

Natural History of *Homo erectus*

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ABSTRACT Our view of *H. erectus* is vastly different today than when *Pithecanthropus erectus* was described in 1894. Since its synonymization into *Homo*, views of the species and its distribution have varied from a single, widely dispersed, polytypic species ultimately ancestral to all later *Homo*, to a derived, regional isolate ultimately marginal to later hominin evolution. A revised chronostratigraphic framework and recent work bearing either directly or indirectly on reconstructions of life-history patterns are reviewed here and, together with a review of the cranial and postcranial anatomy of *H. erectus*, are used to generate a natural history of the species. Here I argue that *H. erectus* is a hominin, notable for its increased body size, that originates in the latest Pliocene/earliest Pleistocene of Africa and quickly disperses into Western and Eastern Asia. It is also an increasingly derived hominin

with several regional morphs sustained by intermittent isolation, particularly in Southeast Asia. This view differs from several current views, most especially that which recognizes only a single hominin species in the Pleistocene, *H. sapiens*, and those which would atomize *H. erectus* into a multiplicity of taxa. Following Jolly ([2001] *Yrbk Phys Anthropol* 44:177–204), the regional morphs of *H. erectus* may be productively viewed as geographically replacing allotaxa, rather than as the focus of unresolvable species debates. Such a view allows us to focus on the adaptations and biology of local groups, including questions of biogeographic isolation and local adaptation. A number of issues remain unresolved, including the significance of diversity in size and shape in the early African and Georgian records. *Yrbk Phys Anthropol* 46:126–170, 2003. © 2003 Wiley-Liss, Inc.

A VIEW OF THE SPECIES

Our view of *H. erectus* is vastly different today than when *Pithecanthropus erectus*, then only the second fossil hominin taxon to be discovered, was described by Dubois (1894). At that time, *H. erectus* was the most primitive and smallest-brained of the fossil hominins. Thus, early analyses expended great effort demonstrating that the Indonesian fossils from Trinil were, in fact, hominins (e.g., Dubois 1894, 1924, 1926a, b, 1932; Schwalbe, 1899). It took the dismissal of Piltdown and the broad acceptance of *Australopithecus* as a hominin ancestor, along with the substantial Asian fossil finds of the 1930s, before the hominin nature and relatively large brain of *H. erectus* would be appreciated by most human paleontologists (see also Trinkaus, 1982). Indeed, as late as 1957, Boule and Vallois (1957, p. 110) continued to portray *Pithecanthropus* and *Sinanthropus* as “Prehominians,” describing them as “extremely primitive in all their characters. They show how close our family still was to the great Anthropoid Apes at the beginning of the Quaternary.”

These relatively large-brained and moderately toothed fossil hominins from both Africa and Asia would eventually be recognized as more similar to *Homo* than to the australopithecids. Yet until 1950, nearly each new find was attributed its own specific and often generic status, although many workers in particular regions had long recognized the essential, and probably specific, similarity of the fossils they

studied (e.g., Dubois, 1936; von Koenigswald and Weidenreich, 1939; Weidenreich, 1940, 1943, 1951; but see Black, 1931). In the context of the evolutionary synthesis of the 1940s, Mayr (1944, 1950) officially synonymized these multiple taxa (*Pithecanthropus*, *Sinanthropus*, *Meganthropus*, and *Telanthropus*) under *Homo erectus*, followed in 1964 by the inclusion of the North African remains from Ternifine (LeGros Clark, 1964). Cranial fossils discovered at Olduvai in the 1960s, such as Olduvai Hominid 9 (originally *Homo leakeyi*; Heberer, 1963), were also subsumed rather easily into *H. erectus* (Le Gros Clark, 1964).

With this synonymization followed a period of some 30 years during which the predominant view, particularly in the US and Western Europe, held *H. erectus* to be a single, widely dispersed, geologically long-lived, polytypic species. *H. erectus* became the presumptive ancestor, in either a unilineal or interwoven multilineal scheme, for both Neandertals and ourselves (Howell, 1978). Into this taxon were placed not only the East Asian and African forms,

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but also the larger-brained forms from Middle Pleistocene Europe, including Arago (Tautavel), Steinheim, and so on (e.g., Wuest, 1951; de Lumley and de Lumley, 1971). This view of *H. erectus* as the polytypic, presumptive ancestor was punctuated only by the growing realization that yet a smaller-brained member (or two) of the genus preceded *H. erectus* (e.g., Leakey et al., 1964; Stringer, 1986; contra Wood and Collard, 1999, who would assign earliest *Homo* to genus *Australopithecus*). Although many supported this synonymization, a number of scholars continued to recognize multiple species, and sometimes genera, within the local fossil lineages (e.g., Jacob, 1981; Sartono et al., 1995; Tyler, 2001; although Jacob (2001) more recently argued for the recognition of multiple, sometimes contemporary, subspecies of *H. erectus* in Indonesia rather than separate species).

While synonymization may have helped us to “see the forest for the trees” in our understanding of the genus *Homo*, the increasing evidence of differences between African, Asian, and European forms also stirred misgivings. This became particularly the case after the discovery of *H. erectus* at Koobi Fora, including KNM-ER 3733, that diverged more from the morphology of the Asian holotype than had Olduvai Hominid (OH) 9. By the 1980s, the growing numbers of *H. erectus* specimens, particularly in Africa, led to the realization that Asian *H. erectus* (*H. erectus sensu stricto*), once thought so primitive, was in fact more derived than its African counterparts. These morphological differences were interpreted by some as evidence that more than one species might be included in *H. erectus sensu lato* (e.g., Stringer, 1984; Andrews, 1984; Tattersall, 1986; Wood, 1984, 1991a, b; Schwartz and Tattersall, 2000).

In my opinion, additional finds and study have now clarified that even the earliest part of the European lineage, that appears to have culminated in Neandertals, should be excluded from *H. erectus* (Howell, 1960) and placed in the taxon *Homo heidelbergensis* (Rightmire, 1988, 1998a; Wood and Richmond, 2000), as erected for the Mauer mandible (Schoetensack, 1908). Some limit this designation to the evolving Neandertal lineage, thus including European Middle Pleistocene remains such as Steinheim, Mauer of course, and Ceprano. Others include in *H. heidelbergensis* (or archaic *H. sapiens*) the relatively large-brained, mostly Middle Pleistocene, hominins from around the world that lack the suite of characteristics attributable to *H. erectus* (Wood, 1991a; Wood and Richmond, 2000; Stringer, 2002; Schwartz and Tattersall, 2002, p. 269): African fossils from Kabwe, Nduvu, and Bodo (Clarke, 1990; Rightmire, 1996, 1998a; Gilbert et al., 2000) and perhaps more recent discoveries from Ethiopia (Daka; Manzi et al., 2003) and Eritrea (Buia; Abbate et al., 1998), Chinese fossils from Dali, Jinniushan, Xujiayao, and Yunxian (Wu, 1981; Li and Etler, 1992; Wu and Poirier, 1995), and the Indian calvaria

from Hathnora (Kennedy et al., 1991). Howell (1994) argued that these specimens, distinct from *H. erectus* on the basis of their double-arched brow ridge, parietal expansion, and brain size (Rightmire, 1988), are also consistently differentiable from *Homo sapiens*, supporting a specific diagnosis for the group (see also Wood and Richmond, 2000; Schwartz and Tattersall, 2002).

Although I support the above distinction, as well as the recognition of more than one species of *Homo* in the Pleistocene, it bears noting that a not insignificant contingent of workers has argued for the inclusion of all Pleistocene hominins into a single species, *Homo sapiens* (Jelinek, 1981; Aguirre, 1994; Wolpoff et al., 1994; Curnoe and Thorne, 2003; Goodman, 2001, who would also include chimpanzees in genus *Homo*). This view and others are considered in greater detail after the morphological discussion.

Unlike the European lineage, in my opinion, the taxonomic issues surrounding Asian vs. African *H. erectus* are more intractable. The issue was most pointedly addressed with the naming of *H. ergaster* on the basis of the type mandible KNM-ER 992, but also including the partial skeleton and isolated teeth of KNM-ER 803 among other Koobi Fora remains (Groves and Mazak, 1975). Recently, this specific name was applied to most early African and Georgian *H. erectus* in recognition of the less-derived nature of these remains vis à vis conditions in Asian *H. erectus* (see Wood, 1991a, p. 268; Gabunia et al., 2000a). It should be noted, however, that at least portions of the paratype of *H. ergaster* (e.g., KNM-ER 1805) are not included in most current conceptions of that taxon. The *H. ergaster* question remains famously unresolved (e.g., Stringer, 1984; Tattersall, 1986; Wood, 1991a, 1994; Rightmire, 1998b; Gabunia et al., 2000a; Schwartz and Tattersall, 2000), in no small part because the original diagnosis provided no comparison with the Asian fossil record. Regardless, since regional variation in *H. erectus* (*sensu lato*) exists, I review anatomical features by region below.

While the taxonomic issues addressed above are still relevant to today's debates, in the two decades since the review by Howells (1980) of *Homo erectus*, additional emphasis has also been placed on using new fossils, such as KNM-WT 15000, and larger sample sizes to provide insights into the biology and behavior of the species (e.g., Smith, 1993). Trinkaus (1982) argued that the tradition of looking for adaptively significant traits in hominins began post-World War II in, for example, the work of Howell (1951) on the relationship between Neandertal anatomy and climate. However, only recently have the sample sizes of *H. erectus* been sufficient to address such issues. Likewise, a subtle shift has occurred in which biology and behavior are of significance in *themselves*, rather than simply as additional means to make taxonomic divisions. The focus has been on several aspects bearing either directly or indirectly

on reconstructions of life-history patterns, including body size and shape, growth and development, and age at maturity (e.g., Smith, 1993; Bogin and Smith, 1996; Clegg and Aiello, 1999; Dean et al., 2001; Antón, 2002b; Antón and Leigh, 2003; Aiello and Key, 2002; Aiello and Wells, 2002).

In addition, the chronostratigraphic framework for fossil *H. erectus* has significantly expanded since its discovery. At the time of synonymization of the various regional genera and species into *H. erectus*, virtually all specimens were considered to be of Middle Pleistocene age, ranging from perhaps 400–500 ka (e.g., von Koenigswald, 1962; Le Gros Clark, 1964; Howells, 1980). In the last decade, in particular, both the earliest and the youngest ranges were extended and refined (e.g., Feibel et al., 1989; Guo et al., 1991; Swisher et al., 1994, 1996; Chen et al., 1997; Grün et al., 1997, 1998; Larick et al., 2001). *H. erectus* is now considered to originate in the latest Pliocene and to span nearly the entire Pleistocene epoch. What is more, hominin dispersal from Africa now appears to commence at the same time as the origin of the species, perhaps around 1.8 Ma (Swisher et al., 1994). This change in our understanding of when hominin dispersal from Africa began has raised significant issues for our understanding of the causes of this dispersal and subsequent movements of *H. erectus* (e.g., Cachel and Harris, 1998; Bar-Yosef and Belfer-Cohen, 2000; Antón et al., 2001, 2002). Previously considered the result of technological advances made with the development of the Acheulian industry (Wolpoff, 1999, p. 443) that likely signaled a shift in subsistence ecology (Klein, 1989, p. 219), changes in biological aspects of the species, including life-history patterns, and responses to ecosystem change are now considered of equal importance for hominin dispersal (Shipman and Walker, 1989; Antón et al., 2002). Taken together, these have fundamentally altered our view of the life history and ranging patterns of *H. erectus*.

Here I attempt to draw together these emerging threads of evidence into a kind of a “natural history” of the species, and in so doing use the anatomy of these hominins to approach their biology. However, to do so requires a reevaluation of the basic facts as they are currently understood, and a synthesis of the biological questions currently under debate. I will largely limit this discussion to fossil remains that can be reasonably referred to *H. erectus* (*sensu lato*), that is, the classic remains from China and Indonesia and the mostly early African remains from Koobi Fora, Olduvai and possibly Swartkrans that do not require too great a relaxation of the cranial definition. I begin this discussion with a review of the chronostratigraphic framework, and cranial and postcranial anatomy, followed by the more inferential arguments made from these data sets regarding life history and behavior. I make only passing reference to the abundant archaeological record, both because much of it cannot be precisely

assigned to species and because this record merits a review of its own.

CHRONOSTRATIGRAPHIC FRAMEWORK

Definitive *H. erectus* fossils range in age from at least 1.8 Ma, and possibly 1.9, Ma in Africa to as recent as 100 ka, and possibly 50 ka, in Indonesia (Table 1; Fig. 1; Feibel et al., 1989; Swisher et al., 1996). The species, broadly interpreted, appears to expand quickly into its entire range (Antón et al., 2002), but to disappear at least a half million years earlier in Africa than in Asia.

Africa

East Africa. Olduvai Gorge (Tanzania) yielded the first *definitive* African *H. erectus* crania, Olduvai Hominid (OH) 9 and OH 12, in the 1960s. These two fossils are thought to originate from Beds II and IV, respectively, with mandibular remains coming primarily from Beds II–IV, and at least one partial mandible (OH 23) deriving from the overlying Masek beds (Leakey, 1971). Postcranial remains assigned to *H. erectus* (OH 28 and ?OH 34; Day and Molleson, 1976) are associated with Beds III and IV. The most recent geomagnetic polarity data suggest that the top of Bed IV is coincident with the Brunhes-Matuyama boundary (Swisher, Hay, and Deino, unpublished data), making all of Bed IV older than 0.78 Ma (Tamrat et al., 1995). The *bottom* of Bed III is dated to 1.25–1.47 Ma, based on single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ age determinations from feldspars of tuff III-1 (Manega, 1993). Thus OH 12 dates between 0.78–1.25 Ma and OH 9 dates to ≥ 1.47 Ma. Presuming that the bed associations are robust, the age difference between the two partial crania may be as much as 700 or as little as 200 ka. The youngest *H. erectus* remains from Olduvai (OH 23) are estimated to be younger than 0.78 Ma, although it remains uncertain how much younger.

Since the 1970s, the Turkana Basin (Kenya) has yielded more dramatic cranial and postcranial remains of early *H. erectus* (Table 1; Wood, 1991a; Walker and Leakey, 1993a). Collectively, these range from possibly as much as 1.9 Ma to younger than 1.45 Ma. Similarly aged mandibular remains are also present at Konso-Gardula in Ethiopia (KGA 10-1, ~ 1.35 –1.45 Ma; Asfaw et al., 1992). The remarkably complete KNM-WT 15000 skeleton from West Turkana dates to 1.51–1.56 Ma (Brown and McDougall, 1993). The earliest of the Koobi Fora cranial remains is the occipital fragment KNM-ER 2598 dated to 1.88–1.9 Ma, whereas the earliest definitive *H. erectus* cranium is KNM-ER 3733 at 1.78 Ma. Postcranial remains from large-bodied hominins are likewise found as early as 1.95 Ma (KNM-ER 3228) and 1.89 Ma (KNM-ER 1481). However, their taxonomic attributions are debated (see below).

