Rabat a mandibular corpus (T1), and part maxilla and vault fragments (T2). Some authors – e.g. Howell (1978 – but cf. Howell 1999), Rightmire (1990) – also associate the cranium from Salé, Morocco with this material as *H. erectus*. However, while small (<900 cm^3) it differs from *H. erectus* in several respects, and is considered by others (e.g. Bräuer 1984) to represent "archaic *H. sapiens*" or equivalent. In any case, it appears affected by pathology (Hublin 1985, Schwartz, Tattersall 2002) making assignment particularly difficult.

Following some earlier, mainly French, workers, Jelínek (1978, 1980a,b,c, 1982a, 1982b, 1985) argued for linking the above finds with later (non – *H. erectus*) North African specimens, including Temara (mandible and vault pieces); Mugharet el Aliya (teeth and an immature, though robust, maxilla); Dar es Soltan (part adult skull, child's skull, immature mandible); Haua Fteah (two mandible fragments) and Djebel Ighoud I and II (cranium, calvarium) as an instance of regional continuity. Despite Jelínek's arguments, I am not aware of any features that specifically indicate continuity between earlier and later North African populations represented by this material. Indeed, Wolpoff in arguing for continuity links Djebel Ighoud with sub-Saharan Middle Pleistocene specimens such as Bodo, Kabwe and Ndutu rather than with the earlier North African material (Wolpoff 1999: 592) while Smith (Smith *et al.* 1989, Smith 1992, 1994) has drawn attention to similarities between North African and European and Levantine fossils in supraorbital and occipital traits. Morphometric similarities noted by Stringer (1979) between Djebel Ighoud and the pathological Singa cranium (then widely viewed as Holocene) and cited by Jelínek (1980b, 1980c) in the context of evidence for later continuity in the region, assume another significance with the redating of Singa to >133 kya (McDermott *et al.* 1996); rather than indicating continuity they suggest species identity, or at least close affinity.

WESTERN ASIA

Besides the fragmentary "Ubeidya remains (Tobias 1966, Belmaker *et al.* 2002) more extensive evidence of early *Homo* has been provided by the Dmanisi, Georgia, finds, associated with pebble tools and late Villafranchian fossils, from above the Masavera Basalt dated to 1.8±0.1 mya (Gabunia, Vekua 1995). The D211 mandible preserves most of the body and virtually intact lower dentition. Bräuer, Schultz (1996) show that its similarities are with *H. erectus*, most particularly with a later (i.e. Middle Pleistocene) sample of East African, Algerian and Chinese specimens. Further specimens include two more mandibles and three crania (Gabunia *et al.* 2000a, Vekua *et al.* 2002).

Two crania are clearly *erectus*-like: D2282 (estimated 650 cm^3 capacity) is distorted but largely complete, lacking only the medial orbital region, nasal bones, and the cranial base; D2280 (775 cm^3 capacity) is a well preserved and undistorted calvarium. In overall proportions both broadly resemble Turkana specimens ER 3733 and 3883. D2282 exhibits some sagittal keeling in the parietal region, while D2280 displays a larger occipital torus, stronger nuchal markings and a pronounced occipital crest. Both display marked postorbital narrowing, fairly thick cranial bones and an angular torus. The face of D2282 projects due to distortion, but again resembles East African *H. erectus* in its proportions, narrow nasal aperture and long palate. Upper cheek teeth also resemble those of Turkana *erectus,* with P^4 single-rooted and narrow crowned, and the first molars larger than the second – so matching the size pattern of the D211 mandible.

The D2700 sub-adult cranium (Vekua *et al.* 2002) is remarkably small; its capacity of 600 cm^3 is comparable to *H. habilis*, and well below that expected in *H. erectus*. Lee (2005) estimates the adult value to have been 618–645 cm^3, depending on remaining growth. The occipital is comparatively smooth and curved rather than strongly angled, with only the slightest indication of thickening in the region of the nuchal torus, and with a low, linear nuchal tubercle. The face and supraorbital torus are smaller than in KNM-ER 3733, recalling KNM-ER 1813 in overall proportions, although more heavily built than the latter specimen. There are similarities with *erectus:* a thickened zygomatic process; frontal keeling anterior to bregma and parietal keeling along the posterior portion of the sagittal suture; the temporal bone's horizontal upper border; well developed supramastoid crests; details of the articular fossa, tympanic and petrous regions; and the inwardly sloping vault walls with the low, arch-like coronal outline to the braincase characteristic of *H. erectus.* The associated D2735 mandible is similar to D211 in size, and also closely resembles the mandible of the KNM-WT 15000 skeleton. The upper canines and most upper and lower cheek teeth are preserved, with the M^3s partly erupted. Overall size suggests D2700/D2735 is female, but Vekua *et al.* are cautious to assign sex in view of the large canines.

A further mandible (D2600) has not been reported in such detail. It is much larger than the other two specimens, but with a long and relatively narrow dental arcade. The incisors are small but the canines large, with massive roots; the premolars are twin-rooted, and the large molars increase in size along the tooth row. The corpus is very deep, and shelving of the rear symphyseal face extends to below P_4. The corpus rear and much of the ramus are damaged, but the latter appears both high and broad, and the specimen looks to have articulated with a large cranium.

Most recently, Lordkipanidze *et al.* (2005) have briefly reported the recovery of a further cranium (D3444) and associated mandible (D3900) i.e. the skull of a second Dmanisi individual. The specimen is remarkable in being completely edentulous save for the left lower canine, and there is extensive resorption of upper and lower alveolar regions. The scale of this points to significant tooth loss well before death, with implications for reconstructions of dietary patterns, subsistence activities and social behaviour among the Dmanisi hominins. D3444 is intermediate between D2700 and D2280/D2282 in a number of its neurocranial dimensions, while exceeding them in parietal size. The specimens are comparable in orbital and nasal dimensions, although D3444 has a shallower malar region than D2700 or D2282 (Lordkipanidze *et al.* 2005).

The Dmanisi hominids have been assigned to *H. erectus* (Vekua *et al.* 2002) and also to *H. georgicus* (Gabunia *et al.* 2002), the latter (new) species based on the D2600 mandible. Despite some attempts to argue for multiple hominid species at Dmanisi on the basis of the specimens' variability (e.g. Schwartz 2000, 2004), the discoverers consider them to represent a single species on both morphological and taphonomic grounds (Gabunia *et al.* 2000b). Differences are size-related and likely to reflect intra-specific variation (e.g. sexual dimorphism) rather than interspecies differences, while the specimens' close proximity and condition indicate a primary site with little or no transport and rapid deposition. Lee (2005) considers the variation in cranial capacity to be consistent with a single species. The Dmanisi specimens are discussed further below.

SOUTH EAST ASIA

Recent developments have significantly altered perspectives on this, the largest regional *H. erectus* sample. An extended chronological framework for the Sangiran area sheds new light on *H. erectus* arrival in SE Asia, while important discoveries from later contexts afford new insights on the species' later evolution.

Sangiran Dome

A more secure time frame for Sangiran *H. erectus* strengthens the case for the species' comparatively early presence on Java. While Swisher *et al.*'s (1994) ^{40}Ar/^{39}Ar dates of 1.81±0.04 mya and 1.66±0.04 mya for the Modjokerto and some Sangiran finds remain problematic in view of contextual uncertainties (De Vos, Sondaar 1994, Swisher 1994), recent work by Larick *et al.* (2001) has clarified the sequence and age of the Kabuh/Bapang deposits in the Sangiran Dome (Itihara *et al.*1994), and so the bulk of the Javan *H. erectus* specimens. The deposits accumulated through five fluvial cycles, each with an earlier (a) facies of gravels, sands and "tuffs", with hominid and other fossils, followed by finer (b) facies overbank deposits of tuffaceous silts and sands, sometimes showing soil weathering. The widely recognised "Grenzbank" marker and the Lowest "Tuff" at Bapang represent the (a) facies, and the Lower "Tuff" the (b) facies of the first cycle (C1), ^{40}Ar/^{39}Ar dated to *ca* 1.5 mya. The second cycle, of which facies C2a contains several hominid specimens including the relatively complete S17 cranium, and C2b includes the Middle "Tuff," is dated by Larick *et al.* to around 1.25 mya. Cycles 3–5 include the Upper "Tuff" (C4b) and contain material from a single or several near-contemporary volcanic events at *ca* 1.0 mya. The paleomagnetic switch evident in the uppermost Puchangan probably represents the Olduvai rather than the Jaramillo event, whilst another R/N transition in the Middle Kabuh Formation previously thought to be the Matuyama – Brunhes boundary (0.78 mya) probably represents the onset of either the Jaramillo (1.05 mya) or Cobb Mountain (1.2 mya) subchrons.

The Kabuh/Bapang deposits with their hominid fossils and Trinil HK and Kedung Brubus faunas, are accordingly up to 0.5 my older than many workers previously thought. The majority of *erectus* fossils of known provenance, including S3, 10, 12, 17, "Skull IX", and possibly S2, are from mid – upper Kabuh beds (C2-C5), associated with the Kedung Brubus fauna, and probably 1.0–1.25 my in age. A few specimens are from towards the base of the Kabuh formation, and one or two, including the S4 cranium, some mandibular remains, and possibly also S2, derive from Grenzbank or uppermost Sangiran (Pucangan) levels. Most of these were found some time ago, but more recently a hominid occipital (Brn-1996.04) has been recovered from sediments near Bapang Village, about 10 m below C1a, and so >1.5 mya (Larick *et al.* 2001).

The Grenzbank and uppermost Pucangan finds are linked to Trinil HK faunas, as is the Trinil calotte itself (De Vos 1985, De Vos *et al.* 1994) suggesting that the *H. erectus* type specimen may also be more than *ca* 1.25 mya – considerably older than usually considered – although Anton and Swisher (2004) date it to 0.9 mya. While the new dating more securely extends the earliest Javan hominids back from 1.1–1.2 mya to 1.5–1.6 mya, it even more dramatically increases the age of the majority of specimens from mid-upper Kabuh levels. Far from being of mid-later Middle Pleistocene age, as widely thought hitherto, all the Kabuh specimens date from the Lower Pleistocene, so opening a significant temporal gap with the Notopuro Formation specimens (see below) and virtually all *H. erectus* fossils from continental East Asia.

Hyodo *et al.* (2002) have contested these early Kabuh/Bapang dates, claiming that they are incompatible with the paleomagnetic evidence. These authors argue that at Munggur the Brunhes/Matuyama boundary clearly underlies the Upper Tuff, dated by Larick *et al.* at >1.0 mya, whilst a tektite layer that predates the boundary by *ca* 12 ky, occurs 4–5 m below the Tuff at Pucung (see also Langbroek, Roebroeks 2000). Hyodo *et al.* consider that reworking of deposits may yield spuriously high ages, and argue that the oldest reliable dates for the Sangiran hominids are *ca* 1.1 mya. However, Anton, Swisher (2004) criticise Hyodo *et al.*'s arguments, pointing out that their paleomagnetic calibration relies crucially on the uncertain location of a single tektite and, as such, is insecure.

Recent fossil finds have also augmented the Sangiran sample. They include a largely complete, thin-walled and moderately buttressed braincase resembling S2, and two maxillary fragments with most of the right upper dentition and isolated left M^1 and M^3 from unit C2a at Grogal Wetan. A more strongly constructed braincase with marked postorbital constriction, a distinct supratoral sulcus and developed angular torus is also from C2a deposits at Bukuran (Grimaud-Hervé *et al.* 2000), while a neurocranium and maxilla are thought to derive from similar levels at Tanjung (Larick *et al.* 2001, Arif *et al.* 2002, contra Tyler, Sartono 2001) as do a calotte and incisor from Sendangbusik. With its distinctive proportions the Tanjung calvarium extends the range of *H. erectus* cranial variability – it is comparable to S17 in length, but resembles the smaller S2 and T2 in its narrower breadth especially anteriorly, and is comparatively high with a steeper frontal than other Javan crania (Tyler, Sartono 2001, Arif *et al.* 2002). From Hanoman, near Bukuran, a fragmented calvarium with narrow frontal, relatively high, weakly keeled parietal region, and evenly curved occipital resembles the Sambungmacan and Ngandong finds rather than other Sangiran finds (Windianto *et al.* 1994). Despite this, it is inferred to come from the uppermost Puchangan beds, implying an age of around 1.5 mya, although stratigraphic uncertainties indicate need for caution. Also resembling Sambungmacan and Ngandong crania, and also of indeterminate age, is the cranium from Ngawi, near Trinil.

Sambungmacan

The three Sambungmacan crania (Sm1, 3, 4) are broadly similar morphologically but from different sites and uncertain contexts – although Sm4 at least appears to be from Kabuh deposits (Baba *et al.* 2003). The calvaria are larger (917 cm^3, 1006 cm^3, 1035 cm^3), higher vaulted and more globular than many Sangiran specimens: keeling and cranial tori are less developed and instead of a defined angular torus there is more diffuse parietal thickening in the asterionic area. The nuchal area is flat, with the occipital torus' inferior margin sharply defined; the mastoid and supramastoid crests are separated by a supramastoid sulcus, and the foramen magnum narrows posteriorly (Marquez *et al.* 2001, Broadfield *et al.* 2001). In many respects the Sambungmacan specimens are similar to the Ngandong fossils, which show comparable or more developed expressions of these characters.

Morphometric comparisons (Delson *et al.* 2001, Anton *et al.* 2002, Baba *et al.* 2003) also place the Sambungmacan specimens intermediate between the Trinil/Sangiran fossils and the Ngandong crania, while Kidder, Durband's (2004) multivariate study, which reveals a complex patterning of affinities between the Sambungmacan, Sangiran and Ngandong fossils, also accords with this interpretation. For example, in both 3 and 5 variable analyses of vault dimensions, Sm1 centres within the Ngandong cluster (with S17 also adjacent) whilst Sm3, although still associating with the Ngandong sample, is rather more of an outlier, reflecting its smaller size (Anton *et al.* 2002).

Ngandong
The larger endocranial capacities (*ca* 1,000–1,250 cm^3) of the Ngandong calvaria (Weidenreich 1951, Santa Luca 1980) compared with most Sangiran specimens are reflected in higher, more vertical frontals and laterally expanded vaults. They are usually regarded as derived *H. erectus* (*H. erectus soloensis*) or occasionally a primitive sub-species of *Homo sapiens (H. sapiens soloensis*) (see below). Dating is problematic, with ages ranging from 130+ kya down to 27–53 kya (Swisher *et al.* 1996a, 1996b, Grun, Thorne 1997, Swisher *et al*. 1997). Storm *et al*. (2005) argue for an earlier Ngandong date on the basis of its archaic fauna which predates the modern tropical rainforest Punung fauna, which they estimate reached Java during the low sea levels 90–120 kya (stadials 5b–5d), so that Ngandong must be > 126 kya, and the absolute dates in error. This argument depends crucially on the date of entry of the Punung fauna and requires further verification, but even if correct does not preclude a final Middle/basal Upper Pleistocene age. In any event, the Ngandong fossils are substantially younger than Kabuh bed specimens, including those from Sambungmacan, if Sm1-3 are of comparable age to Sm4. Notwithstanding this age differential, Howell (1996, 1999) links the Ngandong, Sambungmacan and Ngawi specimens into a single p-deme.

CONTINENTAL ASIA

While the early Javan dates have clear implications for the presence of *H. erectus* in adjacent regions of the Asian mainland, direct evidence is lacking; all known specimens are from sites further north and of later date. Excluding the doubtfully hominid and insecurely dated Longgupo material (Wanpo *et al*. 1995, Schwartz, Tattersall 1996, Wolpoff 1999, Wang, Tobias 2000), the earliest evidence for hominin presence in continental Asia are pebble tools and flakes from sites in the northerly Nihewan basin, dated to *ca* 1.36 mya (Schick *et al.* 1991, Zhu *et al.* 2001). The oldest fossil specimen, of comparable age to the latest Bapang specimens, is the Gongwangling (Lantian) L2 skull cap, dated to *ca* 1.1 mya. The remainder are of Middle Pleistocene age, with the largest and best known sample that from Locality 1, Zhoukoudian (ZKD) and generally considered to span from around 0.58 mya to about 0.26 mya (i.e. mid-later Middle Pleistocene) on the basis of U series, TL and ESR methods (Liu 1985, Grun *et al.* 1997, Goldberg *et al*. 2001). Dating of speleothems by U-series thermal ionisation mass spectroscopy gives older ages by 0.2–0.3 my, suggesting an age (on constant sedimentation rate) of up to 0.8 mya or more for the earliest finds from the site (Shen, Wang 2000), although the later dates as above continue to be the most widely accepted. In any event, all dating methods indicate the ZKD fossils to postdate the Kabuh/Bapang material.

The bulk of the ZKD hominids span around 0.15 my, with a mean age of about 0.45 mya, and with the latest specimens possibly *ca* 0.275–0.3 mya. Other Chinese fossils assigned to the same p-deme by Howell (1996, 1999) include Hexian (Longtandong), Anhui (0.3–0.4 mya) and Tangshan (Nanjing), Jiangsu. Initially thought to be of similar age, Tangshan has been re-dated by U-series to >0.5 mya (Liu *et al*. 2005), approaching in age the mandible from Chenjiawo (Lantian), which is perhaps 0.6 mya, so that between them these fossils span most the interval represented at ZKD.

Specimens from this site have traditionally been taken to exemplify cranial form in East Asian *H. erectus* (Anton 2002) and, indeed, more generally. The low, relatively long vault is distinctive in its narrow frontal, broad mid-region, and tapering occipital breadth (Kidder, Durband 2004). Mid-sagittal, occipital and angular tori are all distinct, with the last especially well developed. By contrast, the mastoids are small, with confluent mastoid and supramastoid crests, so lacking a supramastoid sulcus. The straight, moderately-sized occipital torus merges laterally with the angular tori; between it is delineated from the occipital squama by a supratoral sulcus, but inferiorly there is no external occipital protuberance or tubercle. The continuous supraorbital torus, well defined by a distinct supratoral sulcus, is straight/slightly curved in frontal view, and straight viewed superiorly; given the medial frontal squama's anterior projection, the torus is sagittally thinner medially than laterally. As reconstructed the face is moderately projecting; the infraorbital region is lightly built, flat or concave with a distinct malar notch, in contrast to the robust, sloping infraorbital region of S 17, with its thick, horizontal inferior border.

The more southerly (*contra* Anton 2002) Tangshan specimen has a relatively small cranial capacity (860 cm^3) reflected in a short but broad neurocranium – proportions reminiscent of early African specimens – and a face with distinctively salient, high set and narrow nasal bones (Liu *et al*. 2005). Judging from illustrations, the angular tori, whilst evident, are less pronounced than in the ZKD crania, and the specimen shows less occipital tapering than those fossils. Nonetheless, Tangshan groups with ZKD in morphometric analyses (Anton 2002, Liu *et al.* 2005).

At a comparable latitude to Tangshan but further west across the Yangtse River, the Hexian cranium (PA 830) differs in cranial form in several respects: the vault is broad, especially in its mid-portion, although it is also laterally expanded anteriorly, with minimal postorbital constriction. The occipital bone bulges medially, and the nuchal plane is extensive, being wider and longer than the occipital squama. The nuchal torus, while well-delineated centrally, tapers laterally, and the angular tori are not well developed. It also differentiates morphometrically from the ZKD/Nanjing cluster (Anton 2002, 2003), a finding confirmed by Kidder, Durband (2004) and Liu *et al.* (2005). Whether these differences represent polytypic or individual variability awaits more complete material; a second, more lightly built Hexian cranium (PA 840/41) is too fragmented to be informative.

EUROPE

Whilst Jelínek considered that fossils such as Vertessöllös, Arago, Petralona, Mauer and Bilzingsleben represent *H. erectus* and argued for continuity with later European populations (Jelínek 1978, 1980a, b, c, 1982a, b, 1985), many other workers judge that there is no convincing evidence for the species in Europe. The Atapuerca (Gran Dolina) material – the earliest securely dated fossils – proposed as *H. antecessor* (Carbonell *et al.* 1995, Arsuaga *et al.* 1999, Bermudez de Castro *et al.* 1999) – date from around 0.8 mya and differ from *H. erectus* as known from Africa and Asia in crucial respects. The morphologically contrasting calvaria from Ceprano, Italy, is of uncertain date within the span late Lower – basal Middle Pleistocene but may pre-date Gran Dolina at *ca* 0.9 mya (Ascenzi *et al.* 2000).

Irrespective of date, Ceprano is the most "*erectus*-like" of European specimens and has been ascribed to that species by Ascenzi *et al.* (1996, 2000) and Clarke (2000), although in doing so Clarke stresses its affinities with OH 9, which he has previously (Clarke 1994) assigned to *H. leakeyi*. However, Ceprano contrasts with typical *erectus* fossils in its breadth, expanded coronal profile with near vertical lower parietals, broad frontal with limited postorbital constriction, high, curved temporals, supraorbital form, absence of cranial keeling, and lack of continuity of the occipital torus with the angular torus and supramastoid crest. Ascenzi *et al.* (2000) note that its inclusion within *erectus* requires the hypodigm's range of variation to be enlarged. Ceprano has also been proposed as the type of a new species, *H. cepranensis* (Mallegni *et al.* 2003) although this has not received wide support. In addition, Schwartz, Tattersall (2003) draw attention to supraorbital similarities with later European fossils such as Arago and Petralona, usually regarded as *H. heidelbergensis,* and there is a need for detailed comparisons with this material. Other European fossils (Mauer, Vertessollos, Arago, Bilzingsleben, Reilingen) are considerably younger, depart from *erectus* morphology in important respects, or are too incomplete for firm assignment. Accordingly, the European material is not considered further here.

HOMO ERECTUS: ONE SPECIES OR SEVERAL?

Reflecting differential preservation as well as morphology, *H. erectus* has usually been characterised in terms of its cranial, especially neurocranial, features (form, vault thickness, endocranial capacity, etc). Weidenreich (1936, 1943), Le Gros Clark (1964) Howell (1978) and Rightmire (1990) among others provide useful descriptions and summaries of diagnostic traits. Consideration of individual calvarial dimensions (Bräuer 1994), Bilsborough (2000b, and below) shows that regional and chronological subgroups of the species generally resemble each other closely in neurocranial proportions: rear vault dimensions are essentially constant, and while there are some differences in the anterior and mid-vault, these are slight given the samples' temporal and spatial spread. Moreover, the specimens' cranial variability assessed against other hominid comparators provides no grounds to reject the unity of *H. erectus* (Kramer 1993).

Nonetheless, it was perhaps inevitable that the specific integrity of such widely ranged specimens should be questioned, and the alternative view proposed that they represent several "*erectus*-like" species, better viewed as an adaptive grade rather than an evolutionary entity. Most debate has centred around the possible distinctiveness of the early East African specimens from other *H. erectus*, but has certainly not been confined thereto: claims, albeit less widely held, persist for additional hominin taxa in Java, while the Dmanisi finds have also led to suggestions of other species there. It is therefore worth examining these claims in some detail.

Homo ergaster and multiple African species

Many workers have followed Wood in concluding that the larger-brained Turkana crania represent an "*erectus*-like" but distinct, more primitive and phyletically more central species, *H. ergaster*. Groves, Mazak (1975) had proposed this taxon for the KNM-ER 992 mandible (see also Groves 1989), which they associated with smaller crania such as KNM-ER 1813 (usually viewed as *H. habilis*) rather than the ER 3733 and 3883 specimens with which Wood (1992a, 1992b) linked it. Whereas Groves and Mazak's concept of *H. ergaster* gained scant, if any acceptance, Wood's interpretation has received considerable support, with *H. ergaster* well embedded in the literature.

Advocacy for separating the early East African and Asian fossils goes back more than two decades: Wood (1984) and Andrews (1984) argued for *H. erectus* as an exclusively Asiatic taxon based on autapomorphies not present in the African "*erectus*-like" fossils or in *H. sapiens* (see also Stringer 1984). The Asian traits identified by Wood are: occipital torus with sulcus above; angular torus and mastoid crest; supratoral sulcus on frontal; proportions and shape of occipital bone, and a relatively large occipital arc. Andrews identified as (Asian) *H. erectus* autapomorphies: frontal and parietal mid-sagittal keels; thick vault bones; an angular torus; widely separated inion and endinion; a deep fissure separating the mastoid process from the petrosal crest of the tympanic plate; a deep recess between the tympanic plate and the entoglenoid. All these traits are, in fact, variably present in early African and Asian specimens: for example, KNM ER 3733 possesses both a supratoral sulcus (Wood) and frontal keel (Andrews) while Trinil 2 lacks both features. Additionally, several cited autapomorphies are interdependent traits: frontal and parietal keels and an angular torus are all parts of the skull reinforcement system and so elements of a single functional unit (Bilsborough 1992).

Wood subsequently (1991, 1992a, 1992b) expanded and formalised the case for separating the Koobi Fora sample

(KNM-ER 3733, 3883, 730, 820, 992) from *H. erectus* as *H. ergaster.* In addition to the above list he cited primitive traits of the mandible and dentition (crown and root morphology) in the African fossils together with features of the vault, face, mandible and dentition that are shared with *H. sapiens*. Clarke (1990, 1994) provided similar arguments but assigned the early African specimens to *H. leakeyi*. The case for *ergaster* has been accepted by some workers (e.g. Howell 1994, Tattersall 1995, Foley 1995, Klein 1999), but rejected by others: Rightmire (1990), Leakey, Walker (1989), Turner, Chamberlain (1989), Tobias (1991), Bilsborough (1992), Walker, Leakey (1993a) and Harrison (1993) all argued for the inclusion of the Turkana fossils within *H. erectus*.

Most tellingly, Bräuer, Mbau (1992) considered in detail the distribution of the above traits in *H. erectus* and other hominid taxa, showing them to be variably present in *both* groups of specimens, and failing to differentiate African *ergaster* from Asian *erectus*. They also demonstrated that the features are widely distributed among archaic *H. sapiens*, early *Homo* and even *A. africanus*, and so far from being autapomorphies of *erectus* (or anything else) are best thought of as plesiomorphies. Bräuer and Mbau also noted problems of definition and measurement, probable functional redundancy and, in some cases (e.g. entoglenoid/tympanic recess), differential bilateral character expression on a single cranium. Unsurprisingly, they concluded that the claimed *H. erectus* autapomorphies cannot be considered as such.

Analysis of the Bouri (Daka) specimen also militates against early species differentiation of African and Asian *H. erectus*. In a cladistic analysis of *erectus* paleodemes based on 22 cranial traits (Asfaw *et al.* 2002), the Olduvai LLK deme (OH 9, Daka, Buia) consistently grouped with the Ngandong sample, while earlier African *erectus* fossils (the Nariokotome deme) grouped with the Trinil/Sangiran specimens, with Dmanisi as the sister to this pair. There was no support for an early separation of African and Asian clades as implied by the *H. ergaster/H. erectus* distinction and the analysis instead divided on chronology (early African and Asian groups split from later ones). Manzi *et al.* (2003) criticised the analysis, but their arguments were refuted by Gilbert *et al*. (2003). Moreover, Manzi *et al.*'s analysis shows OH 9 to have closer affinities with Asian specimens (especially ZKD) than with other African crania, and they agree with Asfaw *et al.* in interpreting the results as evidence of broad anagenetic continuity from the earliest African *erectus* down to at least Daka/Buia times.

Given the insecure case for *H. ergaster* as a distinct species, its persistence in the literature seems more to reflect differing views on the nature and pattern of the evolutionary process and the basis for palaeospecies recognition (e.g. Tattersall 1986, 1992, Kimbel, Martin 1993) than the strength of the morphological case for distinguishing the early African specimens from other *H. erectus* fossils. This applies even more strongly to schemes advocating yet greater fragmentation of the African material: Schwartz, Tattersall (2003) and Schwartz (2004) doubt OH 9 is *H. erectus,* and argue that diversity *within* the Turkana *erectus* material indicates interspecies differences (Schwartz 2000, Schwartz, Tattersall 2000, 2003, Tattersall, Schwartz 2001). For example, contrasts in mandibular tooth crown proportions and morphology between KNM-ER 992 and WT 15000 (canine height and breadth, premolar cusp sizes and topography, (pre)molar shape and molar crown shape, talonid basin depth and cusp development and location) in their view preclude assignment of these specimens to the same taxon, as do cranial contrasts between ER 3733 and ER 3883 (supraorbital torus form and projection, frontal development, nasal orientation, zygomatic proportions and mastoid development), with the latter instead linked with the less complete KNM-ER 3732, usually assigned to *H. rudolfensis.* They also emphasise contrasts in the above features between the KNM-ER 3733 and 3883 morphologies and that of KNM-WT 15000, with its longer, narrower face, flatter nasal region with narrower aperture, and more marked alveolar prognathism, thinner supraorbital torus and, in profile, shorter, more rounded neurocranium with retreating frontal, flattened parietal region and only modest angulation of the occipital, lacking a developed nuchal torus, and with small mastoids.

Many of these differences have been assumed to reflect WT 15000's immaturity compared with adult Koobi Fora crania, but Schwartz and Tattersall argue that further growth in the former would have accentuated the contrasts, not reduced them. In these respects – and in others such as palatal shape and maxillary premolar/molar morphology – KNM-WT 15000 does, however, display similarities with ER 1813 (widely regarded as *H. habilis*) and with the broadly contemporary Dmanisi cranium D 2700 (see below). The discovery of KNM-ER 42700, a small-brained calvarium from Ileret, referred to *H. erectus* and dated to *ca* 1.55 mya (Leakey *et al*. 2003, Gibbons 2003) further reinforces resemblances between the Turkana and Georgian samples, and adds to the Kenyan material's diversity. Some implications of this are discussed below, but it may be noted that the cranial differences in the Turkana material cited by Schwartz and Tattersall appear consistent with individual variability and sexual dimorphism (as seen, for example, in the Sangiran sample) or, in some comparisons involving WT 15000 ontogenetic factors, and do not require additional species to be posited.

Multiple species on Java

Some accounts of the SE Asian fossils have been characterised by excessive taxonomic splitting, an approach justifiably criticised by Jelínek (e.g. Jelínek 1978, 1980b, 1982a). Semantic considerations of this kind apart, most discussion has centred around the "*Meganthropus*" fossils as evidence for species other than *H. erectus* on Java. These include the fragmentary and/or distorted robust mandibles S5 (right corpus fragment with M_1 and M_2) and S9 (a right corpus with most teeth), both subsequently referred to *Pithecanthropus dubius*; S 6a (with left P_3, P_4 and M_1); S 6b

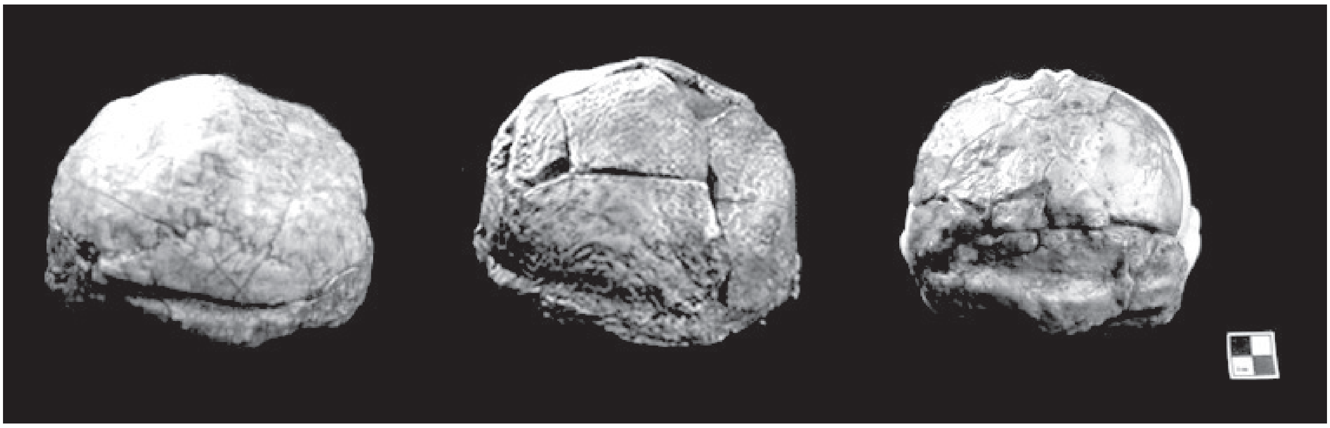


FIGURE 1. Rear views of Sangiran Dome (Java) specimens from the Sangiran (Pucangan) and Bapang (Kabuh) Formations. Left: S 4; centre S 17; right: S 31 (casts).

(with left M_2 and M_3 and damaged M_1 roots) and S8 (with mainly broken right tooth crowns) (Weidenreich 1945, von Koenigswald 1968, Franzen 1985, Grine, Franzen 1994, Kaifu *et al.* 2005a, 2005b). Two partial crania (S27 and S31) have also been associated with these mandibles on the basis of size and robusticity. S27, preserving the face and palate with most cheek teeth, the temporals and part of the cranial base, is broken into four pieces and much crushed and distorted (Jacob 1980, Schwartz, Tattersall 2003), but with resemblances in its strongly built zygoma, prominent canine juga, curving supraorbital torus and well developed mastoids to S17. Sangiran 31 consists of the rear of a massively constructed cranial vault (most of the left and the rear portion of the right parietal together with the occipital), vertically crushed, fragmented and weathered, with a marked nuchal torus, especially mesially. While more strongly developed than other specimens, S31's occipital morphology resembles that of S4 and S17 (*Figure 1*).

Besides *H. erectus,* this material has been variously attributed over the years to *A. africanus*, *P. robustus*, *H. habilis* and *H. rudolfensis* as well as to unnamed species – a range pointing strongly to its indeterminate nature. In an influential paper, Tobias and von Koenigswald (1964) suggested that it might represent Javan *H. habilis* or a similar species on the basis of similarities between the OH 7 and S6 mandibles, although Tobias subsequently revised his view, considering the similarities to have been overdrawn (Tobias 1991 p. 37, and see pp. 512–513). Franzen (1985) argued for *P. dubius'* australopithecine affinities, and Tyler (1994) concluded that S5, S6 and S8 are best considered as *A. africanus* (within which he incorporates *H. habilis*). Tattersall, Schwartz (2001) suggest these fossils may represent species other than *H. erectus,* and also opine (Schwartz, Tattersall 2003) that many reported isolated teeth from Sangiran and some of the above jaw fragments may not be hominid at all.

Howell has long argued the distinctiveness of this material from *H. erectus* (see, for example, Howell 1960, 1967, 1978), latterly (Howell 1994) stressing its affinities with *H. habilis* and *H. rudolfensis,* and most recently designating two paleodemes on its basis (Howell 1996, 1999). The Glagahomba/Sangiran p-deme includes strongly-built part mandibles S5, S6a, 6b ("*Meganthropus* A") and S8 ("*Meganthropus* B"), and the S27 and S31 partial crania. Another, separate, p-deme cluster, is designated Brangkal/Sangiran by Howell (1996, 1999), and is primarily based upon the S4 partial calvarium and palate *("Pithecanthropus robustus")*, possibly together with maxilla fragment S1a, and right mandible bodies with teeth S1b and S9 (the second "*P. dubius*" mandible). The Modjokerto (Perning) infant calvarium *("H. modjokertensis")* may also belong to this group, which is generally smaller and less robust than the Glagahomba cluster.

Both groups are viewed by Howell as distinct from the Trinil/Sangiran *H. erectus* p-deme represented by the overwhelming majority of Sangiran hominid fossils, as well as the Trinil specimens. Howell's allocation separates the two specimens (S5 and S9) assigned by von Koenigswald and Franzen to *P. dubius,* grouping S9 instead with S1b (widely regarded as *H. erectus)*, and which is generally distinguished from most of the above Sangiran mandibles by its lighter build (see Schwartz, Tattersall 2003).

Although the "*Meganthropus*" mandibles are relatively large, their postcanine teeth are generally smaller than those of australopithecines, and resemblances between some East African *Homo* jaws and the Javanese specimens in features such as stout corpora, straight, convergent postcanine tooth rows, moderately large molar crowns and dual-rooted P_3 do not of themselves demonstrate the existence of *H. habilis* or *H. rudolfensis* in Java. Early *Homo* species overlap in jaw and dental traits so that specific assignment of fragmentary specimens is difficult, as the varying attributions for these Sangiran fossils indicate. Moreover, such resemblances do not extend to the neurocranial evidence. Among the Indonesian calvaria there are no indications of the characteristically small, thin vaulted, globular braincase of *H. habilis* or the larger, transversely bell-shaped contour of *H. rudolfensis*; all the Javanese neurocrania (including S31) are ruggedly constructed and typically *erectus* in their proportions. Given this state of affairs, the gnathic

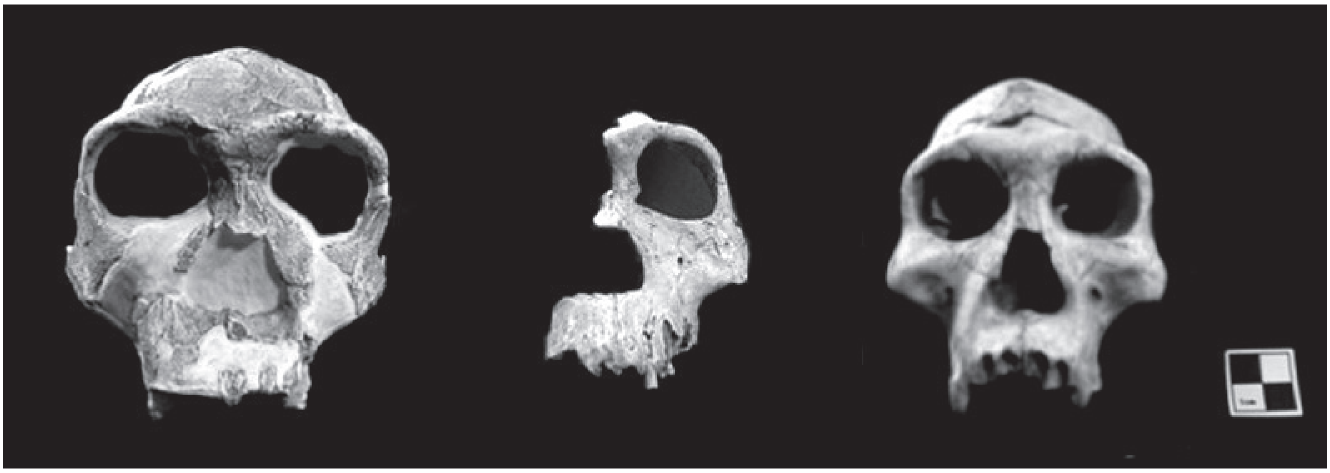


FIGURE 2a. Comparison of hominin crania (frontal view). Left: KNM-ER 3733; centre: SK 847; right D2700 (casts).