More recently, two relatively large-brained crania dated to approximately 1.0 Ma were described from Eritrea and Ethiopia (Abbate et al., 1998; Asfaw et

TABLE 1. Fossil specimens discussed here as *H. erectus* (*sensu lato*)¹

	Partial crania	Cranial fragments	Mandibular	Postcranial
Earliest				
East Africa (1.5–1.8 Ma, or more)	ER 3733, 3883, 42700 WT 15000 OH 9	ER 164, 807, 1466, 1808, 1821, 2592, 2595, 3892, 16001 ?ER 2598	ER 730, 731, 820, 992, 1812, 1507 KGA-10	ER 164, 736, 737, 741, 803, 1808, 5428, 19700 WT 15000 ?ER 1472, 1481, 3228, 3728
South Africa (1–1.8 Ma)	?SK 847		?SK 15, 45, 21204	?SK 18, 84 ?SKX85, 22741, 27431 D2021 + unpublished
Georgia (~1.7 Ma)	D2280, 2282, 2700		D211 D2735	
Indonesia (>1.5–1.8 Ma)	Sangiran 4, 27, 31 Perning		Sangiran 22 Kedungbrubus 1	Kedungbrubus 2
Early				
East Africa (0.78–<1.2 Ma)	OH 12 ?Daka ?Buia	?Omo P996-17 ?Gombore ?Garba	OH 22, 23 ² , 51	OH 28, ?34 ?Daka, ?Gombore
Indonesia (0.9–1.4 Ma)	All other Sangiran Trinil II		All other Sangiran mandibles	Sangiran 29, 30; Kresna 10, 11 Sambungmacan 2 ?Trinil I–VI
China (1.2 Ma)	Gongwangling			
Middle				
China (~200–600 ka)	Zhoukoudian Nanjing 1, 2 Hexian		Zhoukoudian Chenjiawo Hexian	Zhoukoudian Atlas, clavicle Humerus I–III Femora I–VII, Tibia I
Latest				
Indonesia (<100 ka)	Ngandong Sambungmacan 1, 3, 4			Ngandong 17 and Tibia A and B

¹ ER and WT refer to National Museums of Kenya site prefixes (KNM-ER and KNM-WT, respectively) D, Dmanisi; KGA, Konso Gardula; OH, Olduvai Hominid; SK/SKX, Swartkrans; ?, questionable affiliation based on either time or morphology.

² OH 23 is less than 0.78 ka.

al., 2002). Although combining features found in *H. erectus* with those found in later *Homo* (see below), they, like the partial cranium from Bodo, were argued to be a late form of *H. erectus* by some (Asfaw et al., 2002) and archaic *H. sapiens* (or *H. heidelbergensis*) by others (e.g., for Bodo, Conroy et al., 1978; Conroy, 1980; for Buia, Abbate et al., 1998). Other cranial fragments of *Homo* sp. from Melka Kontoure and Omo also occur in this time period.

North and South Africa. Although discovered earlier than OH 9, the taxonomic status of the *Homo* fossils from Swartkrans (South Africa) remains uncertain. Broom and Robinson (1949) argued that the assemblage from Swartkrans contained fossils of early *Homo*, which they assigned to *Telanthropus capensis* (Robinson, 1953a, b). These fossils were alternatively considered to have affinities with *Pithecanthropus capensis*, *Homo* sp., *Homo erectus*, *Homo cf. erectus*, *Homo habilis*, and *Homo* sp. nov. (Clarke et al., 1970; Clarke and Howell, 1972; Howell, 1978; Olson, 1978; Bilsborough and Wood, 1988; Tobias, 1991; Grine, 1993, 2001; Grine et al., 1993, 1996, 2003; Clarke, 1994; Kimbel et al., 1997; Susman et al., 2001). The referred specimens come from Members 1–3 at Swartkrans, and thus should range in age from 1.8–1.0 Ma (Susman et al., 2001).

Also discovered before the Olduvai remains, the Ternifine (Tighenif) mandibles and parietal were originally designated as *Atlanthropus mauritanicus*

(Arambourg, 1954) and subsequently sunk into *H. erectus* (Le Gros Clark, 1964), where they are retained by some workers today, along with other North African remains from Thomas' Quarry and Sidi Abderrahman (e.g., Rightmire, 1993). These localities are estimated to date to the Middle Pleistocene, perhaps 400 ka (Hublin, 1985). As no uncontested *H. erectus* cranial remains are known from this time in Africa, but *H. heidelbergensis* crania such as Kabwe and Nduku (Clarke, 1990) are present, and as mandibular remains are notoriously hard to assign to taxon, the Ternifine, Thomas' Quarry, and Sidi Abderrahman mandibles may be more parsimoniously referred to the later taxon. Alternatively, they could be grouped with the Gran Dolina remains from Spain (assigned to *H. antecessor*; see below). However, if this is done, and if the Mauer mandible is excluded from the group, the species name would revert to *H. mauritanicus*, which has precedence over *H. antecessor*. However, it is equally difficult to exclude these remains from *H. erectus* without reference to crania. Thus, if future cranial evidence leads to the inclusion of these North African remains within *H. erectus*, then the species does not disappear from Africa much earlier than it does in continental Asia. For the moment, it would appear that by the Middle Pleistocene, *H. erectus* exists in Asia (see below), but a more derived hominin exists in Africa (Asfaw et al., 2002).

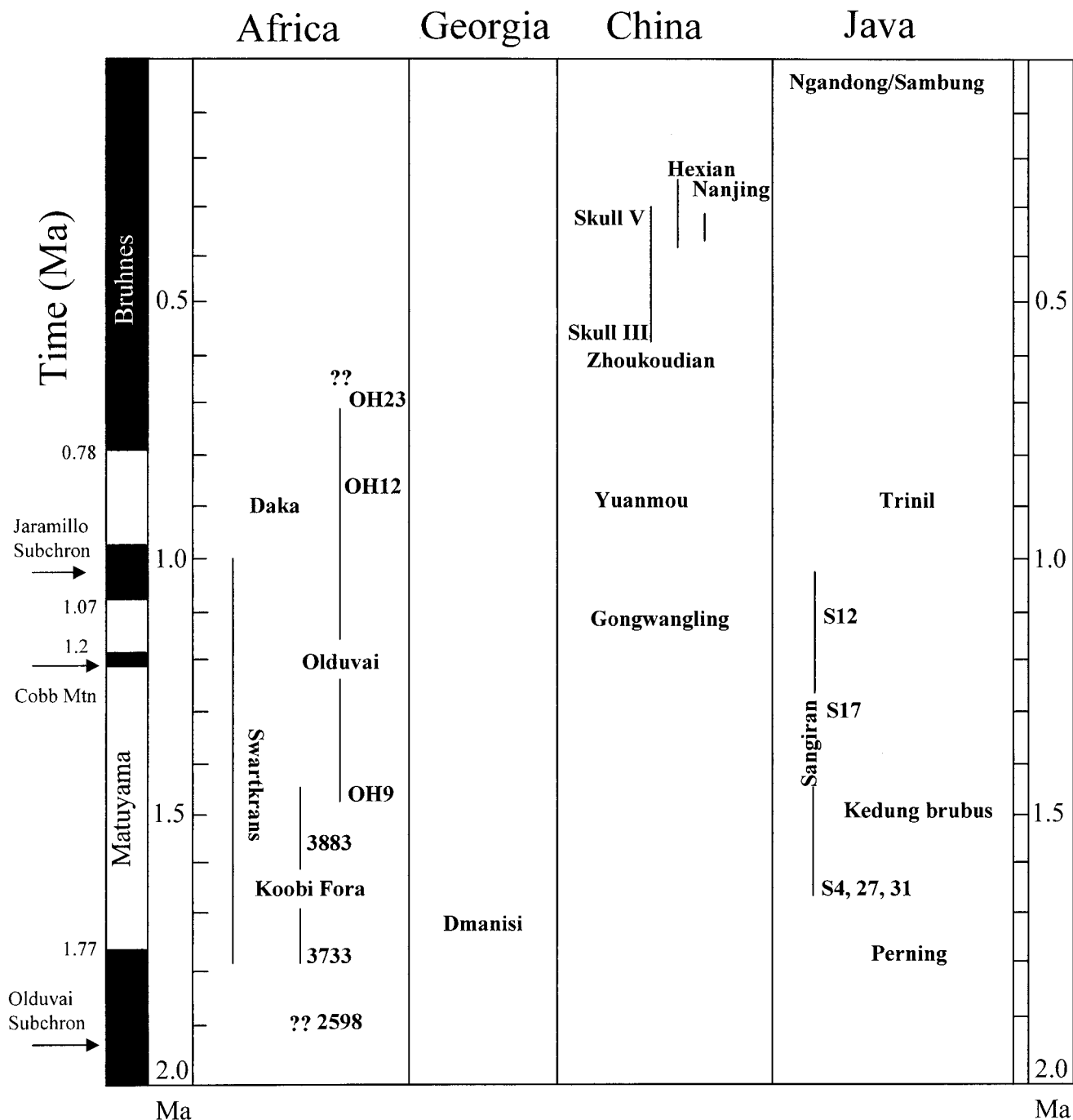


Fig. 1. Chronostratigraphic context of major *H. erectus* sites and fossils plotted against absolute and geomagnetic polarity timescales.

Eurasia and the Near East

Homo erectus arrived in Eurasia at about 1.7 Ma in the Republic of Georgia. Archaeological sites in the Near East suggest a hominin presence, probably attributable to *H. erectus*, through about 1.3 Ma at 'Ubeidiya (Tchernov, 1987, 1992), and possibly as young as 780 ka if the Gesher Benot Ya'aqov lithics and femur from Israel can be attributed to *H. erectus* (Goren-Inbar et al., 2000). In continental Europe, however, even the earliest hominins display charac-

ters of more advanced *Homo*, cf. *H. heidelbergensis*, and not *H. erectus*.

Republic of Georgia. The age of the Dmanisi hominins and fauna is constrained to about 1.7 Ma, based on the geomagnetic polarity of the sediments, radiometric age of the underlying Masavera Basalt (1.78–1.95 Ma), depositional rates of sediments and soil formation, and biogeographic indicators of age (particularly the rodents *Mimomys ostromosensis* and

M. tornensis), which constrain the age of the site to the very latest Pliocene/earliest Pleistocene (Gabunia et al., 2000a, b).

Europe. The earliest uncontested hominin occupation of Europe is at the Gran Dolina locality (Sierra de Atapuerca, Spain) at about 800 ka (Carbonell et al., 1999). The subadult cranial remains from Gran Dolina exhibit none of the derived features of *H. erectus*, but were suggested to be ancestral to both modern humans and Neandertals (Arsuaga et al., 1999). The Ceprano calvaria from Italy was argued to be of similar antiquity (Ascenzi et al., 1996; Manzi et al., 2001), although the geological arguments for the age and stratigraphic position of this salvaged calvaria are unconvincing. Regardless, the anatomy of the Ceprano calvaria, particularly in its more parallel-sided and shorter vault, double-arched brow, and expanded parietals, indicates its associations with archaic *H. sapiens* (or *H. heidelbergensis*), and not *H. erectus* (Clarke, 2000; Schwartz and Tattersall, 2002). Earlier European occupations are possibly suggested on archaeological grounds from France, Spain, and Italy at about 1.2–1.4 Ma (Bonifay, 1991; Bracco, 1991; Rolland, 1992), although hominin fossils remain contested (Martínez-Navarro et al., 1997; Palmqvist, 1997).

There is thus a delay of nearly a million years from the time that hominins leave Africa and enter Georgia (~1.7 Ma) until they move, at least permanently, into Europe (~800 ka; Roebroeks, 2001). A number of arguments have been proposed for this delay, from the structure of the carnivore guild to the harshness of the climate (Turner, 1992; Roebroeks, 2001). It seems likely that the lineage that first populates Europe is ultimately ancestral to Neandertals, but is anatomically distinct from *H. erectus* (sensu Howell, 1960).

Asia

Asian *H. erectus* sites span from about 1.8 Ma to possibly 50 ka on Java (Swisher et al., 1994, 1996; Larick et al., 2001). The chronostratigraphy of Asian hominin sites and the chronology of glacial cycles, as proxied by Plio-Pleistocene oxygen isotope records, have undergone substantial revision in the past decade (reviewed by Antón, 2002a). Despite some specific disagreements in absolute age estimates, all recent chronologies suggest that the earliest Indonesian fossils (e.g., those from Sangiran, Mojokerto, and Kedungbrubus) are relatively older than the Chinese fossils, which are in turn relatively older than the youngest Indonesian fossils (from Ngandong and Sambungmacan).

Island Southeast Asia:Indonesia. The oxygen isotope record suggests that land bridges connected mainland Asia and island Southeast Asia beginning about 2.5 Ma and increased in duration and amplitude throughout the Pleistocene, but particularly after 1.0 Ma (e.g., Shackleton, 1995). The earliest

hominins in Island Southeast Asia appear about 1.8 Ma at Parning (Mojokerto) on Java, and shortly thereafter in the Sangiran Dome region (~1.66 Ma; Swisher et al., 1994, 1996). The Javan *H. erectus* record is then fairly continuous from 1.6 to just less than 1.0 Ma (e.g., Sangiran Dome region, Trinil, Kedungbrubus; Swisher et al., 1994; Swisher, 1997; Larick et al., 2001). A radiometric critique of this early Indonesian chronology (Langbroek and Roebroeks, 2000) suggests that these sites are all less than 1.0 Ma (see also Pope, 1983). However, this critique relies on a single fission-track age on a tektite from Sangiran of uncertain provenience and on previous paleomagnetic data that suggested normal polarities (and thus ages less than 1.0 Ma; Watanabe and Kadar, 1985) but that did not apply thermal demagnetization techniques, and therefore likely measured modern (normal) overprints in the significantly weathered Sangiran sediments. The critique likewise ignores scores of well-behaved $^{40}\text{Ar}/^{39}\text{Ar}$ analyses throughout the section that are temporally consistent with their relative stratigraphic positions (Swisher, 1997; Larick et al., 2001), as well as ignoring paleomagnetic and foraminiferal data of the stratigraphic age of hominin-bearing sediments on Java (Ninkovitch et al., 1982). Collectively, the latter data suggest that the entire hominin-bearing section at Sangiran is greater than 1.0 Ma. Despite arguments by Larick et al. (2001), preservational differences between fossils from the oldest strata (Sangiran, a.k.a. Pucangan, Formation black clays that badly deform and telescope included bones) and younger, overlying strata (Bapang, a.k.a. Kabuh, Formation cross-bedded sandstones that do not present deformed bones) indicate that hominins are certainly associated with the Sangiran Formation and thus with ages in excess of 1.6 Ma. At present, the majority of the data favor an early chronology.

The latest surviving Javan *H. erectus* (Ngandong/Sambungmacan) lived at least 100 ka and possibly <50 ka (Swisher et al., 1996; Bartstra, 1987; Bartstra et al., 1988), based on U-series/ESR analyses. Recent additional gamma spectrometric U-series analyses of the Ngandong 1 hominin calvaria also yielded dates close to 80 ka (Falguères, personal communication to C. Swisher and R. Grün; contra Falguères et al., 1998). It remains possible that a systematic error in the U-series/ESR techniques on tooth and bone would prove these dates inaccurate, despite high reproducibility (Antón, 1999). Likewise, to assess whether these assemblages were reworked, site-formation processes require further investigation (Grün and Thorne, 1997; Antón, 1999; Westaway et al., 2003). However, at present the majority of data suggest that both the hominins and fauna from Ngandong are from the very latest Pleistocene. If this is the case, then the latest *H. erectus* in Indonesia may prove a hominin example of relative biogeographic isolation and survival, and would

provide a parallel case to the last Neandertals in Western Europe.