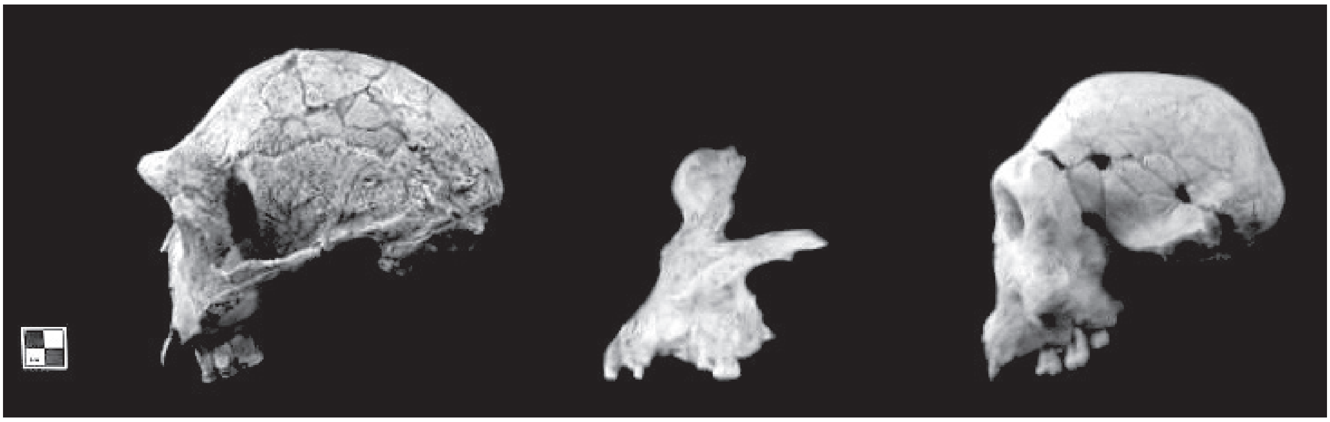


FIGURE 2b. Comparison of hominin crania (side view). Left: KNM-ER 3733; centre: SK 847; right D2700 (casts).

and dental similarities may simply be plesiomorphies; it is also possible that some of the East African mandibles assigned to *H. habilis* or *H. rudolfensis* in fact belong to *H. erectus* (see below).

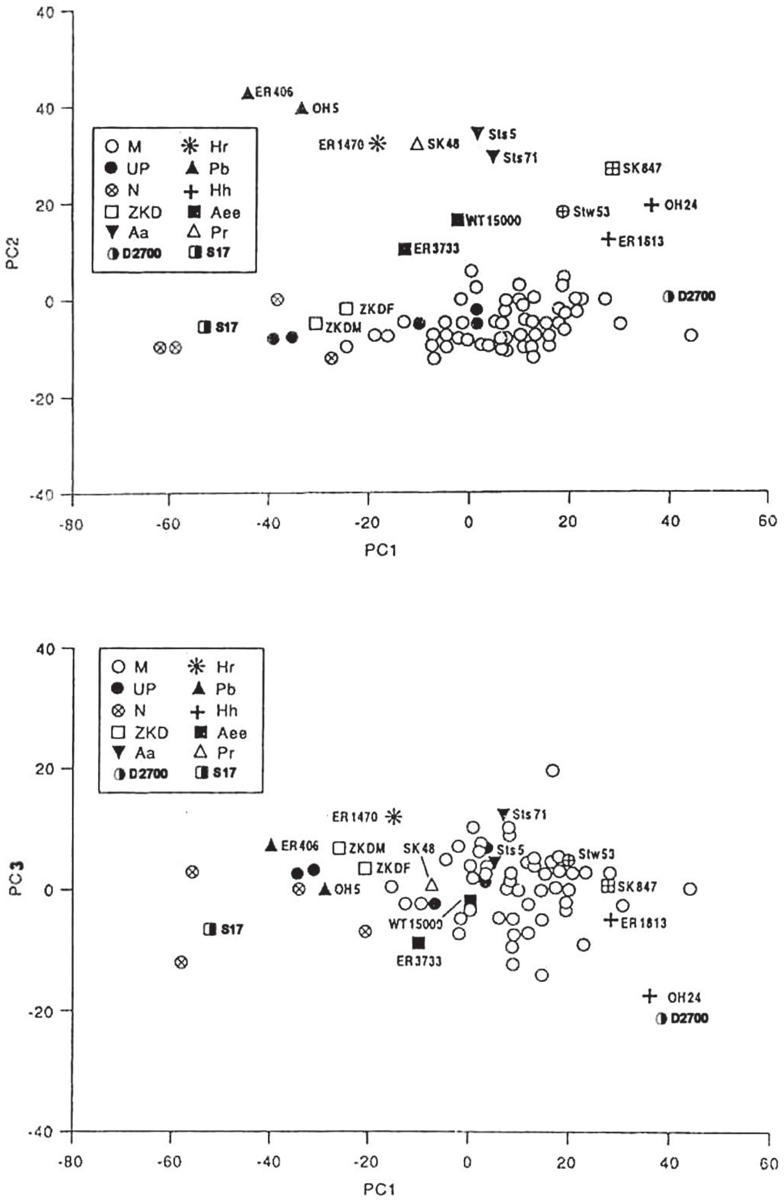
On a splitter's view of the material we are faced with two (or more) species – one (*H. erectus*) represented predominantly by crania, the other(s) predominantly by mandibles. Given this distribution it seems most parsimonious to incorporate all the material within *H. erectus*, with the "*Meganthropus/P. dubius*" specimens representing gnathically larger/more robust individuals (males?) of which 6A would admittedly represent the limit, and smaller "*erectus*" specimens (e.g. the 1B and S22 mandibles) females. This conclusion is reinforced by the variability of the Ternifine and Dmanisi fossils, which indicate significant mandibular size variation in *H. erectus* populations.

Accordingly there seems little or no reason to conclude in favour of a second hominid species on Java and most workers, for example Le Gros Clark (1964), Campbell (1965), Lovejoy (1970), Rightmire (1990), and Wolpoff (1999) assign the *"Meganthropus"* material to *H. erectus*. Kramer, in particular, has used both phenetic (morphometric) approaches (Kramer, Konigsberg 1994) and cladistic analysis (Kramer 1994) to explore the specimens' affinities, demonstrating that the gnathic material resembles *Homo,* not *Australopithecus* or *Paranthropus,* in dental and jaw size and shape, and that within *Homo* links are with *erectus* and later species, rather than with the early African forms. Kramer also concludes that the "temporal crests" on S31, cited by some in support of its distinctiveness from *H. erectus*, are taphonomic artefacts.

Further support for this view is provided by the most recent and comprehensive study of the mandibular and dental material (Kaifu *et al.*2005a, 2005b). Whilst emphasising contrasts between the Sangiran Formation and Grenzbank specimens and the later Sangiran fossils from the Bapang Formation above the Grenzbank zone, these workers conclude that the former material is derived compared to early African *Homo,* but as primitive or slightly more so than East African early *H. erectus* and can be considered a primitive group of that species.

Nor is there any compelling reason for distinguishing between other closely related "*H. erectus*-like" species from the Puchangan and Kabuh beds respectively. Given the small number of specimens definitely known from the former, the limited contrasts between the two samples are plausibly attributed to individual variability. For example,

FIGURE 3. Principal Components Analysis: Face. Plots of hominin specimens on PCs 1 & 2 (3A) and 1 and 3 (3B). Abbreviations: M = Modern *H. sapiens*; UP = Upper Paleolithic *H. sapiens*; N = Neanderthals; ZKD = Zhoukoudian *H. erectus*; Aa = *A. africanus*; Hr = *H. rudolfensis*; Pb = *P. boisei*; Hh = *H. habilis*; Aee = African early *H. erectus*; Pr = *P. robustus*; S17 = Sangiran 17; D2700 = Dmanisi 2700.



Weidenreich's original distinction between *P. robustus* and *P. erectus,* based primarily on robusticity, has been eroded with the recovery of more material – Sangiran 17, from well up in the Kabuh beds, is as robust and strongly constructed as some of the earlier specimens, while the S22 mandible, from the uppermost part of the Sangiran Formation below the Grenzbank, is gracile and slender (Kaifu *et al.* 2005a, 2005b).

ORIGIN OF *H. ERECTUS*

The early Dmanisi, Sangiran and especially Turkana basin *erectus* fossils point to an origin by *ca* 2.0 mya. The earliest evidence for a possible *Homo* ancestor is the AL 666-1a palate from Hadar, Ethiopia (Kimbel *et al.* 1996), the Chemeron (Baringo) temporal (Sherwood *et al.* 2002), and the Lokalalei right M_1 (Prat *et al.* 2005), all dated 2.3–2.4 mya. There is also the UR 501 mandible from Malawi, assigned to *H. rudolfensis* and estimated to be of comparable age (Bromage *et al.* 1995). Detailed analysis of AL 666-1a (Kimbel *et al.* 1997) shows closest affinities to *H. habilis*, and then to *H. erectus*, although most similarities are inferred to be *Homo* plesiomorphies. Only slightly older is the Bouri (Ethiopia) cranial material referred to *Australopithecus gahri*, and lacking synapomorphies that would exclude it from *Homo* ancestry (Asfaw *et al.* 1999).

At Turkana, and possibly other African localities, early *H. erectus* is associated with smaller crania usually referred to *H. habilis.* There are undoubted similarities between the specimens in dental, palatal and mandibular features, and in mid- and lower facial proportions, with differences in the cheek and upper face, in neurocranial size and proportions, and in vault thickness. Most of these reflect differences in brain size, which may in turn be associated with contrasts in body size, as may cranial thickness. Differences in upper facial breadth and supraorbital torus proportions reflect the laterally expanded anterior neurocranium of larger specimens such as ER 3733 and ER 3883 compared with, for example, ER 1813, while differences in the positioning and orientation of the zygomatic processes indicate a shift away from emphasis on the anterior masseter fibres towards temporalis, as the area available for the muscle's origin increases on the vertically and laterally expanded neurocranial wall. However, the small-brained Dmanisi D2700 and Ileret ER 42700 raise the possibility that our identification and delineation of *H. habilis* and *H. erectus* may be at least partly awry. See Blumenschine *et al*. (2003) for a discussion of comparable difficulties in delineating *H. rudolfensis* from *H. habilis* on gnathic and dental evidence.

D2700 resembles *H. erectus* in numerous respects (Vekua *et al*. 2002) suggesting that facial and masticatory features of *H. erectus* may be associated with smaller neurocrania than those hitherto considered typical of the species, especially if early populations showed greater body size dimorphism than later ones. Besides Dmanisi, KNM-ER 42700 (which lacks the face) may also document this phase in the Turkana Basin (Leakey *et al.* 2003), with SK 847 possibly a third example from South Africa. I have previously argued (Bilsborough 2000a) that SK 847 represents a closely related, possibly antecedent species to *H. erectus*, resembling the latter in mid-lower facial proportions but contrasting in the upper face and with a small (sub-*erectus*) braincase (see also Thackeray, Monteith 1997). However, D2700 and ER 42700 are small-brained finds from contexts also yielding "typical" *erectus* individuals, and as such, extend the morphological range of early populations of the species. It is therefore possible that SK 847 is indeed *H. erectus*, as Clarke (1977, 1985) and Walker (1981) have long argued (but see Clarke 1990, 1994, and below, and see Grine *et al.* 1993, 1996 for an alternative interpretation of its affinities). It is also possible that some other specimens customarily assigned to *H. habilis* (e.g. KNM-ER 1805) are, in fact, more appropriately considered early *H. erectus* (see, for example, Howell 1978).

KNM-ER 3733 and later *Homo* are differentiated from Pliocene hominids and other early *Homo* by a set of facial proportions including reduced overall prognathism, flatter mid-face, salient nasal bones, shallow, inferiorly retreating malar region, lateral rather than medial development of the supraorbital torus and a broad upper face relative to the mid-face (Bilsborough, Wood 1988). Photographs and a cast suggest that D2700 conforms to many, if not all of these characteristics, a view reinforced by morphometric analysis. PCA of hominid facial morphology (Bilsborough 2000a) derives PC I (54% variance) as an overall size vector, with median prognathism and upper facial breadth strongly influential. Large-faced hominids with prognathous and/or anteriorly positioned faces such as Neanderthals and large *A. boisei* specimens are at one end of the array, smaller faced forms (modern humans and *H. habilis*) at the other. *H. erectus* specimens are themselves spread along this axis, with S17 closest to Neanderthals, early African representatives overlapping with some *H. sapiens* crania in the centre of the array, and with ZKD female (Weidenreich 1937) and male (Tattersall, Sawyer 1996) reconstructions between them. On this size-driven axis the D2700 cast is predictably well separated from the *erectus* fossils, associating instead with early *Homo* specimens (Stw 53, ER 1813, SK 847, and closest to OH 24).

However, PC II (22% variance) sorting on contrasts in facial proportions instead of overall size, with mid-face breadth and lateral projection together with lower face depth and prognathism heavily weighted, effectively differentiates *Australopithecus* and basal Pleistocene *Homo* from Middle Pleistocene and later *Homo,* including *H. erectus*. Early African *H. erectus* fossils bridge what would otherwise be discrete clusters, with WT 15000 (which had not completed facial growth (Richtsmeier, Walker 1993)) closest to *H. habilis*, overlapping with ER 1813, the facially most "*erectus*-like" of this group. Dmanisi D2700 is now well separated from *H. habilis* fossils, clustering instead with *H. erectus* between the Turkana and ZKD/S17 specimens. The relative isolation of SK 847 on this axis, due to the multiple measures of facial projection incorporated in the analysis in which it contrasts with *H. erectus* specimens (notably in the upper face), is interesting and might be viewed as providing some support for considering it a separate but closely related form, rather than incorporating it within *H. erectus.*

SK 847 does, however, resemble ER 3733 in mid-lower face proportions, in its slender supraorbital torus and orbital bar, in the infero-lateral slope of the lower orbital margin and the gradual shelving of the peri-nasal region into the infra-orbital plane. By contrast the rather smaller but more heavily built D2700 is reminiscent of the E and SE Asian fossils, with a thick zygomatic root, strong canine juga and so salient margins to the piriform aperture, and with the peri-nasal region sharply differentiated from the infra-orbital plane rather than shelving into it, as in the African specimens.

In an important study, also involving PCA, Ackerman, Cheverud (2004) consider the influences of drift and selection in determining intra- and inter-group patterns of early hominid facial diversity. Their findings indicate that the evolution of a *Homo* face from that of *A. africanus* requires selection differentials that are relatively strong to moderately positive in the upper face and orbit (in some features reflecting anterior brain expansion), moderately positive to null in the midface/nasal region and weakly negative along the lower orbits and zygomatics. They conclude that while selection may well have been involved in the initial derivation of *Homo* from *Australopithecus*, thereafter differentiation of facial morphology between *H. habilis, H. rudolfensis* and *H. erectus* could result solely from drift. If so, SK 847 and D2700 suggest that the mid-lower face proportions that subsequently became fixed in

H. erectus were already present in at least some smaller-brained individuals (and possibly characterised entire groups) while others (e.g. the Turkana basin hominids) displayed a wider range of variability. The influence of shifting patterns of overall body size dimorphism on cranio-facial variability, and their underlying causes, remain important areas to explore when more complete evidence is available.

Interestingly, current evidence suggests differing patterns of diversity between Turkana/Dmanisi on the one hand and Sangiran on the other, for there are no indications from SE Asia of the small-brained crania present in Kenya and Georgia: smaller Javan crania are rather larger brained (with S2 the smallest) and more ruggedly constructed (with T2 the most gracile) than the western specimens. Instead the argument there for additional species is based on the fragmentary gnathic and dental material deemed by some too large to be *H. erectus*. Differences between Africa – West Asia and Java may reflect founder effect and drift, but growing evidence suggests that the SE Asian material is not as exceptional in its size as it is sometimes viewed. Disregarding some isolated teeth and jaw fragments claimed as hominid that are, in fact, pongid (Grine, Franzen 1994, Schwartz, Tattersall 2003), the S6a mandible fragment is the largest Javan specimen. However, as noted above, metrical and morphological studies show its closest affinities to be with other *erectus* fossils, while the Dmanisi DM2600 mandible approaches it in corpus size, indicating that S6 is not necessarily exceptional in its dimensions, and that a comparable range in masticatory parameters is indicated, or at least approached, by sampling elsewhere.

The alternative to including these specimens within *H. erectus* is the notion of repeated, initial intimate sympatry of at least two hominid species in all three, widely dispersed localities, followed by the extinction of one (or more) and the persistence of the single remaining species, *H. erectus*. This has been orthodoxy for the East African material but a narrow definition of *H. erectus* requires us to extend the scenario to the Georgian and probably Javan fossil records also. On the other hand, a corollary of assigning all the early material to *erectus* is the implication of a subsequent reduction in the species' intra-group diversity, a phenomenon that merits further study.

EVOLUTIONARY DYNAMICS

Geographical variation and polytypism

Rejecting the case for *H. ergaster* is not to deny differences between African and Asian *H. erectus* (Rightmire 1984, 1990, Bräuer 1994): there are differences in neurocranial shape between the samples which also influence muscle markings and ectocranial structures (Anton 2002, 2003). There are also possible differences in facial form and jaw size (e.g. Rightmire 1998a), although it is unclear whether these are artefacts of limited sampling and the possible inclusion of non-hominid material within the Javan collection (see above). In any event, the features cited are instances of continuously varying traits which are just as likely, if not more so, to reflect an underlying pattern of intra-specific clinal variation rather than species differences.

This conclusion is reinforced by patterns of diversity within the Asian *erectus* samples (Anton 2002, 2003), with contrasts between the mainland and peninsular samples in cranial breadth, supraorbital torus development and contour, mastoid process size, and occipital torus form and development. Given the varying ages of the localities, it is not possible easily to disentangle temporal and spatial components contributing to these differences. However, Anton notes that the earlier Javan material is more variable than later samples, whether Javan or Chinese (principally ZKD) and at least partly overlaps with the latter in character expression (see below).

Potential differences between later African and East/South East Asian *H. erectus* in cranial and possibly body size variation are discussed below. The limited North African evidence shares similarities with the sub-Saharan specimens, with the Ternifine mandibles particularly resembling OH 22 (Rightmire 1990). While displaying some distinctive characteristics, overall the Dmanisi sample bears similarities with the African material, as might be expected from its location (Vekua *et al.* 2002, Anton, Swisher 2004).

Comprehensive craniometric data for the Dmanisi hominins have not yet been published. Those available (Lordkipanidze *et al.* 2005) indicate the crania to be somewhat more variable sagittally than coronally and particularly invariant in biasterionic breadth. In combination they indicate a pattern broadly similar to the above *erectus* groupings but absolutely smaller. The line joining mean values for the Dmanisi crania generally lies below but parallel to the envelope provided by other *erectus* specimens, indicating similar ratios and so comparable shapes. The main exception here is in the mid-vault. The Dmanisi sample's mean value for parietal sagittal arc falls comfortably within the *H. erectus* spread but the lambda-asterion arc is appreciably smaller and its biparietal and biasterionic breadths less than the corresponding values for the other fossils, pointing on average to a sagittally comparable but coronally narrower parietal region in the Georgian crania (*Figure 4e, f*).

However, as expected, individual crania vary: larger specimens (D3444 and D2280) have parietal sagittal arc values well within the *H. erectus* envelope, but coronal measurements (lambdoid border arc, parietal and biasterionic breadths) that all fall below the corresponding values for the other *erectus* specimens. D2700 has a sagittally shorter parietal that just matches the lower boundary of the *erectus* envelope, whereas D2282's parietal falls well below it. The coronal values for both specimens fall well below those for the *erectus* spread. The pattern indicates that the latter crania, with absolutely smaller mid-vaults, more closely approximate the *erectus* parietal region in their *relative* proportions than the larger D2280 and D3444 crania which have comparatively long mid-vaults for their breadths. Further finds are needed to determine whether this is an established pattern or a sampling perturbation.

Temporal change in Africa

Current evidence suggests some increase in cranial robusticity and in endocranial expansion (Rightmire 2004) between the earliest African *erectus* (Nariokotome p-deme) and the LLK p-deme. Whether these are artefacts of limited sampling, and the extent to which they reflect increased overall body size and general robusticity (not stature) are both unclear. The small OH 12 and even smaller OL 45500 crania indicate significant size variation (?sexual dimorphism) persisting in later African *erectus,* coupled with similarities in supraorbital, mastoid and (for OH 12) occipital features with the earlier material (Rightmire 1979, 1993, Anton 2003, Potts *et al.* 2004). The Olorgesailie fossil is comparable in size to D2280 and D2282, with a slender mastoid and supraorbital torus, and small mandibular fossa. Its minimum frontal breadth matches that of D2700 (Vekua *et al*. 2002, Potts *et al*. 2004). It and OH 12 differ from the Daka and Buia fossils in supraorbital morphology and rear vault proportions as well as in size (Anton 2003), suggesting significant variation in East African *H. erectus* around 1.0 mya. Whether such variability characterised sub-Saharan *erectus* throughout the duration of the clade is unknown, but OL 45500 is among the youngest African specimens, and such a pattern would be compatible with a "Centre and Edge" model of the species' diversity (Thorne 1981, Wolpoff 1989, 1999, Wolpoff *et al*. 1984, 1994b). This raises the possibility of differing patterns of internal variability, perhaps sexual dimorphism, between African and Asian *H. erectus* groups, with potential behavioural and sociobiological implications. Much more fossil, especially postcranial, material is needed to investigate this possibility, but such contrasts, if confirmed by further discoveries, would provide a more secure basis for differentiating between these continental groupings at species level.

Temporal change in Asia

South East Asia

There is suggestive evidence for some reduction in dental and palatal size between earlier (S4, 27) and mid Kabuh/Bapang *H. erectus* (Anton 2003), and more definite indication if the *"Meganthropus"* mandibles are included. Kaifu *et al*. (2005b) stress the smaller postcanine teeth and thinner bodies with less developed, posteriorly located lateral prominence, superoposteriorly positioned ramus root and narrow extramolar sulcus of the 3 Bapang Formation mandibles compared with the 8 specimens from the Grenzbank and underlying Sangiran Formation. While the latter mandibles are few in number the contrasts are notable, with dentognathic reduction, including marked M_3 diminution, comparable to that of the Chinese material, occurring over a period of 0.2–0.5 my depending on specimen provenance and the chronological framework adopted. Kaifu *et al.* suggest the differences reflect either *in situ* microevolution or multiple entry into Java and replacement of earlier populations. If the former, it is unclear whether drift was an important influence or whether the changes reflect selection, possibly of the kind, if not magnitude, as that associated with insular dwarfing (see below). However, evidence for a comparable reduction in other cranial features is more ambiguous; while some specimens, generally considered to be early, are robust and heavily constructed, others are less so, and a similar variability characterises the Bapang sample (see above).

What is clearer is that the overall cranial diversity in the pre-1 mya sample encompasses the later morphology of the Sambungmachan and Ngandong specimens in endocranial capacity, supraorbital torus and supratoral morphology, occipital torus morphology and nuchal contour, mastoid size and form, and glenoid fossa proportions (Anton 2002, 2003). Of the more complete Sangiran crania, S10 (855 cm^3), S12 (1,004 cm^3) and S17 (1,059 cm^3) share similarities in neurocranial proportions with the Sambungmacan material, whilst other individual specimens within the overall Sangiran sample may display some of the character states that are common in the Sambungmacan and Ngandong material (Anton *op.cit.*).

The Ngandong fossils are notably similar in neurocranial form, with reduced CV values, especially for frontal and occipital dimensions, compared with earlier Javan *erectus* (Bilsborough 2000b). In four multivariate analyses (Kidder, Durband 2004) they form a tight cluster, with no significant distances between individual specimens, in contrast to the Sangiran and even Sambungmacan samples, individuals of which are sometimes significantly apart in the analyses. While both mean brain size and mastoid size increase over time, their absolute ranges remain broadly constant in the earlier and later Javan groups, with a supramastoid sulcus becoming fixed in the later material (Anton 2002, 2003).

The main metrical differences between the earlier and later Javan *erectus* crania reflect a limited increase in mean brain size, and associated with this, rather greater vault heights, parietal lengths and frontal breadths. However the diversity can easily be accommodated within the range displayed by the Kabuh sample, and the Solo fossils are essentially a rather larger variant anteriorly of the same pattern; in many posterior vault (rear parietal and occipital) dimensions the Ngandong values would actually typify "classic" *H. erectus* crania (Bilsborough 2000b). The restricted magnitude of these metrical changes, as well as the morphological shifts summarised above, and the reduced variability of the later Javan sample are all compatible with the effects of genetic drift in small isolated populations.

Several workers have drawn attention to the derived nature of the later Javan material; Baba *et al.* (2003) in particular list derived features that link Sambungmacan and Ngandong. Among these are a posterior narrowing

FIGURE 4. Comparison of *H. erectus* groups for individual neurocranial dimensions. Abbreviations: FRSC = frontal sagittal chord; FRSA = frontal sagittal arc; FRminB = minimum frontal breadth; FrmaxB = maximum frontal breadth; PSC = parietal sagittal chord; PSA = parietal sagittal arc; L-ast C = lambda-asterion chord; L-ast A = lambda asterion arc; PmaxB = maximum parietal breadth; OSC = occipital sagittal chord; OSA = occipital sagittal arc; Biast B = Biasterionic breadth; Biaur B = Biauricular breadth. For paired comparisons (*Figures 4b–4f*) relevant values for each pair are immediately to left and right of the corresponding dimension indicated on the baseline. Vertical bars indicate 1 SD either side of mean value.

FIGURE 4a. *H. erectus* regional sample means for calvarial dimensions. EA = East African (KNM-ER 3733, KNM-ER 3883 & OH 9); K/P = Java (Kabuh/Bapang & Sangiran/Pucangan); ZKD = Zhoukoudian; Ng = Java (Ngandong).

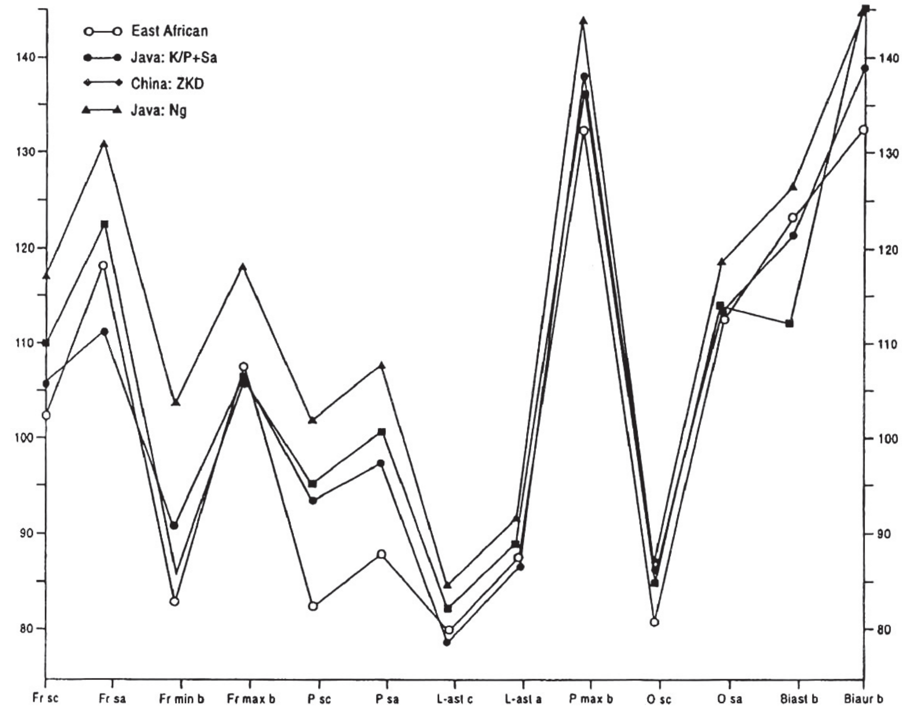
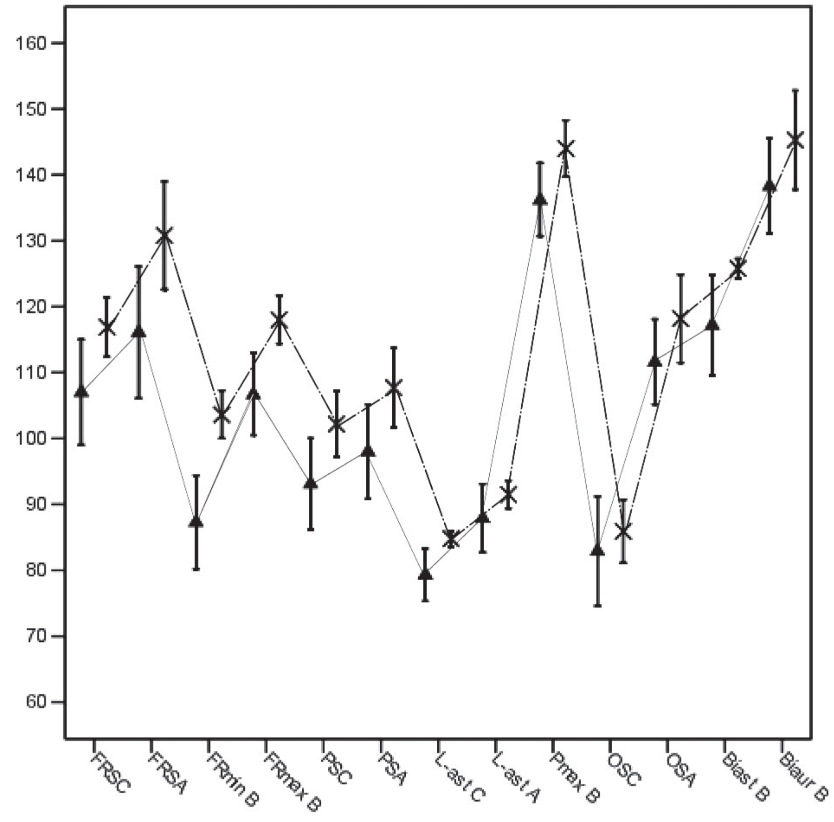


FIGURE 4b. Ngandong sample values compared with *H. erectus* means excluding Ngandong. Triangles, continuous line: *H. erectus* means excluding Ngandong. Crosses, interrupted line: Ngandong means.



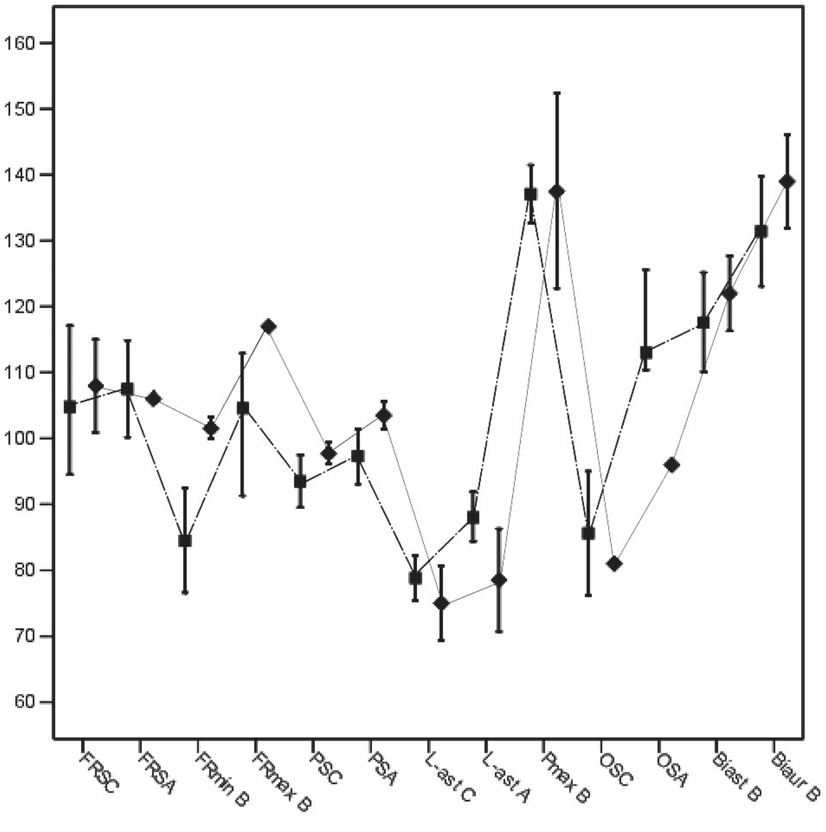


FIGURE 4c. Comparison of Javan *H. erectus* groups for individual calvarial dimensions.
Squares, interrupted line: Sangiran/Pucangan and Kabuh/Bapang (excluding Sambungmacan) sample means.
Diamonds, continuous line: Sambungmacan 1 & 3 means.

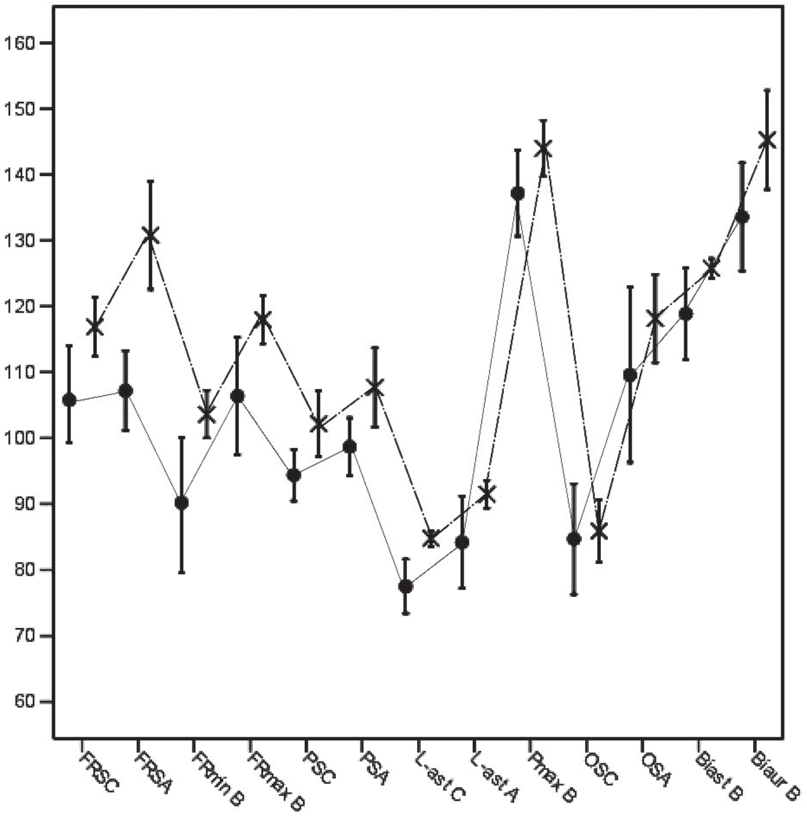


FIGURE 4d. Comparison of Javan *H. erectus* groups for individual calvarial dimensions.
Circles, continuous line: Sangiran/Pucangan and Kabuh/Bapang (including Sambungmacan) sample means.
Crosses, interrupted line: Ngandong sample means.

FIGURE 4e. Comparison of *H. erectus* groups for individual calvarial dimensions.
Stars, continuous line: Dmanisi sample means.
Triangles, interrupted line: *H. erectus* sample means excluding Ngandong.