Continental Asia: China and India. The oldest occupation of China has been proposed to occur as early as 1.8 Ma, coeval with the Peking remains in Java, based on remains from Longgupo (W. Huang et al., 1995). However, the mandible fragment from Longgupo has been argued to be nonhominin, and the associations of the isolated incisor have been questioned (Schwartz and Tattersall, 1996; Wolpoff, 1999, p. 466; Wu, 1999). The first certain hominins from mainland Asia appear about 1.15 Ma in Southern China at Gongwangling (Lantian; An et al., 1990), following a period of connection between mainland and Southeast Asia. Most Chinese *H. erectus* (those from Zhoukoudian, Nanjing, and Hexian) probably appear between 0.58–0.2 Ma (Pei, 1985; Liu et al., 1985; P. Huang et al., 1991a, b, 1995; Grün et al., 1997, 1998; Chen et al., 1997; Cheng and Edwards, 1997), although somewhat older dates, with a younger limit of about 0.4 ka, have also been suggested (for a detailed review of the Asian chronology, see Antón, 2002a). The revised dating of Pleistocene glacial cycles (e.g., Shackleton et al., 1990; Bassinot et al., 1994) and the stratigraphy of Zhoukoudian (Grün et al., 1997) make the argument for *H. erectus* habitation of northern China during glacial periods questionable (Antón, 2002a). Likewise, the argument that *H. erectus* was probably using and controlling fire (e.g., Black, 1931; Wu, 1999; a claim questioned by recent microstratigraphic work by Weiner et al., 1998, 1999; Goldberg et al., 2001), as well as using clothing, shelter, and perhaps stored food remains (e.g., Turner, 1992) in order to survive the cold climate, is unnecessary (Huang, 1997).

China and India have also yielded a number of archaic members of *Homo sapiens*, identified in part by their larger cranial capacities, double-arched supraorbital tori, vertically oriented and expanded parietals, rounded occipitals, and taller vaults. Most notable among these are the well-preserved Middle to Late Pleistocene Dali and Jinniushan hominins from China (X. Wu, 1981; R. Wu, 1988) and the older Hathnora calvaria from the Narmada Valley, India (de Lumley and Sonakia, 1985; Sonakia, 1985), now most frequently included in *H. heidelbergensis* or Archaic *H. sapiens* (e.g., Kennedy et al., 1991; Li and Etlar, 1992; Wu and Poirier, 1995; Wood and Richmond, 2000; Stringer, 2002).

Contextual overview

Once considered a Middle Pleistocene phenomenon, *H. erectus* sensu lato is known to have originated in the latest Pliocene/early Pleistocene and to have survived nearly the entire Pleistocene epoch, ranging from about 1.8 Ma to perhaps less than 100 ka. The bulk of known remains date between 1.0–1.8 Ma. The earliest of these hominins come from Africa, but seem to persist there only until about the

Brunhes-Matuyama boundary (0.78 Ma), although this last occurrence date may shift depending on one's choice of taxon for the Middle Pleistocene North African remains. The earliest African *H. erectus* quickly disperse into Western and Southeastern Asia, where they first appear between 1.7–1.8 Ma. Island Southeast Asia is the only region, at present, where *H. erectus* fossils persist throughout the entire Pleistocene, suggesting that this region may play a unique role in the evolution of the species. The latest, perhaps relictual, *H. erectus* on Java likely implicates the role of intermittent isolation and local adaptation in the longevity of the species.

ANATOMY THROUGH TIME AND SPACE

Original species description

The holotype for the name *H. erectus* is the Trinil 2 calotte. The original species definition by Dubois (1894) also relied heavily on the Trinil 1 femur. Although, at the time, the femur was most critical for assessing the hominin (bipedal) nature of the species, today vault characteristics are more critical to taxonomic definitions (e.g., Wood, 1991a; Rightmire, 1993). In this regard, Dubois (1894, 1924) noted anatomical features of the calotte critical to the current species definition, including a cranial capacity (then considered ~1,000 cc, but now ~840 cc) which is intermediate between that of great apes and humans, the lowness of the vault, particularly its frontal recession and occipital angulation, and its continuous supraorbital region. Dubois (1924) also noted many of the features considered by some to be unique derived features (autapomorphies) of Asian *H. erectus*, including the presence of a strong supra-mastoid crest, a frontal keel, and a bregmatic eminence, as well as an occipital torus. It is back to this definition that we must refer when extending the definition to include other fossils (Schwartz and Tattersall, 2000). While it is true that the type should play no special role in determining the range of variation of the species (Simpson, 1961), it is also the case that the holotype must be an individual of that species. In this case, Trinil 2 is silent on significant aspects of cranial anatomy, lacking basicranial, facial, and mandibular remains. However, past and present work clearly shows a consistent morphological pattern in Indonesia and China, with slight regional variations, that can by inference extend the original definition based on Trinil 2 to aspects of the face and dentition (e.g., Weidenreich, 1943; Weidenreich, 1951; Howell, 1978; Rightmire, 1993; Antón, 2002a; Baba et al., 2003; but see Schwartz and Tattersall, 2000, who would retain only Trinil and Sangiran fossils in *H. erectus* and divide the remainder into more than four morphs and probably species).

Craniodental anatomy

Because of the substantial geological time and geographical spread involved, whether one focuses

on temporally evolving but geographically static regional lineages or on time slices across regions influences the view of the species. Ultimately, of course, it is necessary to understand both aspects in discussing the taxon. Below, I chose to discuss regional variation through time first, and to subsequently compare across regions by time. I believe this facilitates an understanding of the consistent similarities across regions while highlighting more particular regional trends. However, I subdivide the discussion by time blocks (as in Table 1) to facilitate comparison across regions at a given time interval, a comparison that I hope the reader will undertake.

Species-wide morphology

“It is among the truly basic and universal facts of nature that all species vary” (Simpson, 1961, p. 177). I address some of this variation in *H. erectus*, especially its patterning through time and space, later on. Here I attempt to describe a pattern of morphology that, within the bounds of individual variation, unites *H. erectus* while still recognizing the fact that while “All populations vary, and the variation is an essential part of their nature and definition, they do not have single fixed patterns or types” (Simpson, 1961, p. 65). Thus, any individual member of the species should exhibit the overall morphological plan and some large percentage of the individual features; however, it is not a requirement that each feature be represented in each individual or in an invariant way.

H. erectus is essentially a cranially defined species. The characteristics provided below include both primitive and derived traits that, together, describe the species as based on the accumulated observations of a number of workers (e.g., Dubois, 1894, 1924, 1926a, b; Weidenreich, 1943, 1951; LeGros Clark, 1964; Howell, 1978; Santa Luca, 1980; Stringer, 1984; Tattersall, 1986; Wood, 1984, 1991a; Hublin, 1986; Rightmire, 1993, 2000; Antón, 2002a). It is worth noting that, depending in part on the sample being considered, workers’ definitions vary and there is disagreement as to which, if any, of these characters are derived or apomorphic (see below). The discussion below is largely a phenetic one to illustrate the taxon; as will be clear, it is not intended to be a phylogenetic argument. In this consideration, I refer to remains listed in Table 1.

It is critical to note here that the growing early Pleistocene hominin fossil record highlights the need to assess the relationship between size- and shape-related variation. Previous distinctions between groups of early *Homo* based on absolutes of brain or body size are no longer relevant in light of the small-sized remains from Dmanisi, Georgia and Ileret, Kenya, as well as the frequently ignored but small remains of OH 12, all of which retain morphological affinities to *H. erectus* (Rightmire, 1979; Gabunia et al., 2000a; Vekua et al., 2002; Leakey et al., 2003; Antón, unpublished data). Many of these characters require further investigation as to their

structural and developmental origins, in order to assess their usefulness as taxonomic indicators.

Characteristics of the cranial vault dominate definitions of the species due to the relative paucity of facial remains. Vault characteristics include moderately sized cranial capacities, ranging from about 700 cc (in East Africa and Georgia) to over 1,200 cc (in China and Indonesia), with some gradual increase in average size through time (see below). Vault shape is relatively low and angulated, with marked frontal recession and occipital angulation and greatest breadth low down, often on the supramastoid crest. Postorbital constriction is marked to moderate; the inion and endinion are not coincident. In addition, the mastoid and supramastoid crests are marked and sometimes fused. The temporal squama is often low, and the suture is straight and not arched. The vault of African and Asian *H. erectus* is metrically differentiable from geographically diverse samples of *H. sapiens* (including the enigmatic Willandra Lakes 50 from Australia) in simple bivariate and principal components analyses (PCA; Antón, 1997, 1999, 2002a). These metric distinctions are expressions of the “long low vault” form, frontal recession, and occipital angulation often used to describe *H. erectus*.

H. erectus is also characterized by a generalized hypertrophy of cranial bone most notably seen in: 1) supraorbital tori that are essentially continuous and thickened laterally and associated with a posttoral shelf or sulcus that may or may not be continuous, 2) occipital tori that are continuous but somewhat variably expressed, often continuous with the angular tori and mastoid crests and often associated with a supratoral sulci, 3) angular tori, 4) midline (sagittal and frontal) keels, and 5) relatively thick vault bones, a character of questionable taxonomic and phylogenetic significance (e.g., Brown, 1994; Antón and Franzen, 1997; Stubblefield, 2002).

The cranial base of *H. erectus* differs from that of modern humans in a number of characters, including the more sagittal orientation of the petrous temporal, the absence of a styloid process and vaginal sheath (a contested character, suggested by Wolpoff, 1999, p. 447, to be age-related, absent well into adulthood, and thus not a useful character, but in modern humans said to be fused by early adolescence; Scheuer and Black, 2000), and the absence of a foramen lacerum (Fig. 2; Weidenreich, 1943, 1951; Jacob, 1966, 1967, 1975). Although the cranial base of *H. erectus* has often been referred to as unflexed, it is clearly not as flat as in the great apes; recent calculations from the intact base of Sambungmacan 4 suggest that the cranial base angle may be at the flatter end of the modern human range (e.g., 140°; Baba et al., 2003). The mastoid is often said to be small, or small and inflected, yet there is great variation in this feature (Fig. 3; Antón, 2002a), which is also likely to be the primitive condition for hominins (Olson, 1978).

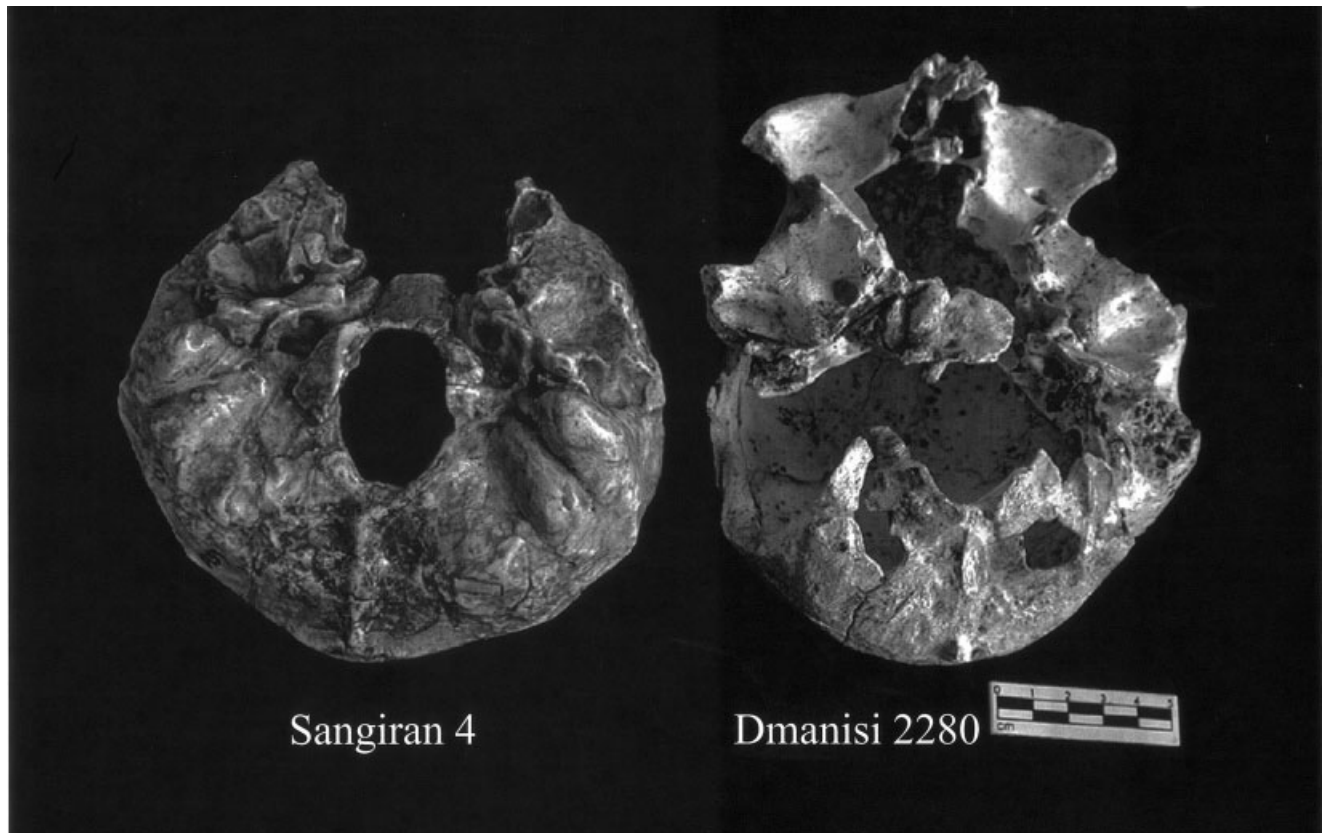


Fig. 2. Basal view of Sangiran 4 (cast) and Dmanisi D2280 to same scale in cm. Specimens are of approximately same geological age. Note similarity in posterior vault shape but differences in overall size (see Table 2). Note relatively broad basioccipital in D2280 but narrower basioccipital in Sangiran 4, orientation of petrous temporal, and large and projecting mastoid process of Sangiran 4.

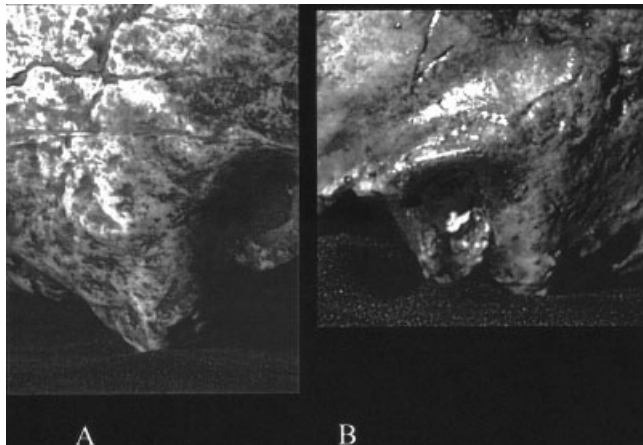


Fig. 3. Lateral view of mastoid and supramastoid crests in (A) Ngandong 10 with a sulcus and (B) Zhoukoudian XI without a sulcus.