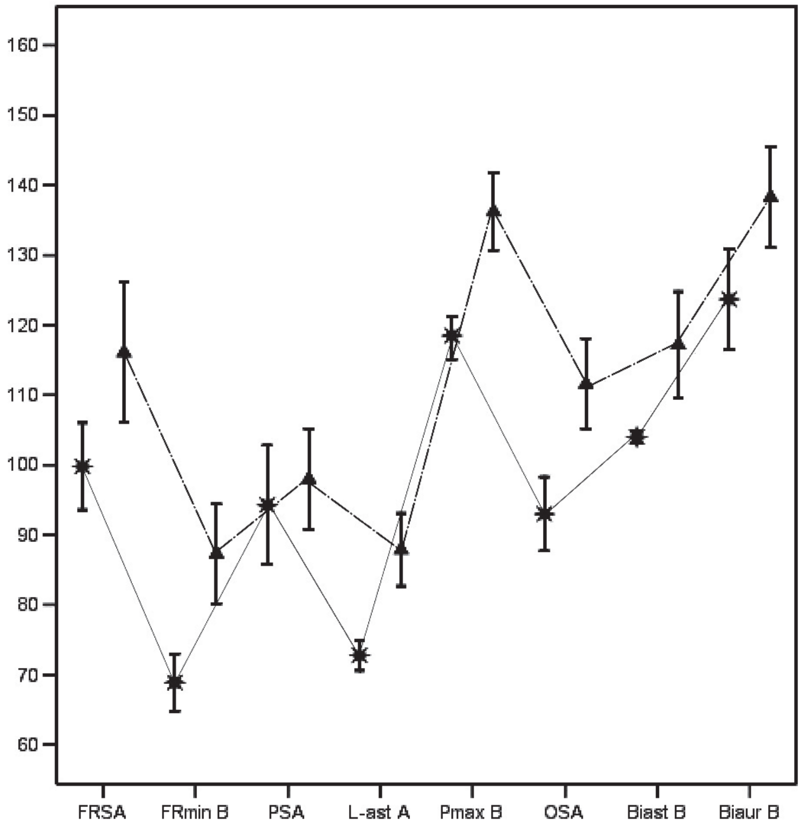
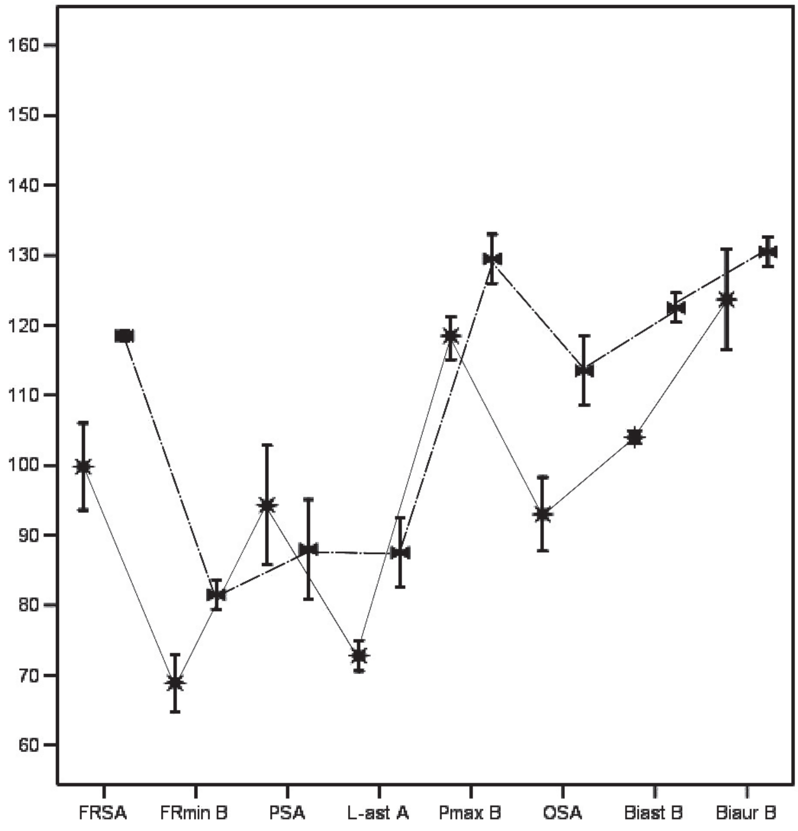


FIGURE 4 f. Comparison of *H. erectus* groups for individual calvarial dimensions.
Stars, continuous line: Dmanisi sample means;
Bows, interrupted line: Early African *H. erectus* (KNM-ER 3733 and KNM-ER 3883) sample means.



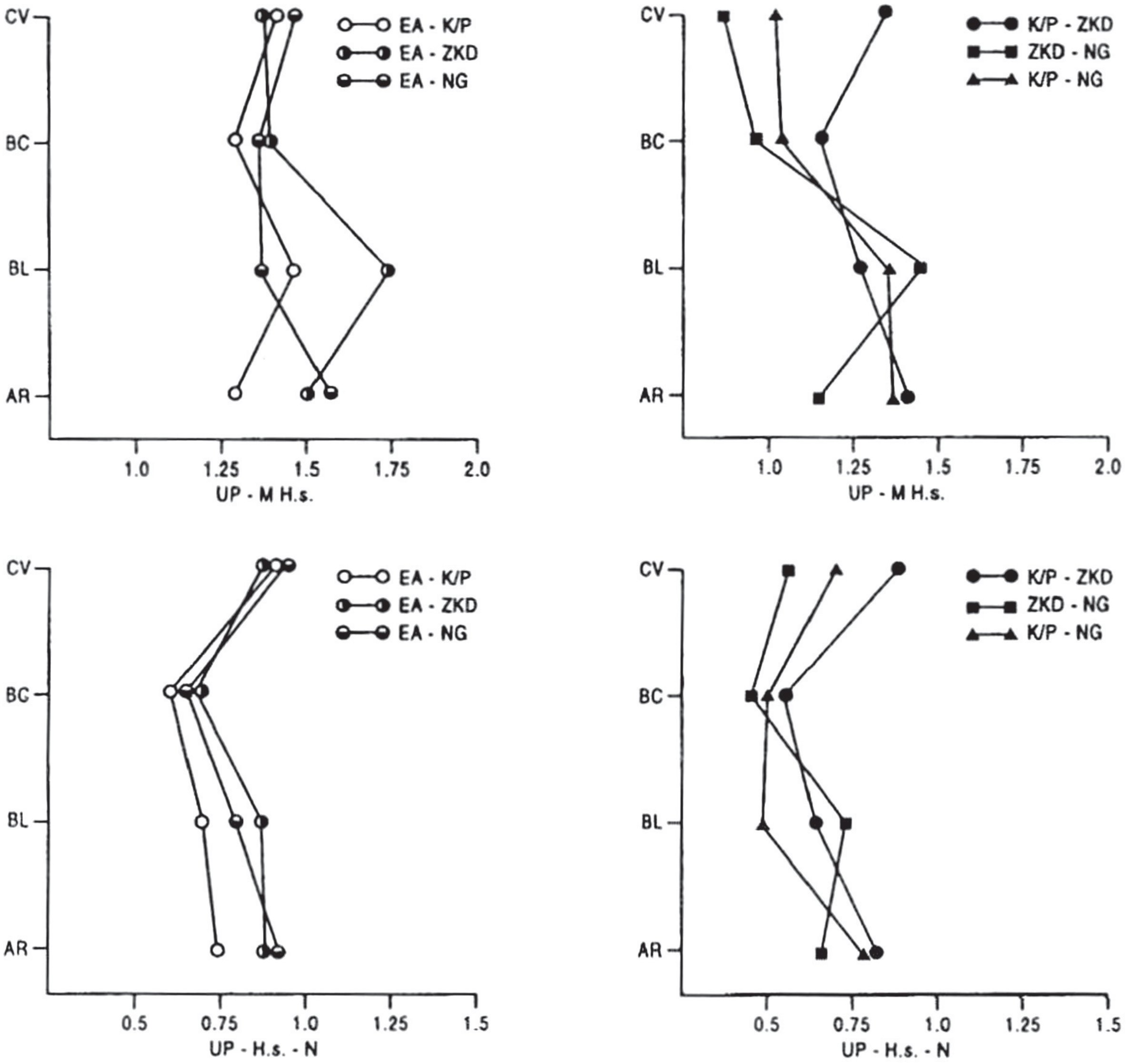


FIGURE 5. Multivariate distances between *H. erectus* groups for Cranial Vault (CV), Basicranial (BC), Balance (BL) and Articular Regions (AR) scaled by the corresponding Upper Paleolithic – Modern *H. sapiens* separation (upper diagrams) and Neanderthal – Upper Paleolithic *H. sapiens* separation (lower diagrams). *H. erectus* groups: EA= East African (Koobi Fora & Olduvai OH 9); K/P= Java (Kabuh/Bapang and Sangiran/Pucangan); ZKD = Zhoukoudian; Ng = Java (Ngandong). For further discussion see text.

of the foramen magnum (opisthionic recess), and a distinctive mandibular fossa that is short and deep, with the squamotympanic fissure in the deepest portion and a laterally extended tympanic plate forming the fossa's posterior wall, and with no or minimal development of the postglenoid process.

Continental Asia
The ZKD sample is remarkably uniform in cranial features, which again may well reflect the outcomes of founder effect and drift on a small, relatively isolated, northern hominid population, albeit one that has had a disproportionate influence on notions of *H. erectus* overall. The growing amount of material from other, mainly more southerly, Chinese localities points to considerable variability in mainland *H. erectus*, with the ZKD sample unrepresentative of that wider diversity. However (the battered Gongwangling cranium apart), the restricted time depth of the Chinese sample does not permit ready identification of marked temporal trends within the material. There is some evidence for dental reduction, especially of the lower cheek teeth, in the ZKD material (Zhang 1991) but claims for more general cranial changes rest essentially on a single specimen (from Locality H, level 3) and, as such require further material for their confirmation.

Temporal change overall
Views differ on whether *H. erectus* displays significant temporal change – i.e. anagenesis – or whether it represents a period of stasis, with some of the most explicit statements

for anagenesis associated with broader debates on the role of multiregional continuity in later human evolution (see below). Such analyses are, in any case, critically dependent upon overall sample size and composition, its sub-division into regional groupings (if any), the underlying evolutionary models assumed, and the accuracy of dating frameworks. See, for example, Godfrey, Jacobs (1981) for caveats on brain expansion data. My own views have changed appreciably between earlier (Bilsborough 1978, 1983, 1992) and later analyses (Bilsborough 2000b) because of these factors.

Following an early interpretation of change in cranial and dental dimensions by Bilsborough (1976), Rightmire (1981, 1986b) argued for stasis in *H. erectus* on the basis of an analysis of four traits (cranial capacity, biauricular breadth, M_1 breadth and mandibular robusticity). His findings in turn prompted Wolpoff (1984, 1986) to analyse a variety of cranial characters, concluding that the data demonstrated marked changes between Lower, early and late Middle Pleistocene *erectus* samples. Many subsequent analyses have focused on variation in cranial capacity and/or encephalisation to investigate evolutionary dynamics.

For example, Cronin *et al.* (1981) and Clausen (1989) detected a trend for *erectus* brain expansion between the earliest African and later Asian specimens, while Leigh (1992) concluded that his data might indicate a trend for increased cranial capacity in *H. erectus* overall which is not evident in regional subsamples other than the Chinese and combined Asian material – but not, interestingly, in the Javan subsample, even though this includes Ngandong. While cautioning about the limitations of small sample sizes, Leigh also noted the possibility of more rapid increases in the early African and later Asian subsamples compared with crania from the species' mid-span (Olduvai Bed II and Sangiran/Trinil fossils). Wolpoff (1999) gives a *ca* 12% increase in average endocranial volume within *H. erectus*, with particular expansion of the frontal and occipital lobes. As part of a comprehensive review of hominid encephalisation, Ruff *et al.* (1997) concluded that cranial capacity and body mass data indicated stasis in relative brain size between 1.8 mya and at least 0.6 mya – i.e. the greater span of *H. erectus* – with a trend for increase from mid/late Middle Pleistocene onwards. More recently Lee and Wolpoff (2003) have argued that the distribution of cranial capacity in fossils from early African *H. erectus* onwards fits a model of anagenetic change within a single lineage, but is incompatible with punctuational or cladogenetic models.

Other workers (e.g. Stanley 1979, 1981, Rightmire 1981, 1985, 1986b, 1990) have argued that *H. erectus* represents a period of stasis in hominid evolution. Bräuer (1994) and Rightmire (1990,1994) detected limited change in a small number of cranial characters: frontal breadth, glenoid fossa length and breadth, biauricular breadth, thickened tympanic plate, and parietal diagonal length out of 41 traits (Bräuer); cranial capacity, corpus breadth out of 9 traits (Rightmire), but little or no evidence of temporal shifts in the majority of features examined. In contrast to earlier findings, Bilsborough (2000b) reached a similar conclusion based on craniometric data, arguing that the limited changes in neurocranial dimensions between the Ngandong specimens and earlier Javan *H. erectus* were as compatible with drift and sampling effects as with directional selection. Similarly (KNM-ER 42700 apart), the early Turkana *erectus* crania have sagittally short parietals but are otherwise comparable to later *erectus* specimens elsewhere in their cranial dimensions.

The relatively invariant nature of *erectus* crania is evident by comparing the neurocranial patterning of regional and temporal groupings with that for the species as a whole (*Figure 4a*). An envelope 1 SD either side of the species mean (calculated conservatively by excluding Solo) encompasses the individual group means except for some anterior cranial characters of the Ngandong (Ng) sample (*Figure 4b*). Even here the latter's mean values are generally only slightly beyond the 1 SD limit, with several constituent specimens falling within the envelope for their anterior dimensions. For example, Ng 7 and 12 lie within the envelope for frontal and parietal sagittal chords and arcs, as does the latter for Maximum Frontal Breadth. Only Minimum Frontal Breadth shows no overlap in specimen values between Ngandong and other *erectus*. In all other respects the values for the Solo sample would be unexceptional in a population of "classic" *erectus* individuals, and in many posterior vault (rear parietal and occipital) dimensions would actually typify such a population (Bilsborough 2000b). This relative uniformity, extending across much of the Old World for *ca* 1.5 million years, is remarkable.

Multivariate comparisons, which in principle might more readily differentiate the groups on the basis of distinctive covariance patterns even when individual characters display extensive overlap, in fact point to similar conclusions. Using Generalised Distances, I have compared the separation of four *H. erectus* groups in four complexes (character numbers in brackets): cranial vault (14); basicranium (5); balance (6); articular region (7), and compared them with two referents: separation between European Upper Paleolithic (UP) and modern (M) *H. sapiens* – taken as an intra-specific standard; and between UP and European Neanderthals (EN) – taken as an inter-specific standard. The *erectus* groupings are: East African (EA), earlier Javan – Kabuh/Puchangan (K/P), Ngandong (Ng), and Zhoukoudian (ZKD). The cranial vault and balance display greater diversity among the *H. erectus* groups and the referents than the basicranial and articular regions (*Figure 5*).

Across the four complexes the *erectus* groups are approximately equidistant from one another, but with a tendency for the EA – ZKD and EA – Ng pairings to be slightly further apart than the others, and for ZKD – Ng to be rather closer, a patterning consistent with their temporal and geographical ordering. Separation between *erectus* groups is rather greater than that between the two *H. sapiens* groups (values mainly 1–1.5 the latter divergence, with the maximum 1.7 – balance between EA and ZKD *erectus*). For the vault, (K/P) – Ng and ZKD – Ng distances are closely comparable to the *H. sapiens* separation. In contrast, inter-*erectus* distances are invariably less than the EN – UP values (the between-species comparator) although for the divergence of EA and other *erectus* groups in vault and articular region they begin to approach the former.

The above comparisons are necessarily based on a restricted sub-set of *erectus* specimens. Rightmire (2004) has recently reviewed more extensive data on brain size and encephalisation in *H. erectus* and *H. heidelbergensis,* incorporating most well-dated and relatively complete specimens from Koobi Fora onwards apart from Ileret ER 42700, Dmanisi D2700 and Sambungmacan crania (context and dating insecure), and assigning a "latest possible" date of 40,000 years to the Ngandong sample. Mean capacity for *H. erectus* overall is 970 cm^3, and between the earlier and later specimens there is a slight but real increase in volume of *ca* 165 cm^3 per million years. Rightmire concludes (p. 118) that "Although the crania from Ngandong and Zhoukoudian are indeed larger than those from Koobi Fora and Dmanisi, the trend reflected in these data is not very pronounced."

A rather older age (basal Upper Pleistocene) for the Ngandong sample is unlikely to affect this conclusion appreciably, although inclusion of D2700 and Ileret among the earliest *erectus* specimens would reduce the overall mean somewhat, and result in a rather higher rate of increase over the duration of the species. Rightmire's recent result of 165 cm^3/my – the most comprehensive available – may be compared with his earlier figures of increases of *ca* 175 cm^3/my including Salé and Ngandong (dated at 0.3 mya) – a result not significant from zero, i.e. no secure trend (Rightmire 1981); *ca* 135 cm^3/my excluding Ngandong – not significant (Rightmire 1985); 181 cm^3 including Ngandong (dated at 0.2 mya) – significant from zero, and 120 cm^3/my excluding Ngandong – not significant from zero (Rightmire 1990), to illustrate the effects of sample composition and dating estimates on such analyses. See also Godfrey and Jacobs (1981) for a review of the effects of data manipulation and transformation on similar investigations of hominid brain evolution.

Given the fossil evidence, most trend investigations have necessarily focused on neurocranial data, and it is possible that other regions – e.g. face, gnathic and dental evidence – provide evidence of more significant evolutionary change in *H. erectus* as Wolpoff (1984, 1986) and some others (e.g. Zhang 1991, Kaifu *et al.* 2005b) have argued. Bilsborough (2000b) noted possible pointers to such changes in calvarial traits of the articular fossa and nuchal complex, regions influenced by proportions of the face and masticatory apparatus. But direct facial evidence of *H. erectus* is extremely limited and its reconstruction disputed (e.g. Bräuer, Stringer 1997, Baba *et al.* 2000), while fragmentary jaw material is often specifically indeterminate (see above). 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 broad temporal and spatial spans.

H. ERECTUS AND LATER PLEISTOCENE HOMININ EVOLUTION

This relatively uniform morphology accords with a view of *H. erectus* as a single, widely distributed species, displaying local (demic) and probably larger scale (regional) patterning that is, however, limited overall across the species range. Accordingly, discussions about its phyletic status have centred less around its ancestry, or otherwise, of species such as *H. heidelbergensis* and *H. rhodesiensis* than about whether such ancestry was confined to particular regional populations rather than the entire species, the evolutionary processes involved and the nature of the transition. For some workers the locus of *H. erectus* has become subsumed within broader arguments over the relative roles of continuity and cladogenesis in later hominin evolution.

For example, proponents of regional continuity (e.g. Jelínek 1978, 1985, Thorne 1981, Thorne, Wolpoff 1981, Wolpoff 1985, 1989, Wolpoff *et al.* 1984, 1994a, b) view *H. erectus* as a widely distributed, polytypic species that also displays anagenetic trends towards sapienisation. Wolpoff *et al.* (1994a) provide an explicit statement of this position, viewing all evolution within *Homo* as a monophyletic continuum, and sinking *H. erectus* from KNM-ER 2598 onwards within *H. sapiens*. This would then have a duration of *ca* 2 my – at least twice that of other hominid species – and encompass an exceptional range of internal diversity. The reality, and so utility, of this approach is highly questionable, given the contrasting fossil records of Africa, Europe and Asia over that period.