Facial remains of *H. erectus* are rare, and substantial variation is evident across regions and individuals (see below; Rightmire, 1998b; a; Aziz et al., 1996; Tattersall and Sawyer, 1996; Wolpoff, 1999; Wang and Tobias, 2000). The face is widest superiorly in China and Africa, and more similar in proportions to modern humans than is earlier *Homo* (Bilsborough and Wood, 1988; Wood and Richmond,

2000). The nasal bridge is relatively high. The nasal aperture has been reported as broad in *H. erectus* (Table 2), although it is necessary to scale this against some other size factor such as brain size or facial width (Grine, 2001). Palates are relatively deeper than in *H. habilis* (Kimbel et al., 1997). However, the relationship to palate breadth is variable between regions: the early African forms are less broad relative to depth, and Asian forms are broader.

Mandibular remains are notoriously hard to assign to species (Rosas and Bermúdez de Castro, 1998). Rosas and Bermúdez de Castro (1998) convincingly argued that a mental trigone on the mandibular symphysis without lateral tubercles develops early in the African *Homo* lineage, probably before *H. erectus*. The lateral prominence is located anteriorly, at least in the earliest specimens of *H. erectus*, and is smaller in later fossils (Kaifu et al., 2003). Mandibular corpus size is larger in *H. erectus* than in modern humans, but sometimes smaller than in earlier *Homo*. Dental arch shape is narrow, and the symphysis is relatively vertical compared with earlier forms (Wolpoff, 1999, p. 464), but sub-vertical compared with modern humans (Weidenreich, 1936; Rightmire, 1993). The Georgian and earliest African *H. erectus* have relatively narrow extramolar sulci (Grine, 2001), although this trait is variable in the Asian sample.

TABLE 2. Comparisons of some traits discussed in text by region and time¹

	Vault	Face	Dentition	Postcrania
Earliest				
East Africa (1.5–1.8 Ma, or more)	700–1,067 cc Low and angular in SAG view Broad posteriorly Mildly pear-shaped (temporal lines diverge less than Asia) Moderate or no keeling Moderately thick walls	Moderate to large SOT Straight SO gutter Broad pyriform aperture Flat infraorbital Paranasal pillars Narrow extramolar sulcus Variable corpus height Moderate SOT	Narrow, long molars No accessory cusps Low MMRs Multi/single-rooted premolars	147–173 cm tall Platymeric femur (midshaft and higher) Thick cortical bone Acetabulocrystal buttress strong
South Africa (1–1.8 Ma)	?	Straight SO gutter Broad pyriform aperture Flat infraorbital	?	
Georgia (~1.7 Ma)	650–780 cc Low and angular in SAG view Broad posteriorly Mildly pear-shaped Incipient or no keeling Moderately thick walls	Moderate SOT Straight SO gutter Broad pyriform aperture Flat infraorbital Paranasal pillars Narrow extramolar sulcus	Broad, long molars Accessory cusps High MMRs Single-rooted premolars Malrotations	148 cm tall (from metatarsal)
Indonesia (>1.5–1.8 Ma)	908 cc Low and angular in SAG view Broad posteriorly Marked keeling/tori Very thick walls	Massive SOT Broad pyriform aperture Convex infraorbital No paranasal pillars Tall mandibular corpus	Broad, long molars (very large) Accessory cusps High MMRs Multi/single-rooted premolars	?
Early				
East Africa (0.78–<1.2 Ma)	727–995 cc Broad posteriorly Moderate or no keeling Moderate to very thick walls	Moderate SOT ?Straight SO gutter Flat infraorbital	?Narrow molars No accessory cusps Low MMRs Multi/single-rooted Premolars	158–163 cm tall Platymeric femora (midshaft and higher) Thick cortical bone Acetabulocrystal buttress strong
Indonesia (0.9–1.4 Ma)	813–1,057 cc Low and angular in SAG view Broad posteriorly Strongly pear-shaped (t-lines diverge) Marked keeling/tori Very thick walls	Moderate to massive SOT Wrapped SO gutter Broad pyriform aperture Convex infraorbital No paranasal pillars Tall mandibular corpus	Broad, long molars Very large molars Accessory cusps High MMRs Multi/single-rooted premolars Wide anterior teeth	?
China (1.2 Ma)	?780 cc	Massive SOT	?	?
Middle				
China (~200–500 ka)	855–>1,200 cc Low and angular in SAG view (greater frontal rise than Java) Narrow at asterion (ex. Hexian) Strongly pear-shaped (t-lines diverge) Marked keeling/tori Thick walls	Moderate to massive SOT (but smaller than Java) Wrapped SO gutter Broad pyriform aperture Flat infraorbital No paranasal pillars Broad extramolar sulci Mandible narrow at M1	Broad large molars (but smaller than Java) Accessory cusps Multi/single-rooted premolars Narrow incisors	150–156 cm tall Platymeric femora (entire shaft) Thick cortical bone (femur)
Latest				
Indonesia (<100 ka)	917–>1,200 cc Moderately low and angular in SAG view Broad posteriorly Pear-shaped (t-lines diverge) Less narrow POC Marked keeling/tori Thick walls	Massive SOT Wrapped SO gutter	?	158 cm tall Thick cortical bone of tibia

¹ Specimens in each time period as in Table 1. SAG, sagittal; SOT, supraorbital torus; SO, supraorbital; MMR, mesial marginal ridge.

Early *H. erectus* has smaller occlusal areas and fewer roots compared to earlier *Homo*, but has relatively larger crowns and more complex roots (especially of premolars) than in modern humans (Gabunia et al., 2000a, 2001; Antón and Indriati, 2002). Despite this, the upper premolars are frequently single-rooted. The third molar is often reduced and similar in size to M2.

Regional cranial variation by time period

Earliest African and Georgian fossils (1.5–1.8 Ma). For the most part, early African and Georgian fossils (Table 1) represent the smaller end of the range as compared with the species-wide condi-

tions discussed above (Table 2; Wood, 1991a; Walker and Leakey, 1993b; Gabunia et al., 2000a; Vekua et al., 2002). This is particularly true in their moderate brain size, ranging from less than 700 cc at Dmanisi to over 1,000 cc at Olduvai, with a mean of about 840 cc for adults in Africa and about 700 cc in Georgia. This is also true of the mostly moderate size of their supraorbital tori, and in their moderately thick-walled and narrow cranial vaults (Table 3; Gabunia et al., 2000a).

In superior view, the earliest African *H. erectus* vaults are only mildly pear-shaped, due to somewhat strong postorbital constriction (POC) relative

TABLE 3. Cranial capacities and measures related to traits in Table 2 for some *H. erectus* and other crania¹

Specimen	Geological age (Ma)	Cranial capacity (cc)	Vertical SOT thickness	Pyramidal aperture breadth	Biasterionic breadth	Cranial length
Earliest Africa						
KNM-ER 3733	1.78	848	8.5	34.3	123	182
KNM-ER 3883	1.5–1.65	804	13	–	115	182
KNM-WT 15000	1.51–1.56	909	10.4	34.7	106	175
OH 9	1.47	1,067	18	–	123	206
SK 847	1–1.8	?	7	23.2	–	–
Early Africa						
OH 12	0.78–1.2	727	10	–	–	–
Daka (Bou-VP-2/66)	0.78–1.0	995	18.5	–	116 ± 2	180 ± 1
Buia (UA 31)	0.78–1.0	750–800	17	–	?	204
Georgia						
D2280	1.7	780	11	–	104	176
D2282	1.7	~650	10	23.5	103	166
D2700	1.7	~600	9	?	104	153
Earliest Indonesia						
Sangiran 4	>1.6	908	–	32.4	132	–
Sangiran 27	>1.6	?	18	–	–	–
Early Indonesia						
Sangiran 2	1.5	813	12	–	126	177
Sangiran 10	1.2	855	19	–	120	–
Sangiran 12	1.1	1,059	–	–	123	–
Sangiran 17	1.3	1,004	18	32.0	131	207
Sangiran IX	1.1–1.4	845	?	–	116	195
Trinil	0.9	940	–	–	–	–
Later Indonesia						
Ngandong 1	0.1–0.05	1,172	13	–	127	196
Ngandong 6	Ditto	1,251	–	–	130	220
Ngandong 7	Ditto	1,013	15	–	123	192
Ngandong 10	Ditto	1,135	–	–	126	202
Ngandong 11	Ditto	1,231	12	–	127	203
Ngandong 12	Ditto	1,090	14	–	126	201
Ngawi 1	Ditto?	1,000	16	–	?	182
Sambungmacan 1	Ditto	1,035	15	–	127	199
Sambungmacan 3	Ditto	917	13	–	118	179
Sambungmacan 4	Ditto	1,006	15	–	?	–
Middle China						
Zhoukoudian II	0.42	1,030	17.4	–	103	194
Zhoukoudian III	0.58	915	12.1	–	117	188
Zhoukoudian V	0.30	1,140	–	–	–	–
Zhoukoudian X	0.42	1,225	16.5	–	111	199
Zhoukoudian XI	0.42	1,015	13.6	–	113	192
Zhoukoudian XII	0.42	1,030	14.6	–	115	195
Nanjing 1	0.3–0.6	860–1000	?	–	111	186

¹ –, measurement not available due to incomplete anatomy. ?, measurement not known. Time periods as in Table 1.

Geological age sources are in text. More specific ages for Asian fossils follow Antón and Swisher (2001). Cranial capacities after: Africa—Abbate et al. (1998); Asfaw et al. (2002); Holloway (1980, 1981) Wood (1991); Walker and Leakey (1993a); Indonesia—Holloway (1980, 1981); Pope (1983); Marquez et al. (2000); Baba et al. (2003); China—Weidenreich (1943); Chiu et al. (1973); Rightmire (1985); Georgia—Gabunia et al. (2000a); Vekua et al. (2002). Other measures per Abbate et al. (1998); Asfaw et al. (2002); Wood (1991a); Grine (2001); Gabunia et al., 2000a; Vekua et al., 2002; Antón (unpublished data); Wolpoff (1999); Liu Wu (personal communication).

to the breadth of the posterior cranium. Related to this, the temporal lines proceed directly posteriorly from the point of postorbital constriction, rather than diverging strongly laterally. The overall superior view, then, is a subrectangular outline. In sagittal view, the vault is relatively long, moderately low, and angular.

By and large, African and Georgian remains also lack significant cranial superstructures such as sagittal keels and occipital and angular tori (e.g., Stringer, 1984). An exception to this is the 1.47-Ma OH 9 that is notoriously heavily browed and thick-walled, presenting at least an incipient angular torus (Wood, 1991a; Rightmire, 1993). However, sagittal keeling may also be seen in some of the

Koobi Fora remains, including the newly discovered KNM-ER 42700 (Leakey et al., 2003). Frontal keeling was reported in KNM-ER 3733 as well (Rightmire, 1993). Likewise, some sagittal keeling is present in D2280 from Dmanisi, although the morphology of the external vault (hypervascularity, as witnessed by increased microforamina, and the presence of extensive healed lesions between and below the temporal lines) makes it possible that this feature is pathological (Gabunia et al., 2000a, 2001). D2282 is also slightly peaked at the sagittal suture, but as is the case in interpreting KNM-ER 42700, little is understood about the developmental and structural processes involved in keel formation, making assessment of these characters difficult.

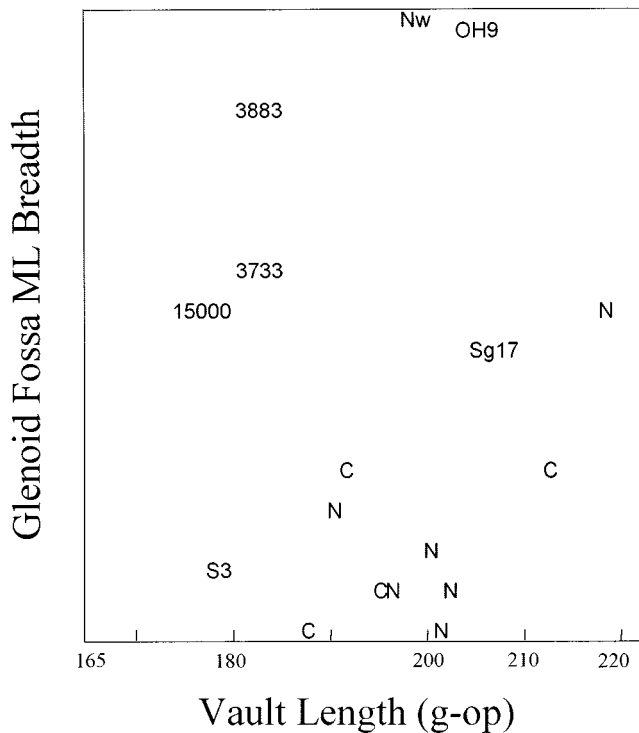


Fig. 4. Bivariate plot of glenoid fossa breadth (mediolateral) and cranial length (glabella-opisthion). African specimens listed by specimen number. C, China; N, Ngandong; Nw, Ngawi; S3, Sambungmacan 3; Sg17, Sangiran 17.

Some have argued that keeling is a primitive retention in any event (Bräuer and Mbua, 1992), an assertion that likewise requires assessment of the structural similarities of keels across individuals and taxa. Occipital toral morphology is restricted to the middle third of the occipital and is not continuous with an angular torus and mastoid crest system in African (Wolpoff, 1999, p. 453) and Georgian specimens.

The temporal bone possesses a number of notable features (Figs. 2–4). The mastoid processes vary considerably in size and projection below the vault, being most robust in OH 9. This morphology may not be related to the large size of OH 9, since the very much smaller OH 12 exhibits a similar mastoid morphology if not size (see below). Mastoid and supramastoid crests are present and may be either fused or unfused, the latter resulting in a supramastoid sulcus (Fig. 3). The glenoid fossa is wide mediolaterally relative to both cranial length and fossa length (Fig. 4; Wolpoff, 1999, p. 448).

The supraorbital torus, as mentioned, is evenly but only moderately thick in most of these early specimens, and is continuous across the glabella, but exhibits great, partly size-related, variability. The supraorbital torus across the glabella can be assessed in only four adult specimens (D2280, KNM-ER 3733 and 3883, and OH 9), and one of these (3883) underwent substantial plastic deformation (KNM-ER 42700 also preserves this region, but

is unpublished at the time of this writing). In African crania, brow shape is somewhat variable when viewed superiorly. The brow is relatively evenly projecting across its entire length in KNM-ER 3733. However, in OH 9, the middle third of the supraorbital torus projects much further anteriorly than do the most lateral edges of the supraorbital torus (Fig. 5). The two also differ in the conformation of the median portion of their supraorbital tori. Although both are slightly indented at the midline, the immediately lateral portions of the OH 9 supraorbital torus project much farther anteriorly than does the midline torus (Fig. 5), whereas the immediately lateral portions of the KNM-ER 3733 median torus are even with the midline torus. In both features, the D2280 brow is similar to OH 9, albeit on a much smaller scale. The brow of SK847, which is of debatable taxonomic affinity, appears similar but sligher than KNM-ER 3733, although it also appears to project more in the glabellar region than laterally and to possess much greater postorbital constriction (Grine et al., 1996).

The supraorbital torus of early African/Georgian *H. erectus* is followed by a continuous, posttoral (supratoral) sulcus or gutter that separates the supraorbital torus from the frontal squama (Weidenreich, 1943; Wood, 1991a; Wolpoff, 1999). This is the case in each of the early African/Georgian specimens. However, the sulcus varies from a concave furrow (3733 and OH 9) to a more flattened plane (3883 and D2280). This region is nearly as wide, anteroposteriorly, at midline as it is laterally (Antón, 2002a).

Early African *H. erectus* and Georgian remains also share facial similarities. These include facial proportions, presence of paranasal maxillary pillars and maxillary fovea, and morphology of the nasal sill (Fig. 6; Gabunia et al., 2001; Vekua et al., 2002). The pyriform aperture may be relatively narrower in the Georgian than in the African remains, however. The greatest similarities are between the subadult/young adult faces of Dmanisi 2282 and KNM-WT 15000, although a generally similar facial form can also be seen in the face of SK 847 (Wang and Tobias, 2000; Gabunia et al., 2000a). However, SK 847 is closer in size to the remains of earlier *Homo*.

Early African and Georgian *H. erectus* share relatively narrow extramolar sulci of the mandible and a relatively small size of the mandibular corpus compared to earlier *Homo* (Wood, 1991a; Rosas and Bermúdez de Castro, 1998). They likewise share probably primitive characters associated with the position of the anterior tubercles and lateral prominence (Gabunia and Vekua, 1995; Gabunia et al., 2000a).

Early African *H. erectus* and Georgian remains also share dental characteristics, including buccolingually narrow anterior teeth and P₃, and the detailed occlusal morphology of their molars (Rosas and Bermúdez de Castro, 1998; Gabunia et al., 2001;

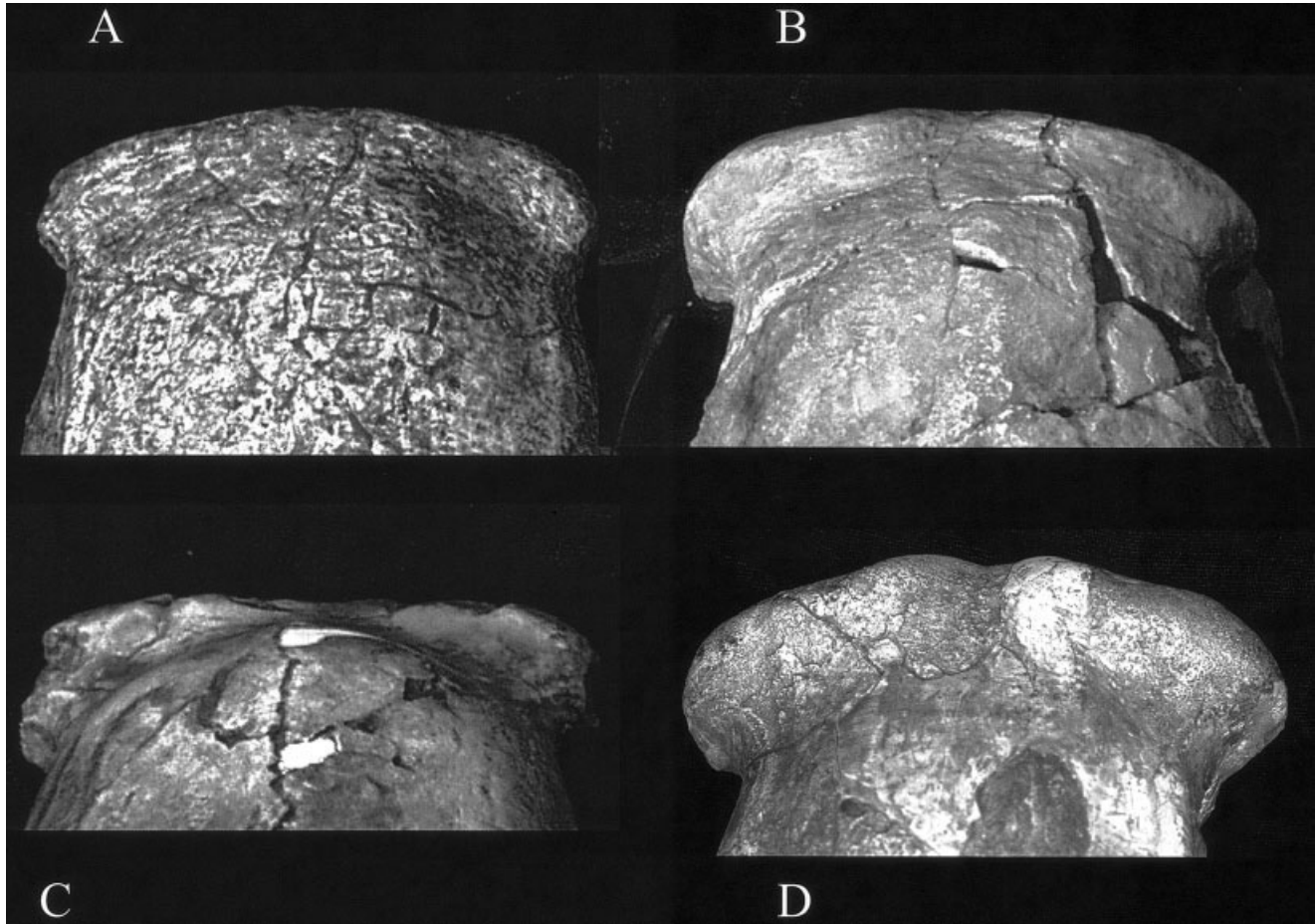


Fig. 5. Superior view of supraorbital torus in (casts) (A) Ngandong 5, (B) Sangiran 17, (C) Zhoukoudian XI, and (D) original OH 9.

Antón and Indriati, 2002). In particular, the anterior fovea of the mandibular molars is delta-shaped, with a low mesial marginal ridge (Fig. 7; paracristid sensu Schwartz and Tattersall, 2002). Accessory cusp complexes are rare or absent in African forms, resulting in mandibular molars that are relatively long (mesiodistally) for their breadth (buccolingually). The Georgian fossils are more derived than their African counterparts in having single-rooted premolars, accessory cusp complexes, and wider molars (Antón and Indriati, 2002). The Georgian remains are unique in exhibiting two malrotations: of the RM/3 of D211, and of the LP4 of D2700.

Early African fossils (0.78–<1.2 Ma). Somewhat later African cranial material includes remains dated to between 0.78–1.2 Ma (Table 1). Cranial fragments of about this age from various localities at Melka Kontoure (Gombore and Garba) have been tentatively included in *H. erectus* (e.g., White, 2000). However, while their cranial thickness may suggest affinities with *H. erectus*, they are too fragmentary to make a strong case, and are not discussed further here. Still younger, mostly mandibular, remains from Middle Pleistocene (~400 ka) deposits of North Africa are not considered here

because of the absence of African Middle Pleistocene *H. erectus* crania.

OH 12 exhibits similarities to early African *H. erectus* from Olduvai and Koobi Fora. In particular, the occipital torus, and shape and orientation of the mastoid process, coupled with extensive cranial thickness, support the inclusion of OH 12 in *H. erectus* (Rightmire, 1979; but see Schwartz and Tattersall, 2003). Despite similarities in the posterior cranium between OH 12 and OH 9, new conjoins discovered in the supraorbital region of OH 12 suggest nearly identical anatomy to that region of KNM-ER 3733 (Fig. 8; Antón, unpublished data). OH 12 is the youngest, by far, of the known African cranial *H. erectus* fossils, and is also the smallest adult with a cranial capacity estimated at 727 cc. OH 12 has a bregmatic eminence (Antón, unpublished data). The similarly aged Olduvai mandibles are similar in corporal size to earlier African mandibles (Table 4). They are variable in their expression of an anterior marginal tubercle, which is present in OH 51 but absent in the more recent OH 23. They have a narrow extramolar sulcus (OH 23) and possess multiple mental foramina.

Two crania from Ethiopia (Daka) and Eritrea (Buia) have been referred to *H. erectus* (Abbate et



Fig. 6. *H. erectus* faces from Africa and Georgia. **a:** KNM WT 15000 (cast). **b:** Dmanisi D2282. **c:** KNM ER 3883. **d:** KNM ER 3733. **a** and **b** to same scale in centimeters. **c** and **d** not to scale.

al., 1998; Asfaw et al., 2002). The Daka and Buia specimens are only preliminarily described, but the Buia specimen was suggested to exhibit a mosaic of *H. erectus* and *H. sapiens* characters (Abbate et al., 1998) that in my view exclude it from *H. erectus* sensu stricto. The Daka specimen was stated to be “phenotypically similar to the partly described Buia cranium” (Asfaw et al., 2002), although the two differ metrically and in some important morphological ways. Both were included in *H. erectus* by Asfaw et al. (2002) in a cladistic analysis that was over-

whelmingly weighted by cranial capacity. Subsequent cladistic and phenetic analyses exclude the Daka and Buia hominins from *H. erectus* (Manzi et al., 2003; and data not reported here). Both crania lack typical features of *H. erectus*, including a true occipital torus (although their expression may be similar to the Koobi Fora individuals), and possess features not typical of *H. erectus*, including a double-arched supraorbital torus (Daka) and thin cranial vaults. The Buia specimen metrically differs from other *H. erectus* in being relatively narrow low-down

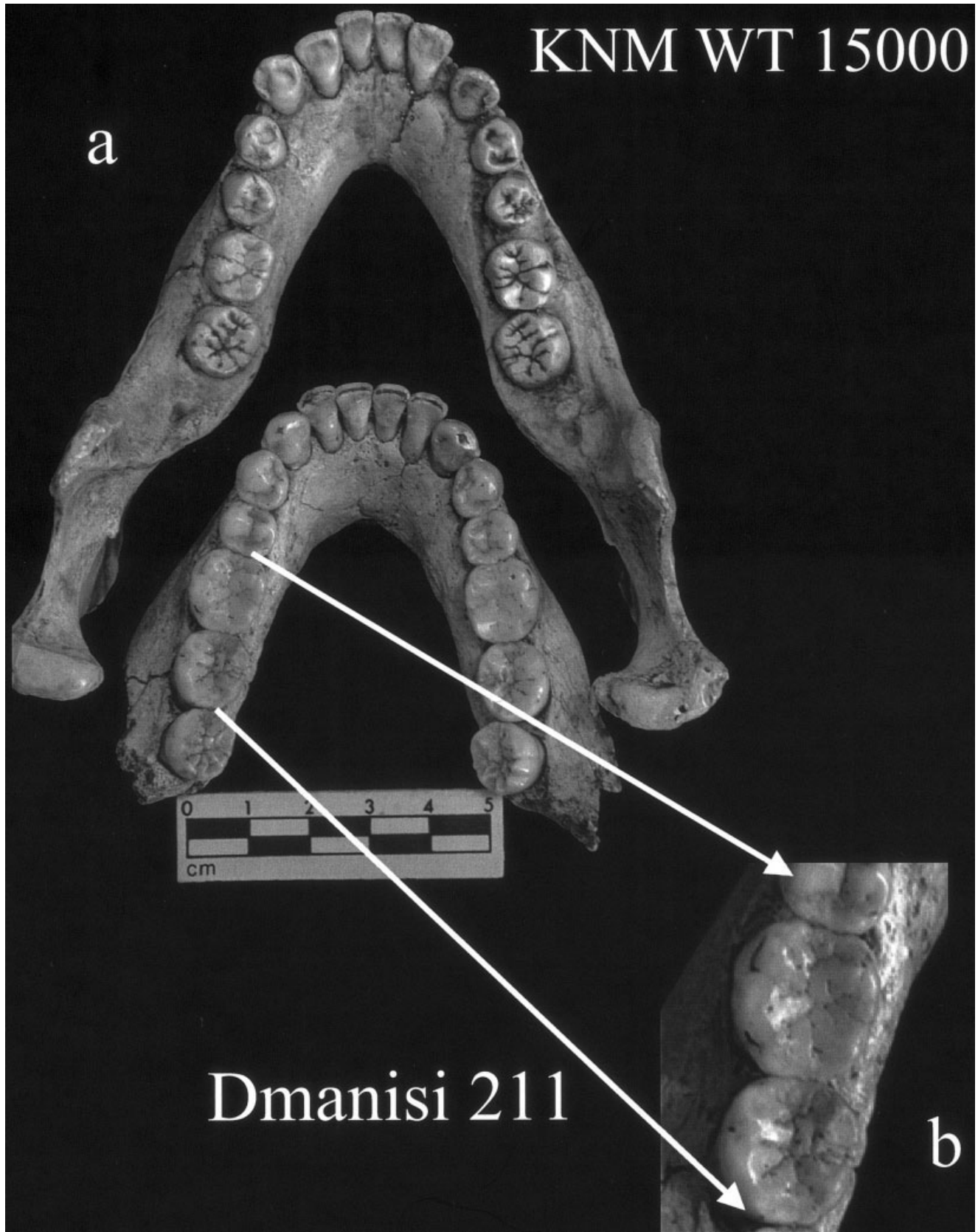


Fig. 7. a: Occlusal view of KNM WT 15000 (cast) and Dmanisi D211, scale in centimeters. b: Enlarged occlusal view of Dmanisi D211 first and second molars. Note accessory cusp complexes and anterior fovea morphology.

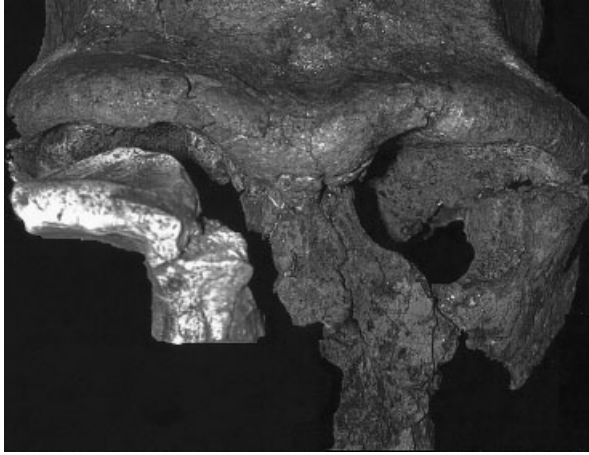


Fig. 8. Frontal view of orbital rim of OH 12 (cast, foreground) and KNM ER 3733. Note similar size and shape of medial supraorbital torus.

on the vault compared to its total length (e.g., biauricular breadth vs. cranial length). It should be noted, however, that some of the most troubling characteristics of the shape of the Buia vault, including the more vertical walls and greater breadth on the parietals, are not apparent in the Daka photographs or metrics. Alternatively, Daka is relatively difficult to distinguish from other *H. erectus* metrically, except that it is tall compared to its breadth (e.g., basion-bregma height compared with biauricular breadth).