Within sub-Saharan Africa a more derived species (*H. rhodesiensis* or African *H. heidelbergensis)* is present from around the Lower/Middle Pleistocene boundary or rather earlier. The Bodo cranium, dated to > 0.7 mya, combines similarities with *H. erectus* (frontal constriction, cranial keeling and angular torus, tympanic conformation) with derived characters of expanded braincase, face and palate that link it to later (0.5–0.7 mya) fossils such as Kabwe and Ndutu (Rightmire 1996, 1998b, 2004). Given that Bodo is contemporary with or antedates the latest East and North African *H. erectus* fossils, as well as most from continental East Asia, it indicates a speciation event within *H. erectus* (Rightmire 1996), possibly associated with the onset of major climatic fluctations after about 0.95 mya (Asfaw *et al.* 2002). The earlier Buia UA 31 cranium also reveals a mosaic of *erectus* features with more derived traits. Depending on age and detailed affinities, UA 31 and the contemporary Daka specimen may represent "progressive" *erectus* populations with some individuals displaying *"rhodesiensis*-like" traits across a spectrum of features, or early representatives of the latter clade, following speciation from *H. erectus.*

Given this picture, the most convincing broad-brush model of *H. erectus* diversity is that summarised by Rightmire (1998b) and Asfaw *et al.* (2002) – a single, polytypic species, widely distributed across Africa and Asia by 1.5 mya and retaining its specific integrity down to at least 1 mya, and perhaps later, a conclusion reinforced by the affinities between the LLK paleodeme and the Asian fossils. Thereafter *H. erectus* persists in East and South East Asia (apparently until late Middle or Upper Pleistocene times in the latter case) but the contrasting African record suggests a different evolutionary pattern in that continent from late Lower/early Middle Pleistocene times onward. As Asfaw *et al*. note, more fossil and contextual evidence from the period 1.0–0.5 mya is needed to determine whether lineage differentiation is associated with any pulse of morphological change, and whether global climatic fluctuations were a driver in the process. However, impressionistically, evidence points to earlier, and perhaps more rapid change (with or without speciation) in the Middle Pleistocene records of Africa and Europe than in Asia, save perhaps for its western fringe.

In East and South East Asia the overall impression is of *comparative* homogeneity between as well as within each region, with similarities extending over the greater part of the period represented by the fossil record – from around 1 my+ in middle latitudes (Gongwangling), from *ca* 0.6 mya further north (ZKD) – until at least the mid-Middle Pleistocene. While specimens' affinities and their chronological frameworks are both less secure than in sub-Saharan Africa, as there evidence points to contemporaneity or overlap of later *H. erectus* (e.g. Zhoukoudian, Hexian) with other Middle Pleistocene hominid morphologies (e.g. Dali, Jinniushan). The latter presumably represent either immigrants into East Asia from further west, or local descendants of *H. erectus.* Various workers (e.g. Wolpoff *et al.*1984, Wolpoff 1985, Pope 1988, 1991, 1992, Wolpoff *et al.* 1994b) have stressed traits pointing to continuity between continental *erectus* and this material so that *in situ* origin by speciation event(s) seem plausible, especially in the context of the impacts of Middle Pleistocene climatic swings. If speciation is accepted as a mechanism underlying the African hominin record, there seems little or no reason to exclude it as an influence on human evolution across the extensive East Asian landmass.

Within Asia the Ngandong fossils provide an example of regional differentiation. Whilst in many respects displaying further development of features noted in Sangiran and Sambungmacan specimens (neurocranial expansion, diminution of nuchal and masticatory reinforcement etc.) this later pattern is not known from continental Asia, and is best thought of as a "terminal, presumably insularly derived product of the *H. erectus* clade" (Howell 1994, see also Jelínek 1982a). Howell summarises the material's biostratigraphic associations, pointing out that virtually all taxa are continuations of earlier immigrant species, with no evidence for continental connections at the time of Ngandong. While advocating multiple species elsewhere among the Asian hominids, Howell differentiates the Ngandong material only sub-specifically as *H. erectus soloensis,* viewing it as a micro- rather than macro-evolutionary phenomenon.

The contrasting view is provided by Wolpoff *et al.* (1994a), who consider earlier and later (Ngandong) *erectus* (their "early" and "middle *H. sapiens"*) to exhibit significant evolutionary trends presaging more modern morphology, including increased cranial capacity overall with differential expansion of the frontal and occipital lobes, greater vault breadth and height, and changes in neurocranial shape, slighter muscle markings and reduced buttressing of the vault (Wolpoff 1999). While viewing the Sangiran population as directly ancestral to Ngandong, Wolpoff denies that the latter is *H. erectus* in the sense used by other workers, arguing that its inclusion within the species constitutes "a classic case of confusing regional features with traits that could be taken to indicate evolutionary grade" (Wolpoff 1999: 573). The impression given is that Wolpoff *et al.* view Ngandong as a SE Asian equivalent of sub-Saharan *H. rhodesiensis /H. heidelbergensis,* which they, of course, also subsume within *H. sapiens*, so that the entire Pleistocene hominin record becomes a microevolutionary phenomenon.

Most other workers have stressed the localised affinities of the Ngandong fossils, while the larger Pucangan/Kabuh and augmented Sambungmacan fossil samples now available reinforce the case for similarity. Morphometric contrasts in vault and basicranium between the earlier Javan, Zhoukoudian and Ngandong crania are similar in scale to those between European Upper Paleolithic and modern *H. sapiens* (see above). The similarity of Asian inter-*erectus* distances to the corresponding inter-*sapiens* standards points to relatively minor differentiation in these complexes in mid-later *erectus* populations, and, as such, reinforce conclusions of Ngandong's *H. erectus* affinities.

Continental specimens such as Dali, Dingcun, and Jinniushan in the centre and north of China, and Maba in the south (Pope 1988, 1991, 1992, Howell 1994) differ from the Ngandong crania, pointing up contrasts between the mainland and insular records. Regional continuity within the south eastern part of the Asian *H. erectus* realm evidently led to a derived morph by isolation and *in situ* random or fine tuning, whereas change – whether through anagenesis or (more likely in my view) through speciation – in the more northerly, continental part of the range resulted in more derived form(s) subsumed within "archaic *sapiens*". Whether the southern mainland morph represented by Maba and Namarda (India) represents a further Asian species or intrusive migrants (Howell 1994) remains to be determined.

Homo floresiensis

The remarkable LB1 skeleton from the Liang Bua Cave, Flores, 1m tall with an endocranial volume of only *ca* 400 cm^3 (estimates of 380 cm^3 and 417 cm^3), assigned to *H. floresiensis* and dated as recently as 18 kya, shares neurocranial and facial similarities with *H. erectus* and is probably best thought of as a derived, dwarfed descendant of that species (Brown *et al.* 2004, Falk *et al.* 2005). Flaked pebble tools from the Soa Basin, 50 km east, indicate hominid occupation of the island, which is off the Sunda Shelf and only accessible by sea crossing, from at least 0.84 mya, so potentially allowing for a long period of endemic dwarfing (Morwood *et al.* 1998). Faunal evidence indicates an island refuge with an impoverished Pleistocene fauna, including at least one other example of insular dwarfing (*Stegodon*) (Morwood *et al.* 2004).

A MODEL OF EVOLUTIONARY DIVERSITY IN *HOMO ERECTUS*

The drier, more open environments of the later Pliocene can be expected to have resulted in greater fragmentation of hominid populations, so leading to greater local differentiation and extinctions (Stanley 1992). Such conditions doubtless also intensified selection pressures for greater terrestriality, to which the postcranium of early *H. erectus* can be seen as a response (Walker, Leakey 1993a, Aiello, Wells 2002). The appearance of this morphology, probably some time around 2 mya, signifies a distinct adaptive shift (see below). Its initial evolution is largely unknown, although the Bouri femora (Asfaw *et al.* 1999) indicate upper hindlimb elongation by *ca* 2.5 mya, apparently still linked with long forelimbs. Whatever is the origin, the adaptive success of this postcranial morphology is evidenced by the remarkable expansion of *H. erectus* within and beyond Africa, within a short time period.

In this context, small groups of *Homo erectus*, thinly scattered across extensive areas with fragmented local habitats, can be expected to have approximated in many respects to Wright's model of small, semi-isolated populations, each one differentiated from the others by a combination of founder effect, drift resulting from intergenerational sampling errors, and local adaptations. Over time some demes would become extinct and might, or might not, be replaced by others moving or expanding their range whilst others might coalesce, so enhancing genetic and phenotypic variability. The overall outcome would be a dynamic, fluid situation at the local level, with appreciable, continually shifting patterns of inter-demic variability, and with stochastic factors playing a significant role (see also Bilsborough 1999).

Gradual, directional change might from time to time have characterised some limited parts of the *H. erectus* range (particularly if separated from the remainder), whether because the selection pressures were relatively widespread, or because chance effects combined with proximate gene flow might have pushed several populations in the same direction. However, given the spatial extent of *H. erectus*, selection pressures over the entire species range are likely to have varied considerably, with the distances and barriers involved probably acting to minimise the effects of gene flow. In this situation the outcome would be little or no directional change for the species overall – i.e. stasis. Regional anagenesis (local trends) may thus be apparent as an infra-specific phenomenon, and yet be fully compatible with stasis at the species level (Eldredge 1995), rather than presaging a transformation of the total gene pool. The reduction in dental and gnathic size between earliest and Kabuh/Bapang *erectus*, the somewhat greater mean endocranial capacity and gracilisation of later Javan crania, the possible indications of dental changes at Zhoukoudian (Zhang 1991) and the contrasts between the earliest African representatives and later finds such as OH 9, may all represent instances of such local trends.

However, such anagenetic change will be spatially limited and temporally ephemeral unless "frozen" by reproductive isolation (Futuyma 1987). Speciation, especially peripatric speciation (Mayr 1954), is accordingly the most likely source of larger scale evolutionary change by preventing back-slippage and acting as an evolutionary ratchet. Populations close to, or at the limits of the species differ from those elsewhere because of genetic drift and distinctive selection pressures; a (geologically) short period of isolation may further accentuate differences due to founder effect and subsequent drift, reinforcing contrasts between the isolate and the original species, and resulting in a new species. The primacy accorded to speciation as the evolutionary process preserving morphological change is the fundamental difference between the broad anagenesis/continuity model articulated by Jelínek, Wolpoff and others (including myself until the last decade), and the model summarised here.

Following Mayr, Carson (1975, 1987) and Templeton (1980) have proposed speciation models that involve restricted change in peripheral demes and which incorporate bottlenecking events and their outcomes. Carson stresses the role of population reduction and bottlenecking in destabilising hitherto co-adapted and stable genomes, leading to strong selection towards a novel character set and so a new species (Carson 1987). Templeton (1980) emphasises the importance of changes in a few genes with major phenotypic effects for promoting speciation, a phenomenon he terms "genetic transilience". Small isolates will deviate in their gene frequencies from the parent population and will exhibit reduced variance and higher inbreeding, so more readily exposing homozygotes to selection, and favouring genes that are fittest in homozygous combination. The altered genetic environment resulting from the founder effect results in changed selective conditions that in turn promote the transilience and speciation. The number of genes involved may not be large, but interaction between loci can reinforce the process before reaching a new, co-adapted, stability: changes in one or more genes (the genetic environment) may significantly affect the selective value(s) of others. Again, the outcome is a new species.

However, despite the much wider spatial and ecological range of *H. erectus* compared with earlier hominids which might be expected to promote speciation, morphological evidence for species diversity is lacking for much of the timespan represented by the material, and only features after about 1 mya in Africa, and even more recently in East and SE Asia. Before then, the at best equivocal regional contrasts in *erectus* samples "may be explained as populational differences, rather than post-speciational divergence" (Harrison 1994: 364). Similarly, while the location and periodic isolation of SE Asian *H. erectus* might be expected to promote speciation, there is no convincing morphological evidence of its occurrence until the late Middle or even Upper Pleistocene, when the disjunction between the Ngandong morphology and that of continental Asia provides strong evidence for species distinction.

What the longer SE Asian record does appear to show is some evidence of brain expansion and cranial gracilisation, but given their weak nature the trends could just as plausibly be attributed to drift as to selection. Evidence is also weak for any species-wide trend for endocranial expansion reflecting directional selection, a component of most, if not all, regional continuity models (Rightmire 2004, and above). The very scale of the morphological contrasts between early *H. erectus* and modern *H. sapiens* argues against the constancy of niche and selection pressures envisaged by many advocates of regional continuity, quite apart from the difficulty in accepting that a range extending across the greater part of the Old World over the almost two million years of Pleistocene climatic fluctuations could ever be regarded as environmentally uniform.

None of this excludes the probability, indeed virtual certainty, of inter-populational differences resulting from stochastic factors impacting on local *erectus* communities, but at least until the final Lower Pleistocene the outcomes were evidently of reduced magnitude and effectively invisible via the fossil record. This contrasts with earlier hominins, where evidence of morphologically distinct species is more convincing, despite their more localised distributions. In effect, it suggests that for the greater part of its duration, the outcomes of evolutionary processes for *H. erectus* were micro-evolutionary rather than species level phenomena (Gould 1985) which in turn points to distinct adaptive modes and strategies between earlier hominins and *H. erectus*.

The current picture raises the possibility that the more intense climatic fluctuations after 1 mya were an important factor promoting habitat fragmentation and break up, population isolation and differentiation, and the origin of *H. rhodesiensis* from later African *H. erectus,* although more evidence is needed to substantiate this. The same climatic swings are likely to have had even greater impact on the incursions of *erectus* groups into higher latitude regions of Asia with their unstable climatic regimes, and so further opportunities for random effects and group differentiation. Some features of the ZKD fossils (overall homogeneity, pronounced angular torus, occipital tapering, small mastoids) hitherto taken to typify *H. erectus,* may be better thought of as local traits resulting from such isolating factors. Again, the origin of at least some Asian "archaic *sapiens*" morphologies may result from the same influences.

However, the most convincing case for speciation through isolation is surely that of *H. floresiensis,* very probably derived from a small founding group of individuals, necessarily atypical in their gene frequencies of the parent *H. erectus* population, and subject to further drift through isolation. The small Flores population would also be increasingly subject to selection acting on exposed homozygous combinations, an important factor promoting genetic transilience as a speciation mechanism, and subject to strong selection pressures promoting dwarfism. Whether the founding group derived from "typical" (Sangiran dome) *erectus*, or from Sambungmacan or Ngandong type populations is unknown, but the process is similar in principle, with only the timescale varying.

SUMMARY AND CONCLUSIONS

The much expanded *erectus* fossil record indicates an African origin followed by an early, rapid dispersal to West (Dmanisi) and South East Asia (Sangiran etc.). Occupation of northern continental East Asia is known from *ca* 1.3+ mya (Nihewan tools), but the earliest fossil find is the rather younger (1.1 mya) and more southerly specimen from Gongwangling. Fossil evidence from higher Asian latititudes is unknown before *ca* 0.6 mya, or possibly rather earlier (Zhoukoudian). Similarly, *H. erectus* fossils are known from North Africa by the Lower/Middle Pleistocene boundary (Ternifine), but there is no unequivocal evidence for the species in Europe.

There are reasons for supposing that the two most extensive and best known fossil samples – from Sangiran and ZKD – widely taken to typify *erectus* morphology were, given their peripheral locations, strongly influenced by founder effect and drift, and not necessarily representative of more centrally located *erectus* populations.

Among the early sub-Saharan and West Asian fossils are small-brained specimens that possibly indicate precursor or closely related species, or which indicate a wide range of cranial (and possibly body size) variation in early *H. erectus* which persists until at least the late Lower Pleistocene in sub-Saharan Africa, but which is not known in the fossil records from South East and East Asia.

Claims for multiple species within the early East African and South East Asian fossil samples are not substantiated morphologically, nor is the case for distinguishing early African specimens as *H. ergaster*. Modal differences exist between African and Asian *H. erectus,* but they are not exclusive to one or other group and so do not permit ready assignment on morphological grounds. Given the geographical range of *H. erectus* allopatric diversification and speciation might be expected in principle, but morphological evidence is lacking until after 1 mya, when the African record indicates a derived species *H. rhodesiensis* or *H. heidelbergensis.* Derived specimens occur only much later in continental Asia – around 0.3 mya or less, and may represent migrant groups, or *in situ* differentiation and evolution from *H. erectus*, perhaps promoted by the pronounced climatic fluctuations of the Middle Pleistocene.

In South East Asia later *H. erectus* morphology is represented by the Ngandong crania, derived by anagenetic evolution during a period of isolation, possibly with drift as a major factor in the process. *H. floresiensis* represents a derived, dwarfed descendant species originating by isolation, with founder effect and drift as major influences. A genetic transilience may well have been involved in the species differentiation, together with strong selection for insular dwarfing.

There is some evidence for limited regional morphological trends within the *erectus* material: greater robusticity and increased brain size in sub-Saharan Africa, an early reduction in tooth and jaw size and a later increase in endocranial volume and cranial gracilisation in SE Asia, and a reduction in lower cheek teeth size at Zhoukoudian. Evidence for species-wide morphological trends other than a weak increase in endocranial capacity is limited, and the overall impression is of relative stasis. However, if body size variation did shift between earlier and later populations of the species, or differ between continents, this may represent an important evolutionary adaptation with significant behavioural and socioecological correlates. Much more postcranial material is needed to investigate this possibility.

Accumulating African fossil evidence and a more secure chronological framework indicates that *H. sapiens* there is contemporary with, or even possibly predates, Ngandong *H. erectus* (Bräuer *et al.*1997, White *et al.* 2003, Clark *et al.* 2003, McDougall *et al.* 2005). This indicates species distinction and precludes Ngandong ancestry of modern humans, as argued by proponents of multiregional continuity. Evidence overall indicates *H. erectus* to have been a distinct clade that survived at least until the final Middle Pleistocene, and possibly well into the Upper Pleistocene. It persisted after giving rise to more derived Middle Pleistocene species in Africa and mainland Asia, and was apparently ancestral to one highly localised form – *H. floresiensis*.

ENVOI

Jan Jelínek integrated the fossil and contextual evidence for human evolution within a comprehensive, predominantly anagenetic, conceptual framework. His morphological analyses have stood the test of time extremely well, and many of his observations have turned out to be remarkably prescient. While still attracting many proponents, his preferred framework is no longer the predominant paradigm and my own view is that an alternative model better accords with the totality of current evidence. Whilst he would doubtless have disagreed with the interpretation summarised above, I hope that he would have appreciated the impulsion underlying the shift of view presented here when compared with some of my earlier publications. That impetus is aptly summarised by the remark attributed to the British economist J. M. Keynes: "When the facts change, I change my mind – what do you do?" In that same spirit one might reasonably expect major recasting(s) of this – and other – interpretations as further evidence becomes available.

Particular phyletic models and taxonomies are necessarily transient and ephemeral in their details. In contrast, for maximal understanding of its subject matter, paleoanthropology retains a continuing need for conceptual frameworks informed by that awareness of evolutionary processes and mechanisms which Jan Jelínek personified, within which to integrate the burgeoning and increasingly diverse evidence for human evolution.

ACKNOWLEDGEMENT

I am grateful to Ms. J. Manghan for preparing the figures.