For the moment, until additional data and comparisons are available, it seems conservative to exclude Buia from the discussion of later *H. erectus* crania in Africa, whereas OH 12 can be comfortably included, and Daka requires further evaluation. However, it should be noted that although OH 12 differs in supraorbital toral and occipital morphology from the Daka and Buia specimens, and is easier to accommodate in early *H. erectus* from Koobi Fora than is either Daka or Buia, some aspects of vault shape that exclude at least Buia from *H. erectus* are not assessable in OH 12 due to its fragmentary nature. Alternatively, Daka at least may share similarities with the supraorbital torus of OH 9, but also with the vault of KNM-ER 3733, a pattern opposite that of OH 12. Clearly this Brunhes/Matuyama group of African hominins requires further assessment.

Middle Pleistocene African crania from Lake Ndutu, Kabwe, Bodo, and Salé share with one another vault characters, including more parallel-sided vaults, usually larger cranial capacities (>1,100 cc, although Salé, a pathological cranium, is about 925 cc), and double-arched supraorbital tori (Wolpoff, 1999), as well as characters of the temporal bone such as a marked articular eminence and sphenoid spine that suggest they are archaic examples of *H. sapiens* (or *H. heidelbergensis*) rather than *H. erectus* (Rightmire, 1983, 1993). The Buia specimen shares affinities with these fossils. That this ca.

1-million-year-old fossil shares clearer affinities with Middle Pleistocene crania than with the contemporaneous OH 12 suggests the possibility that two lineages may be involved. However, as noted above, the fragmentary OH 12 and very small sample size make an understanding of regional affiliations tentative.

Change through time in Africa

The relatively small number of African cranial fossils makes assessing change through time on that continent problematic at best. The similarities in orbital morphology between the later OH 12 and the earlier KNM-ER 3733, and in posterior cranial morphology between OH 12 and OH 9, suggest that their shared morphology existed for nearly 1 million years. The Olduvai mandibles are similar in size and shape to their earlier counterparts from Koobi Fora. However, they tend to have somewhat shorter corpora for a given breadth (Table 4). The sparse and fragmentary fossil record makes it impossible to assess the complexity of variation between these regions. Likewise, the extent to which the anatomy of OH 12 is foreshadowed by that of earlier Olduvai *H. habilis* (and that of KNM-ER 3733 is foreshadowed by Koobi Fora *Homo*), coupled with new materials from Ileret, Kenya (cf. Leakey et al., 2003), suggests that our understanding of the origin and variation of early African *H. erectus* is far from clear. The assessment of relative character development due to age, sex, and particularly size (while assessable only through much larger sample sizes) is likely to prove crucial in disentangling these issues.

Despite the similarity in anatomy between the early Koobi Fora specimens and the much later OH 12, OH 12 differs from the recently announced Daka and Buia specimens (Abbate et al., 1998; Asfaw et al., 2002) in size, supraorbital toral morphology, and posterior vault shape, despite being approximately coeval with these hominins. In turn, Daka and Buia differ from one another in vault shape, strongly suggesting that at least Buia is not part of *H. erectus*. The constituency and variation in this Brunhes/Matuyama group of African hominins require further attention.

ASIA

The Asian sample represents the bulk of the *H. erectus* cranial record, and by and large represents the larger end of the range of variation mentioned above. Even the smallest-brained of the adult Asian fossils are around 800 cc, and while brain size may scale with body size, they would nonetheless be larger than at least their Western Asian counterparts from Dmanisi. Asian crania are also more hyperostotic than their African and Georgian counterparts.

The extent and kind of variation of certain traits appear consistent across all Asian *H. erectus* fossils (e.g., Howells, 1980; Andrews, 1984; Stringer, 1984;

TABLE 4. Adult mandibular corpus dimensions, in millimeters¹

Specimen	Height at M1	Breadth at M1	Height at M2	Breadth at M2
Early Africa				
KNM-ER 730	32.8	19.3	32.5	19.3
KNM-ER 731	27	19		
KNM-ER 992	32	20	35	24
Later Africa				
OH 22	27.3	20.4	28	21
OH 23	(30.1)	20.2	32	20
OH 51	(35)	22		
Early Indonesia				
Sangiran 1b	36	16.5	33	17
Sangiran 5	38	20		21
Sangiran 6			45	26
Sangiran 8	35.5	20		
Sangiran 9	(36)	23	(32)	23
China				
Zhoukoudian GI	34	16.4		
Zhoukoudian HI	26	15.4		
Zhoukoudian AII	25.6	15.2		
Zhoukoudian PA86	26.2	16.7		
Zhoukoudian KI	27.1	15.5		

¹ Data from Antón (unpublished data); Weidenreich (1943); Wood (1991a); Rightmire (1993).

Wood, 1984, 1991a, b; Rightmire, 1993; Antón, 2002a). Cranial superstructures such as metopic and bregmatic eminences, which are present or incipiently present in all Asian *H. erectus* fossils, and sagittal keels and angular tori are largely consistent, although somewhat variable, features of Asian *H. erectus*. A tympanomastoid sulcus is also present in all Asian *H. erectus* for which this region is preserved. Despite the fact that the type specimen is from Java, Chinese *H. erectus* more clearly resemble the standard description of *H. erectus* than do Indonesian fossils, perhaps reflecting the greater reliance on Chinese specimens to make these extended definitions (e.g., Antón, 2002a). There is significant regional variation in Asia, as discussed below.

Earliest Indonesia (1.6–1.8 Ma)

The earliest Indonesian crania are few in number, often badly deformed postmortem, and range in age from about 1.6 Ma to approximately 1.8 Ma (Tables 1 and 2). Cranial capacity can only be assessed on one fossil, Sangiran 4, but is relatively large at 908 cc (Holloway, 1981). Cranial walls are quite thick (Table 2). Postorbital constriction was probably pronounced (Sangiran 27), and the posterior vault is quite wide (Sangiran 4; Indriati, Antón, Jacob, unpublished data). However, overall shape cannot be assessed due to postmortem deformation. The posterior cranium is massive (Antón and Indriati, 2002). The mastoid process is large and projecting below the cranial base (Sangiran 4; Weidenreich, 1943, Von Koenigswald, 1940). The occipital torus is massive, confluent with the angular torus, defined superiorly by a large supratoral sulcus, and meets inferiorly in a central linear tubercle that continues into a well-expressed external occipital crest (Fig. 9; Sangiran 4 and 31; Grimaud-Hervé, 2001; Wolpoff, 1999, p. 455). The sagittal crest reported for Sangiran 31 (Tyler et al., 1995) is almost certainly an artifact of deformation (Grimaud-Hervé, 2001). The

glenoid fossa is similar in size from anteroposterior to mediolateral.

The earliest Indonesian face is represented only by the badly distorted Sangiran 27 and the maxilla of Sangiran 4. The supraorbital torus in the earliest Indonesian fossils is massive in vertical height (Table 2; Sangiran 27). However, it is not sufficiently preserved to describe its shape or glabellar region (Indriati, Antón, Jacob, unpublished data; contra Wolpoff, 1999, p. 457). Prognathism cannot be assessed, but the infraorbital region is convex and cheek height relatively tall (Sangiran 27; Indriati, Antón, Jacob, unpublished data). The maxilla lacks paranasal pillars, and the nasal sill is marked by a sharp ridge in Sangiran 4 but is smooth in Sangiran 27 (Antón and Indriati, 2002; Indriati, Antón, Jacob, unpublished data).

Occlusal area is absolutely large in the earliest Indonesian molar and premolar rows (Indriati, Antón, Jacob, unpublished data). The molars possess high mesial marginal ridges and accessory cusp complexes (Sangiran 4, 27; Grine and Franzen, 1994; Antón and Indriati, 2002). However, distal marginal ridge shape is variable, tending to be incomplete in Sangiran 4 (Antón and Indriati, 2002). The upper canine is large, with a large root in both Sangiran 4 and 27 (Wolpoff, 1999, p. 456; Indriati, Antón, Jacob, unpublished data).

The earliest Indonesian mandible is represented by a single, relatively gracile specimen, Sangiran 22, with a narrow extramolar sulcus and similar features to those of D211 from Georgia (Antón and Indriati, 2002), and by a badly distorted mandibular fragment probably associated with Sangiran 27 (Indriati, personal communication).

Early Indonesia (0.9–1.5 Ma)

These remains are more numerous than those of the earliest Indonesian fossils, and often exhibit a greater range of variation. Adult cranial capacity

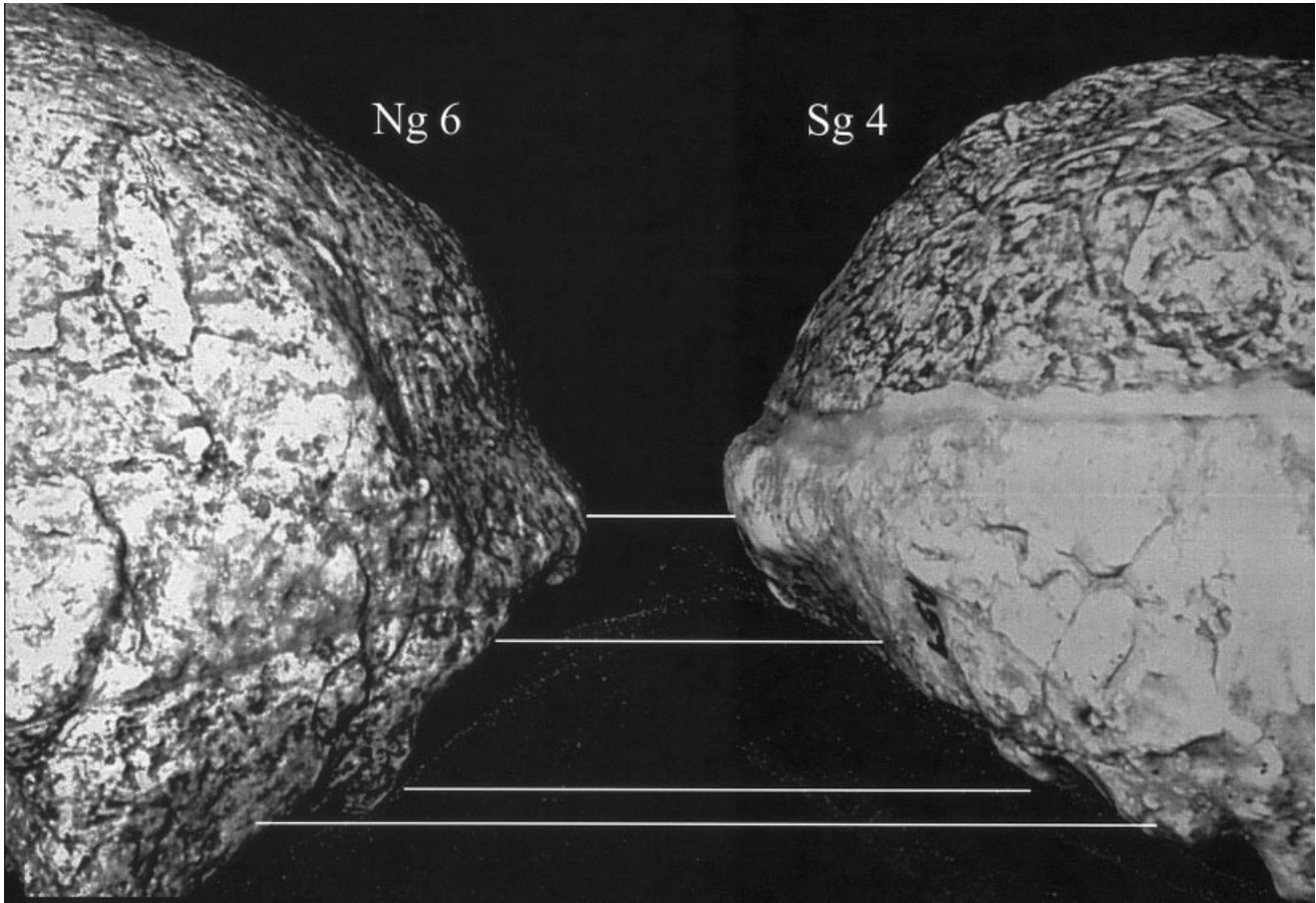


Fig. 9. Sagittal view of posterior vault of (casts) Ngandong 6 and Sangiran 4. Specimens to same scale. Note similar degree of development of anatomical structures of occipital (lines connect these), despite temporal gap of more than 1.0 million years and differences in cranial capacity of nearly 350 cc (see Table 2).

varies from about 800 cc (Sangiran 2) to just over 1,000 cc (Sangiran 10 and 17; Table 3; Holloway, 1981). The vault is strongly pear-shaped when viewed from above, due to strong postorbital constriction and a substantially wider posterior than anterior cranium (Antón, 2002a). The temporal lines follow this shape, diverging substantially posteriorly. In sagittal view, the vault is long, low, and angular. Cranial superstructures, including midline keels and angular tori, are the norm (Santa Luca, 1980).

The posterior cranium exhibits mastoid processes and occipital tori of varying size and shape (Weidenreich, 1943; Antón, 2002a). Most mastoid processes are relatively small and nonprojecting below the cranial base, but large and projecting processes are seen in some specimens (Sangiran 12). The mastoid and supramastoid crests are marked, and most have a supramastoid sulcus between them. The glenoid fossa is equally wide in anteroposterior and mediolateral dimensions. Some early Indonesian *H. erectus* have a continuous, straight occipital torus with a supratoral sulcus, and also lack expression of an external occipital crest (Sangiran 2 and 10); others have only a slight supratoral sulcus and very modest

development of the occipital torus (Sangiran 3; Antón and Franzen, 1997).

The supraorbital torus in early Indonesia is large and continuous. In some fossils, in anterior view, the supraorbital torus dips inferiorly at the glabella, and in a few it is depressed antero-posteriorly at the glabella (i.e., *depressio glabellaris*; see Antón, 2002a). However, in superior view, it always projects farther at the glabella than laterally, and is vertically, absolutely thick (Fig. 5; Table 2). The post-toral/supratoral gutter is wider laterally than medially (Antón, 2002a), and is not always well-defined or continuous (Wolpoff, 1999, p. 462–463). In all early Indonesian *H. erectus* fossils, the lateralmost ends of the supraorbital torus are separated from the frontal squama by triangular depressions. Medially, a less distinct depression (Trinil 2 and Sangiran IX), or none at all (Sangiran 17), separates the glabellar portion of the supraorbital torus from the frontal squama.

Only one undeformed early Indonesian face exists (Sangiran 17), along with some facial fragments (Sangiran IX). Both appear large and moderately prognathic (Aziz et al., 1996; Wolpoff, 1999, p. 463; Arif et al., 2001). The infraorbital region is convex.

The Sangiran 17 face is broadest inferiorly (in the zygomaxillary region; Wolpoff, 1999, p. 487). These faces appear to lack paranasal maxillary pillars and maxillary fovea, but share similar nasal floor and sill morphology (Antón and Indriati, 2002).