REFERENCES

ABBATE E., ALBIANELLI A., AZAROLI A., BENVENUTI M., TESFAMARIAMI B., BRUNI P., CIPRIANI N., CLARKE R. J., FICARELLI R.M., NAPOLEONE G., PAPINI M., ROOK L., SAGRI M., TECLE T.M., TORRE D, VILLA I., 1998: A one-million-year-old *Homo* cranium from the Danikil (Afar) Depression of Eritrea. *Nature* 393: 458–460.

ACKERMANN R., CHEVERUD J. M., 2004: Detecting genetic drift versus selection in human evolution. *Proc. Nat. Acad. Sci. USA.* 101, 52: 17946–17951.

AIELLO L. C., WELLS J. C. K., 2002: Energetics and the evolution of the genus *Homo. Ann. Rev. Anthrop.* 31: 323–338.

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

ANTON S. C., 2002: Evolutionary significance of cranial variation in Asian *Homo erectus. Amer. J. of Phys. Anthrop.* 118: 301–323.

ANTON S. C., 2003: Natural history of *Homo erectus. Yearbook of Phys. Anthrop*. 46: 126–170.

ANTON S.C., MARQUEZ S., MOWBRAY K., 2002: Sambungmacan 3 and cranial variation in Asian *Homo erectus. J. of Hum. Evol.* 43: 555–562.

ANTON S. C., SWISHER C. S., 2004: Early dispersals of Homo from Africa. *Ann. Rev. Anthropol.* 33: 271–296.

ARIF J., KAIFU Y., BABA H., SUPARKA M. E., ZAIM Y., SETOGUCHI T., 2002: Preliminary observations of a new cranium of *Homo erectus* (Tjg-1993.05) from Sangiran, Central Java. *Anthropological Science* 110, 2: 165–177.

ARSUAGA J.-L., MARTINEZ I., LORENZO C., GRACIA A., MUNOZ A., ALONSO O., GALLEGO J., 1999: The human cranial remains from Gran Dolina Lower Pleistocene site (Sierra de Atapuerca, Spain). *J. of Hum. Evol*. 37: 431–457.

ASCENZI A., BIDDITTU I., CASSOLI P. F., SEGRE A. G., SEGRE-NALDINI E., 1996: A calvarium of late *H. erectus* from Ceprano, Italy. *J. of Hum. Evol*. 31: 409–424.

ASCENZI A., MALAGNI F., MANZI G., SEGRE A. G., SEGRE-NALDINI E., 2000: A re-appraisal of Ceprano calvaria affinities with *Homo erectus* after the new reconstruction. *J. of Hum. Evol*. 39: 443–450.

ASFAW B., BEYENE Y., SUWA G., WALTER R. C., WHITE T. D., WOLDEGABRIEL G., YEMANE T., 1992: The earliest Acheulean from Konso-Gardula. *Nature* 360: 732–735.

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.

ASFAW B., GILBERT W. H., BEYENE Y., HART W. K., RENNE P. R., WOLDEGABRIEL G., VRBA E. S., WHITE T. D., 2002: Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. *Nature* 416: 317–320.

BABA H., AZIZ F., NARASAKI S., 2000: Restoration of the face of Javanese *Homo erectus* Sangiran 17 and re-evaluation of regional continuity in Australia. In: W. Dong (Ed.): *Proc. 1999 Beijing International Symposium on Paleoanthropology*. Suppl. to *Acta Anthropologica Sinica* 19: 34–40.

BABA H., AZIZ F., KAIFU Y., SUWA G., KONO R.T., JACOB T., 2003: *Homo erectus* calvarium from the Pleistocene of Java. *Science* 299: 1384–1388.

BELMAKER M., TCHERNOV E., CONDEMI S., BAR-JOSEF O., 2002: New evidence for hominid presence in the Lower Pleistocene of the Southern Levant. *J. of Hum. Evol.* 43: 43–56.

BERMUDEZ DE CASTRO J. M., ROSAS A., NICOLAS M. E., 1999: Dental remains from Atapuerca-TD6 (Gran Dolina site, Burgos, Spain). *J. of Hum. Evol*. 37: 523–566.

BILSBOROUGH A., 1976: Patterns of evolution in Middle Pleistocene hominids. *J. of Hum. Evol.,* 5: 423–439.

BILSBOROUGH A., 1978: Some aspects of mosaic evolution in hominids. In: D. J. Chivers, K. A. Joysey (Eds.): *Recent Advances in Primatology 3: Evolution*. Pp. 335–350. Academic Press, London.

BILSBOROUGH A., 1983: The pattern of evolution within the genus *Homo*. In: V. Navaratnam, R. J. Harrison (Eds.): *Progress in Anatomy* 3. Pp. 143–164. Cambridge Univ. Press, Cambridge.

BILSBOROUGH A., 1992: *Human Evolution*. Blackie, Chapman and Hall, London, Glasgow. 258 pp.

BILSBOROUGH A., 1999: Contingency, patterning and species in hominid evolution. In: J. L. Bintliff (Ed.): *Structure and Contingency: Evolutionary Processes in Life and Human Society.* Pp. 43–101. Leicester Univ. Press, London.

BILSBOROUGH A., 2000a: Phenetic patterning and species sorting in early African *Homo. Anthropologie* XXXVIII, 2: 151–163.

BILSBOROUGH A., 2000b: Chronology, variability and evolution in *Homo erectus. Variability and Evolution* 8: 5–39.

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

BLUMENSCHINE R. J., PETERS C. R., MASAO F. T., CLARKE R. J., DELNO A. L., HAY R. H., SWISHER C. S., STANISTREET I. G., ASHLEY G. M., McHENRY L. J., SIKES N. E., VAN DER MERWE N. J., TACTIKOS J. C., CUSHING A. E., DEOCAMPO D. M., NJAU J. K., EBERT J. I., 2003: Late Pliocene Homo and hominid land use from western Olduvai Gorge, Tanzania. *Science* 229: 1217–1221.

BRÄUER G., 1984: A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In: F. H. Smith, F. Spencer (Eds.): *The Origin of Modern Humans: a World Survey of the Fossil Evidence*. Pp. 387–410. Liss, New York.

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.

BRÄUER G., SCHULTZ M., 1996: The morphological affinities of the Plio-Pleistocene mandible from Dmanisi, Georgia. *J. of Hum. Evol*. 30: 445–482.

BRÄUER G., STRINGER C., 1997: Models, polarisation and perspectives on modern human origins. In: G. A. Clark, C. M. Willermet (Eds.): *Conceptual Issues in Modern Human Origins Research.* Pp. 191–201. Aldine, Chicago.

BRÄUER G., YOKOHAMA Y., FALGUERES C., MBUA E., 1997: Modern human origins backdated. *Nature* 386: 337–338.

BROADFIELD D. C., HOLLOWAY R. L., MOWBRAY K., SILVERS A., YUAN M. S., MARQUEZ S., 2001: Endocast of Sambungmacan 3 (Sm 3): A new *Homo erectus* from Indonesia. *Anat. Rec*. 262: 369–379.

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.

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

BROWN F. H., McDOUGALL I., 1993: Geologic setting and age. In: A. Walker, R. Leakey (Eds.): *The Nariokotome Homo erectus Skeleton*. Pp. 9–20. Harvard Univ. Press, Cambridge, Mass.

BROWN P., SUTIKNA T., MORWOOD M. J., SOEJONO R. P., JATMIKO E. W. S., ROKUS A. D., 2004: A new small-bodied hominin from the late Pleistocene of Flores, Indonesia. *Nature* 431, 1065–1061.

CAMPBELL B. G., 1965: The nomenclature of the Hominidae including a definitive list of hominid taxa. *Royal Anthrop. Inst. Occ. Paper* 22: 1–33

CARBONELL E., BERMUDEZ DE CASTRO J. M., ARSUAGA J. L., DIEZ J. C., ROSAS A., CUENCA-BESCOS G., SALA R., MOSQUERA M., RODRIGUEZ X. P., 1995: Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). *Science* 269: 826–830.

CARSON H. L., 1975: The genetics of speciation at the diploid level. *The American Naturalist* 109: 73–92.

CARSON H. L., 1987: The genetic system, the Deme and the origin of species. *Ann. Rev. of Genetics* 21: 405–423.

CLARK J. D., BEYENE Y., WOLDEGABRIEL G., HART W. K., RENNE P. R., GILBERT H., DEFLEUR A., SEWA G., KATOH S., LUDWIG K. R., BOISSERIE J-R., ASFAW B., WHITE T. D., 2003: Stratigraphic, chronological and behavioural contexts of Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423: 747–752.

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

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. Seneckenberg. 171*: 185–193.

CLARKE R. J., 2000: A corrected reconstruction and interpetation of the *Homo erectus* calvaria from Ceprano, Italy. *J. of Hum. Evol*. 39: 433–442.

CLAUSEN I. H. S., 1989: Cranial capacity in *Homo erectus*: stasis or non stasis, direction of trend. In: G. Giacobini (Ed.): *Hominidae: Proceedings of the 2nd International Congress of Human Paleontology.* Pp. 217–220. Jaca, Milan.

CONROY G. C., 2002: Speciosity in the *Homo* lineage: too many, too few or just about right? *J. of Hum. Evol*. 43 759–766.

CRONIN J. E., BOAZ N. T., STRINGER C. B., RAK Y., 1981: Tempo and mode in hominid evolution. *Nature* 292: 113–122.

DELSON E., HARVATI K., REDDY D., MARCUS L. F., MOWBRAY K., SAWYER G. J., JACOB T., MARQUEZ S., 2001: The Sambungmacan 3 *Homo erectus* calvaria: a comparative morphometric and morphological analysis. *Anat. Rec*. 262: 380–397.

DE VOS J., 1985: Faunal stratigraphy and correlation of the Indonesian hominid sites. In: E. Delson (Ed.): *Ancestors: the Hard Evidence.* Pp. 215–220. Liss, New York.

DE VOS J., SONDAAR P., 1994: Dating hominid sites in Indonesia. *Science* 266: 1726–1727.

DE VOS J., SONDAAR P. Y., VAN DEN BURGH G. D., AZIZ F., 1994: The *Homo* bearing deposits of Java and its ecological context. In: J. Franzen (Ed.): 100 Years of Pithecanthropus: The Homo erectus Problem. *Courier Forschungs-Institut Senckenberg* 171: 129–140.

ELDREDGE N., 1995: *Reinventing Darwin: The Great Evolutionary Debate.* Weidenfeld and Nicolson, London. 244 pp.

FALK D., HILDEBOLT C., SMITH K., MORWOOD M. J., SUTIKNA T., BROWN P., JATMIKO, SAPTOMO E.W., BRUNSDEN B., PRIOR F., 2005: The Brain of LB1, *Homo floresiensis. Science* 308: 242–245.

FEIBEL C. S., BROWN F. H., McDOUGALL I., 1989: Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya and Ethiopia. *Amer. J. of Phys. Anthrop.* 78: 595–622.

FOLEY R. A., 1995: *Humans before Humanity: an Evolutionary Perspective.* Blackwells, Oxford. 238 pp.

FRAZEN, J. L., 1985: What is "*Pithecanthropus dubius Koenigswald*, 1950"? In: E. Delson (Ed.): *Ancestors: the Hard Evidence.* Pp. 221–226. Liss, New York.

FUTUYMA D. L., 1987: On the role of species in Anagenesis. *The American Naturalist* 130: 465–473.

GABUNIA L., VEKUA A., 1995: A Plio-Pleistocene hominid from Dmanisi, east Georgia, Caucasus. *Nature* 373: 509–512.

GABUNIA L., VEKUA A., LORDKIPANIDZE D., SWISHER C. S., FERRING R., JUSTUS A., NIORADZE M., TVALCHRELIDZE M., ANTON S. C., BOSINSKI G., JORIS O., DE LUMLEY M.-A., MAJSURADZE G., MOUSKHELISHVILI A. 2000a: Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting, and age. *Science* 288: 1019–1025.

GABUNIA L., VEKUA A., LORDKIPANIDZE D., 2000b: Taxonomy of the Dmanisi crania. *Science* 289: 55–56.

GABUNIA L., ANTON S. C. LORDKIPANIDZE D., VEKUA A., JUSTUS A., SWISHER C. C., 2001: Dmanisi and dispersal. *Evol. Anthrop.* 10: 158–170.

GABUNIA L., DE LUMLEY M. A., VEKUA A., LORDKIPANIDZE D., DE LUMLEY H., 2002: Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Georgie). *Comptes Rendus Palevol*. 1: 243–253.

GIBBONS A., 2003: A shrunken head for African *Homo erectus. Science* 300: 893.

GILBERT W. H., WHITE T. D., ASFAW B., 2003: *Homo erectus, Homo ergaster, Homo "cepranensis"* and the Daka cranium. *J. of Hum. Evol*. 45: 255–260.

GODFREY L., JACOBS K. H., 1981: Gradual, autocatylytic and punctuational models of hominid brain evolution: a cautionary tale. *J. of Hum. Evol.* 10: 255–272.

GOLDBERG P., WEINER S., BAR-JOSEF O., XU Q., LIU J., 2001: Site formation processes at Zhoukoudian, China. *J. of Hum. Evol*. 41: 483–530.

GOULD S. J., 1985: The paradox of the first tier: an agenda for paleobiology. *Paleobiology* 11, 1: 2–12.

GRIMAUD-HERVE D., WIDIANTO H., JACOB T., 2000: Two new human fossil remains discovered in Sangiran (Central Java, Indonesia). In: Wu Xinzhi, Zang Senshui, Dog Wei (Eds.): *Proc. 1999 Beijing International Symposium on Paleoanthropology. Suppl. to Acta Anthropologica Sinica* 19: 41–45.

GRINE F. E., FRANZEN J. L., 1994: Fossil hominid teeth from the Sangiran Dome (Java, Indonesia). In: J. Franzen (Ed.): 100 Years of Pithecanthropus: The Homo erectus Problem. *Cour. Forsch.-Inst. Senckenberg* 171: 75–103.

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.

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.

GROVES C. P., 1989: *A Theory of Human and Primate Evolution*. Clarendon Press, Oxford. 375 pp.

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

GRUN R., THORNE A., 1997: Dating the Ngandong Humans. *Science* 276: 1575.

GRUN R., HUANG P.-H., WU X., STRINGER C. B., THORNE A., McCULLOCH M., 1997: ESR analysis of teeth from the palaeoanthropological site of Zhoukoudian, China. *J. of Hum. Evol.* 32: 83–91.

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.

HOWELL F. C., 1960: European and Northwest African Middle Pleistocene hominids. *Curr. Anthrop.* 1: 195–232.

HOWELL F. C., 1967: Recent advances in human evolutionary studies. *Quart. Rev. Biol*. 42, 4: 471–513.

HOWELL F. C., 1978: Hominidae. In: V. J. Maglio, H. B. S. Cooke (Eds.): *Evolution of African Mammals.* Pp.154–248. Harvard Univ. Press, Cambridge, Mass.

HOWELL F. C., 1994: A chronostratigraphic and taxonomic framework of the origins of modern humans. In: M. H. Nitecki, D. V. Nitecki (Eds.): *Origins of Anatomically Modern Humans.* Pp. 253–319. Plenum, New York, London.

HOWELL F. C., 1996: Thoughts on the study and interpretation of the human fossil record. In: W. E. Meikle, F. C. Howell, N. G. Jablonski (Eds.): *Contemporary Issues in Human Evolution. Calif. Acad. Sci* 21: 1–45.

HOWELL F. C., 1999: Paleo-demes, species clades, and extinctions in the Pleistocene hominin record. *J. of Anthrop. Research* 55: 191–243.

HUBLIN J. J., 1985: Human fossils from the North African Middle Pleistocene and the origin of *Homo sapiens*. In: E. Delson (Ed.): *Ancestors: The Hard Evidence.* Pp. 283–288. Liss, New York.

HYODO M., NAKAYA H., URABE A., SAEGUSA H., YIN JIYUN X. S., XUEPIN J., 2002: Paleomagnetic dates of hominid remains from Yuanmou, China and other Asian sites. *J. of Hum. Evol*. 43: 27–41.

ITIHARA M., WATANABE N., KADAR D., KUMAI H., 1994: Quaternary stratigraphy of the hominid fossil bearing formations in the Sangiran area, Central Java. In: J. Franzen (Ed.): 100 Years of Pithecanthropus: The Homo erectus Problem. *Courier Forschungs-Institut Senckenberg,* 171:123–128.

JACOB T., 1980: The *Pithecanthropus* of Indonesia: Phenotype, genetics and ecology. In: L. K. Konigsson (Ed.): *Current Argument on Early Man*. Pp.170–179. Pergamon, Oxford.

JELÍNEK J., 1978: *Homo erectus* or *Homo sapiens?* In: D. J. Chivers, K. A. Joysey (Eds.): *Recent Advances in Primatology 3: Evolution.* Pp. 419–430. Academic Press, London.

JELÍNEK J., 1980a: European *Homo erectus* and the origin of *Homo sapiens.* In: L. K. Konigson (Ed.): *Current Argument on Early Man.* Pp. 137–144. Pergamon, Oxford.

JELÍNEK J., 1980b: Was Homo erectus already Homo sapiens? Les Processus de l'hominisation *Coll. Int. du C.N.R.S.* 599: 85–89.

JELÍNEK J., 1980c: Variability and geography. *Anthropologie (Brno)* XVIII, 2-3: 109–114.

JELÍNEK J., 1982a: The East and Southeast way of regional evolution. *Man and His Origins. Anthropos (Brno)* 21: 195–212.

JELÍNEK, J., 1982b: The Position of Anteneanderthals among the hominids. *Proc. Congrès International de Paléontologie Humaine* XXX: 937–948.

JELÍNEK J., 1985: The European, Near East and North African finds after *Australopithecus* and the principal consequencies for the picture of human evolution. In: P. V. Tobias (Ed.): *Hominid Evolution: Past, Present and Future.* Pp. 341–354. Liss, New York.

JELÍNEK J., 1997: Azych, Mid-pleistocene mandible from sub-Caucasian region. *Anthropologie et Préhistoire* 108: 63–68.

KAIFU Y., AZIZ F., BABA H., 2005a: Hominid mandibular remains from Sangiran: 1952–1986. *Amer. J. of Phys. Anthrop*. 128: 497–519.

KAIFU Y., BABA H., AZIZ F., INDRIATI E., SCHRENK F., JACOB T., 2005b: Taxonomic affinities and evolutionary history of the early Pleistocene hominids of Java: dentognathic evidence. *Amer. J. of Phys. Anthrop*. 128: 709–726.

KIDDER J., DURBAND A. C., 2004: A re-evaluation of the metric diversity within *Homo erectus. J. of Hum. Evol*. 46: 299–315.

KIMBEL W. H., MARTIN L. B., 1993: *Species, Species Concepts and Primate Evolution*. Plenum, New York, London, 560 pp.

KIMBEL W. H., WALTER R. C., JOHANSON D. C., REED K. E., ARONSON J. L., ASSEFA Z., MAREAN C. W., ECK G. G., BOBE R., HOVERS E., RAK Y., VONDA C., YEMANE T., YORK D., CHEN Y., EVENSEN N. M., SMITH P. E., 1996: Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *J. of Hum. Evol*. 31: 549–561.

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.

KLEIN R. G., 1999: *The Human Career: Human Biological and Cultural Origins* (2nd. ed). Chicago Univ. Press: Chicago, London. 810 pp.

KOENIGSWALD G. H. R. von, 1968: Observations upon two *Pithecanthropus* mandibles from Sangiran, Central Java. *Proc. Koninkl. Nederl. Akad. Wetensch*. B 71: 99–107.

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., 1994: A critical analysis of claims for the existence of Southeast Asian Australopithecines. *J. of Hum. Evol.* 26: 3–21.

KRAMER A., KONIGSBERG L. W., 1994: The phyletic position of Sangiran 6 as determined by multivariate analysis. In: J. Franzen (Ed.): 100 Years of Pithecanthropus: The Homo erectus Problem. *Cour. Forsch. Inst. Seneckenberg.* 171: 105–114.

LANGBROEK M., ROEBROEKS W., 2000: Extraterrestrial evidence on the age of the hominids from Java. *J. of Hum. Evol.* 38: 595–600.

LARICK R., CIOCHON R. L., ZAIM Y., SUDIJONO, SUMINTO, RIZAL Y., AZIZ F., REAGAN M., HEIZLER M., 2001: Early Pleistocene ^{40}Ar/^{39}Ar ages for Bapang Formation hominins, Central Java, Indonesia. *Proc. Nat. Acad. Sci. USA*. 98, 9: 4866–4871.

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 M. G., SPOOR F., BROWN F. H., GATHOGO P. N., LEAKEY L. N., 2003: A new hominin calvarium from Ileret (Kenya). *Amer. J. of Phys. Anthrop.* 120: 136.

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.

LEAKEY R. E. F., WALKER A. C., 1989: Early *Homo erectus* from West Lake Turkana, Kenya. In: G. Giacobini (Ed.): *Hominidae. Proc. 2nd Int. Congress of Human Paleontology.* Pp. 209–216. Jaca, Milan.

LEE S.-H., 2005: Is variation in the cranial capacity of the Dmanisi sample too high to be from a single species? *Amer. J. of Phys. Anthrop*. 127: 263–266.

LEE S.-H., WOLPOFF M. H., 2003: The pattern of evolution in Pleistocene human brain size. *Paleobiology* 29: 186–196.

LEIGH S. R., 1992: Cranial capacity evolution in *Homo erectus* and early *Homo sapiens. Amer. J. of Phys. Anthrop*. 87: 1–13.

LIU Z., 1985: Sequence of sediments at Locality 1 in Zhoukoudian and correlation with loess stratigraphy in Northern China and with the chronology of Deep-Sea Cores. *Quaternary Research* 23: 139–153.

LIU W., ZHANG Y., WU X., 2005: Middle Pleistocene human cranium from Tangshen (Nanjing) Southeast China: A new reconstruction and comparisons with *Homo erectus* from Eurasia and Africa. *Amer. J. of Phys. Anthrop*. 127:253–262.

LORDKIPANIDZE D., VEKUA A., FERRING R., RIGHTMIRE G. P., AUGUSTI J., KILADZE G., MOUSKHELISHVILI A., NIORADZE M., PONCE DE LEON M. S., TAPPEN M., ZOLLIKOFER C. P. E., 2005: Anthropology: The earliest toothless hominin skull. *Nature* 434: 717–718.

LOVEJOY C. O., 1970: The taxonomic status of the "Meganthropus" mandibular fragments from the Djetis beds of Java. *Man* (n.s.) 5, 2: 228–236.

MALLEGNI F., CARNIERI E., BISCONTI M., TARTARELLI G., RICCI S., BIDDITU I., SEGRE A., 2003: *Homo cepranensis sp. nov* and the evolution of African-European Middle Pleistocene hominids. *C. R. Palevol*. 2: 153–159.

MANZI G., BRUNER E., PASSARELLO P., 2003: The one-million-year-old *Homo* cranium from Bouri (Ethiopia): a reconsideration of its *H. erectus* affinities. *J. of Hum. Evol*. 44: 731–736.

MARQUEZ S., MOWBRAY K., SAWYER G. J., JACOB T., SILVERS A., 2001: New fossil hominid calvaria from Indonesia – Sambungmacan 3. *Anat. Rec.* 262: 344–368.

MAYR E., 1954: Changes in genetic environment and evolution. In: J. S. Huxley, A. C. Hardy, E. B. Ford (Eds.): *Evolution as a Process.* Pp.188–213. Allen and Unwin, London.

McDERMOTT F., STRINGER C., GRUN R., WILLIAMS C. T., DIN V., HAWKESWORTH C., 1996: New Late-Pleistocene uranium-thorium and ESR dates for the Singa hominid (Sudan). *J. of Hum. Evol*. 31: 507–516.

McDOUGALL I., BROWN F. H., FLEAGLE J. G., 2005: Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature* 433:733–736.

MORWOOD M. J., O'SULLIVAN P. B., AZIZ F., RAZA A., 1998: Fission-track ages of stone tools and fossils on the east Indonesian island of Flores. *Nature* 392: 173–176.

MORWOOD M. J., SOEJONO R. P., ROBERTS R. G., SUTIKNA T., TURNEY C. S. M., WESTAWY K. E., RINK W. J., ZHAO J.-X, VAN DEN BURGH G. D., DUE R. A., HOBBS D. R., MOORE M. W., BIRD M. L. FIFIELD L. K., 2004: Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature* 431: 1087–1091.

POPE G. G., 1988: Recent advances in Far Eastern paleoanthropology. *Ann. Rev. of Anthrop.* 17: 43–77.

POPE G. G., 1991: Evolution of the zygomaticomaxillary region in the genus *Homo* and its relevance to the origin of modern humans. *J. of Hum. Evol*. 21: 189–213.

POPE G. G., 1992: Craniofacial evidence for the origin of modern humans in China. *Yearbook of Phys. Anthrop*. 35: 243–298.

POTTS R., BEHRENSMEYER A. K., DEINO A., DITCHFIELD P., CLARK J., 2004: Small mid-pleistocene hominin associated with East African Acheulean technology. *Science* 305: 75–78.

PRAT S., BRUGAL J.-P., TIERCELIN J.-J., BARRAT J.-A., BOHN M., DELAGNES A., HARMAND S., KIMEU K., KEBUNJIA M., TEXIER P.-J., ROCHE H., 2005: First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3–2.4 Myr. *J. of Hum. Evol*. 49: 230–240.

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., 1981: Patterns in the evolution of *Homo erectus. Paleobiology,* 7: 241–246.

RIGHTMIRE G. P., 1984: Comparison of *Homo erectus* from Africa and S. E. Asia. *Courier Forschungs-Institut Senckenburg* 69: 83–98.

RIGHTMIRE G. P., 1985: The tempo of change in the evolution of mid-Pleistocene *Homo.* In: E. Delson (Ed.): *Ancestors: the Hard Evidence*. Pp. 255–264. Liss, New York.

RIGHTMIRE G. P., 1986a: Species recognition and *Homo erectus. J. of Hum. Evol.* 15: 823–826.

RIGHTMIRE G. P., 1986b: Stasis in *Homo erectus* defended. *Paleobiology* 12: 324–325.

RIGHTMIRE G. P., 1990: *The Evolution of Homo erectus. Comparative Anatomical Studies of an Extinct Human Species.* Cambridge University Press. 260 pp.

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., 1994: The relationship of *Homo erectus* to later Middle Pleistocene hominids. In: J. Franzen (Ed.): 100 Years of Pithecanthropus: The Homo erectus Problem. *Courier Forschungs-Institut Senckenberg* 171: 319–326.

RIGHTMIRE G. P., 1996: The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? *J. of Hum. Evol*. 31: 21–39.

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

RIGHTMIRE, G. P., 1998b: Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. *Evol. Anthrop*. 6: 218–227.

RIGHTMIRE G. P., 2004: Brain size and encephalisation in Early to Mid-Pleistocene *Homo. Amer. J. of Phys. Anthrop.* 24: 109–123.

RUFF C. B., TRINKAUS E., HOLLIDAY T. W., 1997: Body mass and encephalisation in Pleistocene *Homo. Nature* 387: 173–176.

SANTA LUCA A. P., 1980: The Ngandong fossil hominids. *Yale University Publications in Anthropology* 78: l–175.

SCHICK K., TOTH N., WEI Q., CLARK J. D., ETLER D., 1991: Archaeological perspectives in the Nihewan Basin, China. *J. of Hum. Evol*. 21: 13–26.

SCHWARTZ J. H., 2000: Taxonomy of the Dmanisi crania. *Science* 289: 55.

SCHWARTZ J. H., 2004: Getting to know *Homo erectus. Science* 305: 53–54.

SCHWARTZ J. H., TATTERSALL I., 1996: Whose teeth? *Nature* 381: 201–202.

SCHWARTZ J. H., TATTERSALL, I. 2000: What constitutes *Homo erectus?* In: W. Dong (Ed.): *Proc. 1999 Beijing International Symposium on Paleoanthropology*. *Suppl. to Acta Anthropologica Sinica* 19: 18–22.

SCHWARTZ J. H., TATTERSALL I., 2002: *The Human Fossil Record. Volume 1. Terminology and Craniodental Morphology of Genus Homo (Europe).* Wiley-Liss, New York. 388 pp.

SCHWARTZ J. H., TATTERSALL I., 2003: *The Human Fossil Record. Volume 2. Craniodental Morphology of Genus Homo (Africa and Asia).* New York, Wiley-Liss. 603 pp.

SHEN G.-J., WANG J.-Q., 2000: Chronological studies on Chinese Middle-Late Pleistocene hominid sites. In: W. Dong (Ed.): *Proc. 1999 Beijing International Symposium on Paleoanthropology.* Suppl. to *Acta Anthropologica Sinica* 19: 279–284.

SHERWOOD R. J., WARD S. C., HILL A., 2002: The taxonomic status of the Chemeron temporal (KNM-BC 1). *J. of Hum. Evol*. 42: 153–184.

SMITH F. H., 1992: Models and realities in modern human origins: the African fossil evidence. *Phil. Trans. Roy. Soc. B*. 337: 243–250.

SMITH F. H., 1994: Samples, species and speculations in the study of modern human origins. In: M. H. Nitecki, D. V. Nitecki (Eds.): *Origins of Anatomically Modern Humans.* Pp. 227–249. Plenum, New York.

SMITH F. H., SIMEK J., HARRILL M., 1989: Geographical variation in supraorbital torus reduction during the later Pleistocene (c 80 000–15 000 BP). In: P. Mellars, C. B. Stringer (Eds.): *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Pp. 172–193. Edinburgh Univ. Press, Edinburgh.

STANLEY, S. M., 1979: *Macroevolution: Pattern and Process*. W. H. Freeman, San Francisco. 332 pp.

STANLEY, S. M., 1981: *The New Evolutionary Timetable: Fossils, Genes and the Origin of the Species*. Basic Books, New York. 222 pp.

STANLEY S. M., 1992: An ecological theory for the origin of *Homo. Paleobiology* 18(3): 237–257.

STORM P., AZIZ F., DE VOS J., KOSASIH D., BASKORO S., NGALIMAN, VAN DEN HOEK OSTENDE, L. W., 2005: Late Pleistocene *Homo sapiens* in a tropical rainforest fauna in East Java. *J. of Hum. Evol*. 49: 536–545.

STRINGER C. B., 1979: A re-evaluation of the fossil human calvaria from Singa, Sudan. *Bull. of Brit. Mus. Nat. Hist. and Geol*. 32, 1: 77–83.

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.

SWISHER C. C., 1994: Dating hominid sites in Indonesia. *Science* 266: 1727.

SWISHER C. C., RINK W. J., ANTON S. C., SCHWARTZ H. P., CURTIS G. H., SUPRIJO A., WIDIASMORO, 1996a: Latest *Homo erectus* of Java: potential contemporaneity with *Homo sapiens* in Southeast Asia. *Science* 274: 1870–1874.

SWISHER C. C., RINK W. J., SCHWARCZ H. P., ANTON S. C., 1996b: Dating the Ngandong humans. *Science* 274: 1870.

SWISHER C. C., RINK W. J., SCHWARCZ H. P., ANTON S. C., 1997: Dating the Ngandong humans. *Science* 276**:** 1575–1576.

SWISHER C. C., CURTIS G. H., JACOB T., GETTY A. G., SUPRIJO A., WIDIASMORO T., 1994: Age of the earliest known hominids in Java, Indonesia. *Science* 263: 1118–1121.

TATTERSALL I., 1986: Species recognition in human palaeontology. *J. of Hum. Evol.* 15: l65–175.

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

TATTERSALL I., 1995: *The Fossil Trail*. Oxford University Press, New York. 288 pp.

TATTERSALL, I., SCHWARTZ J. H., 2001: *Extinct Humans*. Westview Press, Boulder. 255 pp.

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

TEMPLETON A. R., 1980: The theory of speciation via the Founder Principle. *Genetics* 94: 1011–1035.

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.

THORNE A., 1981: The centre and the edge: the significance of Australian hominids to African palaeoanthropology. In: R. E. F. Leakey, B. A. Ogot (Eds.): *Proc. 8th Pan African Congress of Prehistory and Quaternary Studies*. Pp. 180–181. TILLMIAP, Nairobi.

THORNE A., WOLPOFF M. H., 1981: Regional continuity in Australian Pleistocene hominid evolution. *Amer. J. of Phys. Anthrop.* 55: 337–349.

TOBIAS P. V., 1966: Fossil hominid remains from Ubeidiya, Israel. *Nature* 211: 130–133.

TOBIAS P. V., 1978: Primatology, palaeoanthropology and reticulate evolution: concluding remarks. In: D. J. Chivers, K. A. Joysey (Eds.): *Recent Advances in Primatology 3: Evolution.* Pp. 507–509. Academic Press, London.

TOBIAS P. V., 1991: *Olduvai Gorge: Vol. 4. The Skulls, Endocasts and Teeth of Homo habilis*. Cambridge University Press, Cambridge. 921 pp.

TOBIAS P. V., VON KOENIGSWALD G. H. R., 1964: A comparison between the Olduvai hominines and those of Java and some implications for hominid phylogeny. *Nature* 204: 515–518.

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

TYLER D. E., 1994: The taxonomic status of "*Meganthropus*". In: J. Franzen (Ed.): 100 Years of Pithecanthropus: The Homo erectus Problem. *Cour. Forsch.-Inst. Senckenberg* 171: 115–121.

TYLER D. E., SARTONO S., 2001: A new *Homo erectus* cranium from Sangiran, Java. *Hum. Evol.* 16, 1:13–25.

VEKUA A., LORDKIPANIDZE D., RIGHTMIRE G. P., AGUSTI J., FERRING R., MAISURADZE G., MOUSKHELISHVILI A., NIORADZE N., PONCE DE LEON M., TAPPEN M., TVALCHRELIDZE M., ZOLLIFIKER C., 2002: A new skull of early *Homo* from Dmanisi, Georgia. *Science* 297: 85–89.

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 Honour of Davidson Black*. Pp. 193–215. Univ. 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 University Press, Cambridge, Mass.

WANG Q., TOBIAS P. V., 2000: Recent advances in Chinese palaeoanthropology**.** *S. Afr. J. Sci*. 96: 9–10.

WANPO H., CIOCHAN R., YUMIN G., LARICK R., QIREN F., SCHWARCZ H., YONGE C., DE VOS J., RINK W., 1995: Early *Homo* and associated artefacts from Asia. *Nature* 378: 275–278.

WEIDENREICH F., 1936: The mandibles of *Sinanthropus pekinensis*: a comparative study. *Palaeont. Sinica*. Series D 7: 1–162.

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 of the Amer*. *Mus. Nat. Hist*. 40: 1–134.

WEIDENREICH F., 1951: Morphology of Solo Man. *Anth. Papers of the Amer. Mus. of Nat. Hist.* 43: 205–290.

WHITE T. D., ASFAW B., DEGUSTA D., GILBERT H., RICHARDS G. D., SEWA G., HOWELL F. C., 2003: Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423: 742–747

WINDIANTO H., SEMAH A-M., DJUBIANTONO T., SEMAH F., 1994: A tentative reconstruction of the cranial remains of Hanoman 1 from Bukuran, Sangiran (Central Java). In: J. Franzen (Ed.): 100 Years of Pithecanthropus: The Homo erectus Problem. *Courier Forschungs-Institut Senckenberg* 171: 47–59.

WOLPOFF M. H., 1984: Evolution in *Homo erectus*: the question of stasis. *Paleobiology* 10, 4: 389–406.

WOLPOFF M. H., 1985: Human evolution at the peripheries: the pattern at the eastern edge. In: P. V. Tobias (Ed.): *Hominid Evolution Past, Present and Future*. Pp. 355–366. Liss, New York.

WOLPOFF M. H., 1986: Stasis in the interpretation of evolution in *Homo erectus*: a reply to Rightmire. *Paleobiology* 12, 3: 325–328.

WOLPOFF M. H., 1989: Multiregional evolution: the fossil alternative to Eden. In: P. Mellars, C. Stringer (Eds.): *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Pp. 62–108. Edinburgh Univ. Press, Edinburgh.

WOLPOFF M. H., 1999: *Paleoanthropology* (2nd. ed.). McGraw-Hill, Boston. 878 pp.

WOLPOFF M. H., THORNE A. G., JELÍNEK J., ZHANG Y., 1994a: 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.

WOLPOFF M. H., THORNE A. G., SMITH F. H., FRAYER D. W., POPE G. G., 1994b: Multiregional evolution: A world-wide source for modern human populations. In: M. H. Nitecki, D. V. Nitecki (Eds.): *Origins of Anatomically Modern Humans.* Pp.175–199. Plenum, New York and London.

WOLPOFF M. H., WU Z., THORNE A., 1984: Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. In: F. H. Smith, F. Spencer (Eds.): *The Origins of Modern Humans: A World Survey of the Fossil Evidence.* Pp. 411–483. Liss, New York.

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

WOOD B. A., 1991: *Koobi Fora Research Project. Vol. 4. Hominid Cranial Remains.* Clarendon Press, Oxford. 466 pp.

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

WOOD B. A., 1992b: Hominid species and speciation. *J. of Hum. Evol.* 22: 351–365.

ZHANG Y., 1991: An examination of temporal variation in the hominid dental sample from Zhoukoudian Locality 1. *Acta Anthropologica Sinica* 10, 5: 85–95.

ZHU R.X., HOFFUMAN K. A., POTTS R., DENG C. L., PAN Y. X., GUO B., SHI C. D., GUO Z. T., YUAN B. Y., HOU Y. M., HUANG W. W., 2001: Earliest presence of humans in northeast Asia. *Nature* 413: 413–417.

Alan Bilsborough
Evolutionary Anthropology Research Group
Department of Anthropology
Durham University
Durham DH1 3HN, UK
E-mail: Alan.Bilsborough@durham.ac.uk