The early Indonesian mandibles are notoriously variable in morphology, leading to claims of multiple species at Sangiran (e.g., Jacob, 1975; Howell, 1994; Table 4), although these arguments remain metrically hard to substantiate (e.g., Kramer, 1994). Early Indonesian mandibular corpora are tall for their breadth, possibly related to the large occlusal areas of their molars (Table 4). These mandibles are variable in the breadth of their extramolar sulci (when preserved) and in the development of lateral prominences and anterior marginal tubercles. Molars possess high mesial marginal ridges and accessory cusp complexes (Grine and Franzen, 1994; Antón and Indriati, 2002). Mandibular incisors are relatively broad (Wolpoff, 1999, p. 460).

Later Indonesia (<100 ka)

Later Indonesian fossils from Ngandong and Sambungmacan lack upper facial, mandibular, or dental remains (Table 1; Openoorth, 1932, 1937; Jacob, 1984; Bartstra, 1987; Santa Luca, 1980; Márquez et al., 2001; Baba et al., 2003). Cranial size ranges from 900 to over 1,200 cc, and averages over 1,000 cc (Table 3; Holloway, 1980; Márquez et al., 2001; Baba et al., 2003). Cranial shape exhibits moderate postorbital constriction (Weidenreich, 1951; Wolpoff, 1999, p. 571), but still demonstrates the much wider posterior expansion and posterior divergence of the temporal lines seen in earlier Indonesian forms (Antón, 2002a). In sagittal view, the vault is long, moderately low, and angular. Cranial superstructures are the norm (Santa Luca, 1980).

The posterior cranium is marked by relatively projecting mastoid processes and occipital tori, often with supratoral sulci (Weidenreich, 1951). The mastoid and supramastoid crests are strongly expressed and all have a supramastoid sulcus between them (Fig. 3; Antón, 2002a). Occipital tori are continuous and either massive or moderate in size, often with large supratoral shelves and expressing an external occipital crest (Fig. 9; Santa Luca, 1980; Antón, 2002a). The glenoid fossa is similar in size from anteroposterior to mediolateral, and, except in Ngawi, is relatively narrow mediolaterally compared to cranial length (Fig. 4).

These later Indonesian hominins possess absolutely thick, continuous, supraorbital tori, and exhibit a great frequency of glabellar depression (Table 2; Santa Luca, 1980). Posttoral sulcus morphology is similar to larger-brained, early Indonesian forms such as Sangiran 17 (Fig. 5; Antón, 2002a).

Change through time in Indonesia

Between the earliest and the early Indonesian *H. erectus* samples there is little evidence of change,

except possibly in size. New preliminary reports suggest that occlusal area and overall mandibular size decrease from lower to higher in the section at Sangiran (Kaifu et al., 2003). This same work argues that differences between mandibles that were sometimes used to argue for multiple species (Jacob, 1975; Howell, 1994) are likely related to scaling factors. Although the earliest Indonesian crania (Sangiran 4, 27, and 31) are hyperrobust (Wolpoff, 1999, p. 457), they are also unscorable for many traits due to deformation, and are well-encompassed by the morphological variation in early and later Indonesian *H. erectus*.

Together, the range of variation in the premillion-year-old Indonesian *H. erectus* encompasses the morphology seen in later Indonesian specimens from Ngandong and Sambungmacan (Weidenreich, 1943, 1951; Santa Luca, 1980; Antón, 1997, 1999, 2002a; Antón et al., 2002; Baba et al., 2003). This is true of variation in cranial capacity and the expression of the supraorbital torus, posttoral/supratoral gutter, mastoid process, form of the glenoid fossa, and occipital toral morphology. The later Indonesian cranial sample, despite being reasonably numerous ($n = 16$), exhibits a narrower range of variation and a fixing of some character states relative to the earlier fossils (Antón, 2002a). Through time, the average brain size increases (although the absolute range changes little; Antón and Swisher, 2001), mastoid processes increase in average size (but not size range), and the presence of a supramastoid sulcus becomes the exclusive condition. Glabellar depressions become more frequent (Weidenreich, 1951). The smaller range of variation in later Indonesian cranial samples may be the result of genetic drift through time in this presumably small and isolated population (Wolpoff, 1999, p. 572; Antón, 2002a), although it is also possible that this is the result of the Ngandong/Sambungmacan samples representing more restricted time horizons (and more closely related individuals) than the earlier Sangiran record that encompasses at least 500,000 years (Antón, 2002a). The main differences between earlier and later Indonesian *H. erectus* seem to relate to brain size increase, including increases in average capacity, increases in vault height, and decreases in postorbital constriction. However, many of the ways in which the Ngandong specimens have been said to differ from *H. erectus* in general (mastoid and supramastoid morphology, supraorbital torus morphology, and occipital morphology) are instead ways in which Indonesian *H. erectus* differs from Chinese *H. erectus* (see below and Antón, 2002a).

Continental Asia

Early *H. erectus* from China (~1.2 Ma). Early *H. erectus* from Gongwangling (Lantian) is badly deformed postmortem (Wu and Poirier, 1995). Brain size is reconstructed to be small (780 cc), but due to deformation this may be an unreliable estimate

(Wolpoff, 1999, p. 467). The supraorbital torus is massive and probably barlike, with a dip inferiorly at midline (Antón, unpublished data). The shape of the supratotal gutter and overall vault shape cannot be assessed.

Middle *H. erectus* from China (~ 200–600 ka).

The sample is comprised principally of the Zhoukoudian and Nanjing crania. The vault size of continental Asian fossils from this middle period ranges from 855 to over 1,200 cc, with a mean of over 1,000 cc (Tables 2 and 3; Weidenreich, 1943; Chiu et al, 1973; Rightmire, 1985). Viewed superiorly, the vault is pear-shaped, with strongly diverging temporal lines posteriorly. However, the posterior vault is extremely narrow at the asterion, but remains wide at the auriculare (Antón, 2002a). In sagittal view, the vault is long, low, and angular, although the frontal squama rises sharply from the posttotal sulcus. Cranial superstructures are the norm (Weidenreich, 1943).

The Chinese *H. erectus* posterior cranium has small, nonprojecting, mastoid processes and marked occipital tori (Weidenreich, 1943). The mastoid and supramastoid ridges are marked and confluent at their superior ends (i.e., they lack a supramastoid sulcus; Fig. 3; Wood, 1991a, p. 37; Santa Luca, 1980; Stringer, 1984). This likely represents the primitive condition (e.g., Olson, 1978), although it is possible that the narrow asterionic region contributes to the fusion of the crests secondarily, and thus this may be a derived character. The glenoid fossa is similar in size from anteroposterior to mediolateral, and relatively narrow mediolaterally compared to cranial length (Fig. 4). The occipital torus is moderate in size, straight, and continuous, is demarcated superiorly by a supratotal sulcus, and joins the well-defined angular torus at its lateral extent (Weidenreich, 1943). The torus lacks any inferior midline projections, such as an external occipital protuberance or linear tubercle, and the Chinese occipitals also tend to lack any significant expression of an external occipital crest (Weidenreich, 1943).

Chinese supraorbital tori are vertically large, continuous across the glabella, and separated from the frontal squama by a discrete, continuous supratotal gutter (Table 2; Antón, 2002a). Viewed from above, the Chinese supraorbital torus projects as evenly at the glabella as laterally (Fig. 5). The supratotal gutter “wraps around” the anterior cranium, being wider laterally and narrower at midline. The supratotal gutter is quite distinct due to the very sharply rising frontal squama which, however, rises less steeply in Nanjing 1 and 2 than in the Zhoukoudian fossils (Wolpoff, 1999, p. 487, 498).

The Chinese *H. erectus* face is known from several large fragments and reconstructions of these (e.g., Weidenreich, 1943; Tattersall and Sawyer, 1996). The reconstructed face is not particularly prognathic, although somewhat more so in the most recent reconstructions (Tattersall and Sawyer, 1996).

The infraorbital region is flat to concave (Wolpoff, 1999, p. 487). The Chinese *H. erectus* mandibles are reasonably large (Table 4), the gonial angles are everted, extramolar sulci, when preserved, are broad, and the dental arcade shape is parabolic (Weidenreich, 1936; Wu and Poirier, 1995). Mandibular tori occasionally develop, as do multiple mental foramina. Molar occlusal areas are moderately large. Mandibular incisors are narrow (Rosas and Bermúdez de Castro, 1998).

Comparative cranial anatomy across regions

Variation within Asia. Chinese and Indonesian *H. erectus* share a total morphological pattern that includes similarities in overall cranial architecture, including vault size and shape (Rightmire, 1993; Antón, 2002a). Vault size in Asian *H. erectus* ranges from about 800 cc to over 1,200 cc, with a gradual increase in mean cranial capacity with time (Antón and Swisher, 2001). Asian *H. erectus* possess a long, low vault that, when viewed superiorly, is strongly pear-shaped and possesses diverging temporal lines posteriorly. However, the posterior vaults show one significant difference: the Chinese vault is narrow (pinched) in its asterionic region compared to Indonesian specimens (Antón, 2002a). The relatively narrow frontal (postorbital constriction) and occipital (biasterionic breadth), coupled with a relatively large brain size, separate the Chinese morph from the Indonesian samples in simple PCA analyses, whereas early and late Indonesian morphs do not separate from one another (Antón, 2002a; Baba et al., 2003).

Chinese and Indonesian *H. erectus* differ somewhat with respect to shape of the supraorbital torus in superior view, continuity of the posttotal/supratotal gutter, presence of a supramastoid sulcus, position of the squamotympanic fissure, and presence of an occipitomastoid crest (Antón, 2002a). In contrast to Indonesian *H. erectus*, the Chinese supraorbital tori, while large, are less vertically massive (Table 3). The Chinese supraorbital tori are also straighter in superior view, whereas the Indonesian tori extend further anteriorly in the region of the glabella than laterally. All Asian supratotal gutters “wrap around” the front of the brain (i.e., they are wider laterally than at midline), but those of Chinese *H. erectus* differ somewhat from the Indonesian condition by being continuous in all specimens and strongly demarcated by a steep vertical rise of the frontal. This greater vertical rise of the frontal squama in Chinese *H. erectus* may be an accommodation to relatively narrow frontal breadths coupled with large brain sizes.

The most marked differences between Chinese and Indonesian *H. erectus* faces relate to relative prognathism (Wolpoff, 1999, p. 487). Indonesian faces (Sangiran 17 and 27) are clearly more convex in their infraorbital regions than Chinese *H. erectus*, and have been reconstructed to be much more prognathic as well (Thorne and Wolpoff, 1981). However,

how these faces should be hafted has been contested, with the result that reconstructions of Sangiran 17 vary between highly orthognathic (Aziz et al., 1996) and highly prognathic (Thorne and Wolpoff, 1981). The actual degree of prognathism is likely to be greater than that suggested in the most recent reconstructions of Sangiran 17. However, this may not differ too greatly from recent reconstructions of Chinese *H. erectus* (Tattersall and Sawyer, 1996). The lower face of Sangiran 17, however, is broader than the upper face, whereas these regions are of similar dimension in the Chinese reconstructions and Sangiran IX (Arif et al., 2001). In other ways, the faces are similar (Rightmire, 1998b). For example, both Chinese and Indonesian faces appear to lack paranasal maxillary pillars. Nasal sill and floor morphology (sensu McCollum et al., 1993; McCollum, 2000) is variable within regions.

Dental arcade shape is generally parabolic, although anterior teeth appear smaller in China than in Indonesia (Weidenreich, 1936, 1937, 1943). Both possess large mandibles, but Indonesian specimens are larger and taller (Table 4). Both also possess large postcanine teeth, although the occlusal area is even greater in Indonesia than in China. Extramolar sulci, when preserved, are variable in size in Indonesia but broad in China.

Variation between Asia and Africa. The vaults of African and Asian *H. erectus* also share a number of similarities. Together, African and Asian vaults are metrically differentiable from geographically diverse samples of *H. sapiens* in simple bivariate and principal components analyses (PCA; Antón, 1997, 1999, 2002a). These metric distinctions are expressions of the “long low vault” form, frontal recession, and occipital angulation often used to describe *H. erectus* (e.g., Dubois, 1894; Wood, 1991a; Schwartz and Tattersall, 2000; Jacob, 2001). It should be noted that the Daka calvaria groups with the Koobi Fora vaults in similar analyses (data not reported here). Except on the basis of size, these tests do not differentiate African from Asian forms (Antón, 2002a), although other methods suggest that the two may be metrically differentiable (Bilsborough and Wood, 1988). Although angular dimensions of the vault bones fail to distinguish African from Asian vaults, they do differentiate subadult from adult *H. erectus* specimens from all regions (Antón, 1997, 2002a, b; Antón and Leigh, 2003).

The vault differs between African and Asian specimens, however, by being more strongly pear-shaped when viewed from above in Asian specimens. This shape difference is related to a substantially greater difference between anterior and posterior cranial breadths in Asian *H. erectus* (Antón, 2002a). Asian temporal lines diverge strongly from one another as they proceed posteriorly, whereas in African specimens these lines remain more parallel to one another and higher on the vault. Asian proportions are retained even in the Chinese specimens, despite

their being quite narrow at the asterion compared to Indonesian *H. erectus*.

The structure of the glenoid fossa differs between African and Asian forms (Picq, 1990), and is more mediolaterally elongated and anteroposteriorly foreshortened in African relative to Asian forms (Antón, 2002a). This is likely a retention of the primitive condition in the former. Similarly, the glenoid fossa is mediolaterally wide compared to vault length in African, but not in most Asian fossils (Fig. 4). Exceptions include the late Indonesian fossil from Ngawi and, as observed by Spoor (unpublished data), possibly Sangiran 2.

The supraorbital tori are more massive, on average, in Asia than in Africa, although both the African and Indonesian samples exhibit large ranges of size variation (Table 3; Wolpoff, 1999, p. 452). Chinese supraorbital tori are evenly projecting in superior view, similar to those of KNM ER 3733, whereas Indonesian supraorbital tori project further in the glabellar region than laterally, more similar to OH 9. Further work is needed to assess the implications of these similarities and differences.

Supratoral gutter shape wraps around the anterior cranium in Asian *H. erectus*, but is straight (evenly wide laterally and at midline) in African *H. erectus* (Antón, 2002a). African *H. erectus* frontal squamae tend to rise steeply from this gutter (Wolpoff, 1999, p. 457). Although Chinese *H. erectus* also possess a frontal that rises steeply from the gutter (see above), this rise would appear to exist for different reasons than those seen in Africa; the Chinese rise appears related to large brain size and narrow frontal and biasterionic breadths, whereas it is present even in small-brained African *H. erectus*. Ultimately, differences in gutter width and position relate to the anteriormost extent of the brain, and may relate to hafting of the face to the braincase (Ravosa, 1988). The possession of a continuous supratoral gutter and a greater vertical rise of the frontal is not likely to unite Chinese and African *H. erectus*, since gutter form differs between them and arises for different reasons.

Asian *H. erectus* faces are more massive than the existing early African/Georgian counterparts, and are probably somewhat more prognathic (Bilsborough and Wood, 1988; Wolpoff, 1999), although hafting issues remain contested (Tattersall and Sawyer, 1996; Aziz et al., 1996). Asian faces appear to lack the paranasal maxillary pillars and fovea seen in Dmanisi 2282 and the Nariokotome boy, but to retain similar nasal floor and sill morphology as African fossils (Gabunia et al., 2001; Antón and Indriati, 2002). The infraorbital region appears more convex in the Indonesian than in the Chinese or African/Georgian faces.

Indonesian mandibles are larger than their early African counterparts, suggesting greater masticatory robusticity (Table 4). Chinese mandibles are intermediate in size between Indonesian and African forms. Extramolar sulci tend to be narrower in

African than Asian *H. erectus*; however, Indonesian specimens are variable in this regard. The presence and position of the anterior tubercle and lateral prominence are similarly variable across groups.

Asian molar occlusal areas are larger than African/Georgian areas, with Indonesian values being the largest. In addition, Asian occlusal shape, particularly of the mesial marginal ridge and the presence of accessory cusp complexes, differs from early African, but not Georgian, anatomy (Grine and Franzen, 1994; Antón and Indriati, 2002; Gabunia et al., 2001).

Overall, the similarities between early African *H. erectus* and the Dmanisi hominins are stronger than those between African and Asian forms, although there are also ways in which the Dmanisi hominins differ from early African *H. erectus* (Gabunia et al., 2000a, 2001). Georgian and Javan fossils share similar, possibly primitive shapes and orientation of the subalveolar plane of the mandible (Rosas and Bermúdez de Castro, 1998), as well as the presence of Carabelli and protostylid complexes of both upper and lower dentitions (Antón and Indriati, 2002). The Georgian fossils share small buccolingual dimensions of the lower incisors with later *H. erectus* from Zhoukoudian, and tend to group with the Zhoukoudian fossils in multivariate analyses of the mandibular dentition (Rosas and Bermúdez de Castro, 1998).

Autapomorphic characters and character suites

Attempts to define unique features of *H. erectus* have met with mixed results (e.g., Santa Luca, 1980 vs. Hublin, 1986). Most workers concur that some of the following are unique, at least to the Asian branch of the species. However, they disagree as to the usefulness of these characters as taxonomic indicators. Potential autapomorphies include a long and low vault with greatest breadth low down and thick vault walls, pronounced postorbital constriction, frontal recession and occipital angulation, cranial superstructures including frontal, coronal, and sagittal keels, occipital and angular tori, large continuous supraorbital tori and a supratatorial sulcus, marked supramastoid and mastoid crests, thick tympanic plates, a process supratubalis, no vaginal crest (but see Wolpoff, 1999), petrous portions oriented in a more sagittal plane than in modern humans, and a large posterior middle meningeal artery (e.g., Weidenreich, 1943; Santa Luca, 1980; Stringer, 1984). However, the principal Koobi Fora crania extend this definition by mostly lacking continuous occipital and angular tori, by being less thick-walled, and by having less prominent, although still present, supraorbital tori (Wood, 1991a). Interpretation of these distinctions is obscured by our imprecise understanding of the origins of these features. Future research should focus on the systematic assessment of the structural and developmental origins of each of these features, in an effort to assess the homologous nature of the traits

being scored and their relative developmental plasticity, and thus their usefulness as both taxonomic and phylogenetic characters.

POSTCRANIAL ANATOMY

The postcranial remains assigned to *H. erectus* are far fewer in number than the cranial sample, and isolated elements are difficult to assign to species (Tables 5–7). Three partial skeletons from Kenya (KNM-ER 803 and 1808, and KNM-WT 15000) provide the *only association between cranial and postcranial members of the species*, and the only information on body proportions. Attributing isolated postcranial elements to species is particularly difficult in time ranges when more than one species of *Homo* may be sampled (McHenry and Coffing, 2000); such is the case in attributing large, early postcranial elements (e.g., innominate KNM-ER 3228 and the femur KNM-ER 1481A) to *H. erectus* rather than *H. habilis* (*sensu lato*) and in attributing later postcranial elements such as the Kapthurin remains (e.g., KNM-BK 64, 65, and 66) to *H. erectus* rather than to *H. heidelbergensis* or other *Homo*. To be conservative, isolated elements that do not fit the predominant pattern established by postcrania associated with cranial *H. erectus* are not considered here. It should be recognized that this decision likely decreases the range of variation in the sample. Postcranial specimens are listed by element in Table 5. The main comparisons to earlier *Homo* are with the only associated skeletons of *H. habilis sensu lato*, the highly fragmentary OH 62 and KNM-ER 3735 (Johanson et al., 1987; Leakey et al., 1989).

Species-wide conditions

Due to the fragmentary nature of the associated *H. habilis* skeletal remains, it is impossible to assess whether many of the differences between *H. erectus* and *Australopithecus* are derived characters for genus *Homo* or for *H. erectus*. Differences between the two genera include, in *Homo*, the presence of: enlarged articular surface areas of long bones, thick cortical bone (particularly in the lower limb shafts), deep trochlea of the distal femur, double meniscal attachments of the proximal tibia, narrow pelvis with marked iliac pillars (i.e., acetabulocrystal buttresses), and medial torsion of the ischial tuberosity (Table 7). These characters also appear to be retained in all post-*H. erectus* skeletons, although some are lost in modern humans. Thus, the postcrania of *H. erectus* are primarily differentiated from those of modern humans on the basis of primitive characters (e.g., McHenry et al., 1976; Trinkaus, 1984; Ruff, 1995), including both those that are derived in hominins relative to nonhuman primate conditions (e.g., six lumbar vertebrae (but see below) or long femoral necks), and those that, as mentioned above, may originate in earlier *Homo* and remain unchanged until *H. sapiens*.

Postcranially, *H. erectus* is larger and possesses different body proportions than do australo-

TABLE 5. Postcranial elements¹

Specimen	KNM-ER 15000	KNM-ER 1808	KNM-ER 803	Other Africa	Georgia	Indonesia	China
Vertebrae	X			ER 164	Dmanisi, UP		Zhoukoudian atlas
Ribs	X				Dmanisi, UP		
Scapula	X	X					
Clavicle	X	X			Dmanisi, UP		Zhoukoudian Misc I
Humerus	X	X			Dmanisi, UP		Zhoukoudian humerus I–III
Ulna	X	X	X	?BK66			
Radius		X	X				
Hand	X		X	SK84, ?BK 64, 65	Dmanisi, UP		Zhoukoudian- lunate
Os coxa	X	X		?ER-3228 OH 28		Ngandong 17	
Femur	X	X	X	?ER 1472, 1481, 3728 ?OH 34 ?BOU-VP 1/175, 2/15, 19/63 OH 28 ER-736, 737 ?ER-741		Trinil I–V Sangiran 29, 30; Kresna 10, 11; Kedungbrubus 2	Zhoukoudian femur I–VI
Tibia	X	X	X	?ER 19700 ?ER-1481 ?OH 34 ?BOU-VP 1/109		Ngandong tibia A and B ² Sambungmacan 2	Zhoukoudian tibia I
Fibula	X	X	X				
Foot	X		X	ER 5428	Dmanisi D2021 Dmanisi, UP		

¹ Site abbreviations as in Table 1, and BK, Baringo Kapthurin; BOU, Daka member of Middle Awash, Ethiopia; x, element present; ?, questionable affiliation based on either time or morphology; Dmanisi, UP, unpublished.

² Ngandong Tibia A and B were originally cataloged in their order of discovery as Ngandong 9 and 10 (Indriati, 2003). However, more recent catalogs assigned numbers Ngandong 13 and 14 to these tibia (Oakley et al., 1975), or Ngandong 12 and 13 (Wolpoff, 1999); or used multiple designations (Schwartz and Tattersall, 2003).

pithecines or the highly fragmented associated skeletons of *H. habilis* (McHenry and Coffing, 2000). In particular, the upper limb is relatively short compared to body size, due mostly to relatively short distal upper-limb segments coupled with elongation of the lower limb. Compared to *Australopithecus afarensis*, and possibly *H. habilis*, the pelvic inlet is enlarged sufficiently to accommodate the birth of a reasonably large-brained, if secondarily altricial, infant (Ruff and Walker, 1993). However, substantial range in body size, as witnessed by the Georgian remains, is present at least early in the species' history (Gabunia et al., 2000c; Table 6). In addition, if OH 62 is representative of all early *Homo*, then anteroposteriorly narrow but mediolaterally wide femoral shafts (platymeria) in the subtrochanteric and midshaft regions may be derived in *H. erectus*. Such a conclusion, however, would require that early femora such as KNM-ER 1472 and 1481 be assigned to *H. erectus* (e.g., Kennedy, 1983a, b), a position that many are understandably unwilling to take without corroborative contemporaneous crania (Trinkaus, 1984; Walker and Leakey, 1993c; McHenry and Coffing, 2000). Possibly the occipital fragment KNM-ER 2598 (Wood, 1991a) hints at the eventual presence of such cranial remains.

Regional postcranial variation

Africa and Georgia. The axial skeleton. The vertebral column, known largely from KNM-WT 15000, is similar to that of modern humans, with some notable exceptions. Unlike most modern humans, but similar to the situation in *A. africanus* (Sts 14), six lumbar vertebrae are present (Walker and Leakey, 1993c). Latimer and Ward (1993) suggested that the presence of six lumbar results from the lumbarization of T13 in order to achieve the lumbar lordosis necessary for habitual bipedality. The attribution of six lumbar in both Sterkfontein (Sts) 14 and KNM-WT 15000, however, was seriously questioned by Haeusler et al. (2002), who argued that the presacral Nariokotome spine, although incomplete, provides evidence that the vertebra designated as L1 is in fact T12. In addition to the number of lumbar, Latimer and Ward (1993) also noted that lumbar vertebral bodies are relatively small compared with body weight, although not as small as in the great apes. Vertebral canal size in KNM-WT 15000 swells in the cervical and lumbar regions, as seen in modern humans and other hominins, but the thoracic canal lacks this swelling (Brown et al., 1985). Differences in the ver-

TABLE 6. Limb lengths, stature, and body weight¹

Specimen	Geological age (Ma)	Taxon ³	Length (mm)	Midshaft AP (mm)	Midshaft ML (mm)	Stature (cm)	Weight (kg)
Clavicle			Maximum				
KNM-ER 15000	1.51–1.56	<i>H.e.</i>	130.5 at death	14.5	9.3		
KNM-ER 1808	1.69	<i>H.e.</i>	130–140	12.0	10.0		
Zhouk Misc I	0.50	<i>H.e.</i>	(145) restored				
Humerus			Maximum				
KNM-ER 15000	1.60	<i>H.e.</i>	(319) at death	29.9	16.7		
Zhouk Hum II	0.50	<i>H.e.</i>	(324) restored	20.7	15.4		
Zhouk Hum III	0.50	<i>H.e.</i>		21.6	17.8		
Ulna			Maximum				
KNM-ER 803	1.53	<i>H.e.</i>					
KNM-ER 15000	1.51–1.56	<i>H.e.</i>	270 at death				
KNM-ER 15000	1.51–1.56	<i>H.e.</i>	348 adult				
Femora			Bicondylar				
KNM-ER 1472	1.89	<i>H. sp.</i>	400	25.1	26.4	149	47
KNM-ER 1481	1.89	<i>H. sp.</i>	395	22.4	25.6	147	46
KNM-ER 3728	1.89	<i>H. sp.</i>	390	20.1	24.7	145	45
KNM-ER 736	1.70	<i>H.e.</i>	500	36.1	37.7	180	62
KNM-ER 737	1.60	<i>H.e.</i>	440	27.1	32.4	160	52
KNM-ER 803	1.53	<i>H.e.</i>		28.2	32.1		
KNM-ER 1808	1.69	<i>H.e.</i>	480			173	59
KNM-ER 15000	1.51–1.56	<i>H.e.</i>	429 at death	24.5	24.3	159 at death	52
KNM-ER 15000	1.51–1.56	<i>H.e.</i>	517 adult			185 adult	68
OH 28	<0.78	<i>H.e.</i>	450	24.7	32.7	163	54
OH 34	1.00	? <i>H.e.</i>	430			158	51
Trinil I	?0.9	? <i>H.e.</i>	455	29	28.0	163	54
Trinil II	?0.9	? <i>H.e.</i>	460	26.2	27.1	163	54
Trinil III	?0.9	? <i>H.e.</i>		25.4	27.7		
Trinil IV	?0.9	? <i>H.e.</i>		25.7	28.8		
Trinil V	?0.9	? <i>H.e.</i>		27.0	26.3		
Zhouk I	0.50	<i>H.e.</i>	(400)	27.1	29.7	150 ²	47
Zhouk II	0.50	<i>H.e.</i>		22.8	26.4		
Zhouk IV	0.50	<i>H.e.</i>	407	25.0	29.3	150 ²	47
Zhouk V	0.50	<i>H.e.</i>		23.7	29.5		
Zhouk VI	0.50	<i>H.e.</i>		26.1	29.2		
Tibia			Maximum				
KNM-ER 803	1.53	<i>H.e.</i>		28.6	20.0		
KNM-ER 15000	1.60	<i>H.e.</i>	380 at death	24.0	20.4	160	52
KNM-ER 15000	1.60	<i>H.e.</i>	475 as adult			184	64
Ngandong A	0.05–0.1	<i>H.e.</i>		37.1	27.0		
Ngandong B	0.05–0.1	<i>H.e.</i>	(360)	29.5	21.2	158	51
Fibula							
KNM-ER 15000	1.60	<i>H.e.</i>	321.5 at death w/o epiphysis	10.5	9.1		
Third metatarsal			Maximum				
Dmanisi D2021	1.7	<i>H.e.</i>	60			148	46

¹ Data are from: *Africa*—McHenry (personal communication, 1992, 1994); McHenry and Coffing (2000); Walker and Leakey (1993c); *China*—Weidenreich (1941); Wu and Poirier (1995); *Indonesia*—Santa Luca (1980); *Georgia*—Gabunia et al. (2000c).

² Weidenreich (1941, p. 34), using Manouvrier's and Pearson's regressions, published an estimated stature of 156 cm.

³ *H.e.*, *H. erectus*; *H. sp.*, *Homo Species*; ?, questionable association.

tebral column have been attributed either to differences in muscular control of lower limb elements for the lumbar (due to increased efficiency of bipedality in *H. sapiens*; MacLarnon, 1993), or greater control of respiratory/abdominal musculature for the thoracics (perhaps related to speech in *H. sapiens*; MacLarnon, 1993), or to a pathological condition, either axial dysplasia or an early, healed trauma, in this particular hominin (Latimer and Ohman, 2001; Walker, 2002).

Analyses of rib angulation and relative position of thoracic vertebrae indicate that the shape of the thorax of KNM-WT 15000 more closely resembles the cranially broad but caudally narrow, barrel-shaped thorax of modern humans than the funnel-shaped thorax of the nonhuman great apes and earlier australopithecines (Jellema et al., 1993). The narrow inferior thorax is directly relatable to the

narrow bi-iliac breadth of the pelvis (see below) and likely reflects reorganization (or reduction) of abdominal viscera (see below; Aiello and Wheeler, 1995). Whether these changes may also have occurred in *H. habilis* is unknown, due to the absence of appropriate fossils.

The shoulder, arm, and hand. The shoulder girdle exhibits a clavicle that is moderately long but unremarkable, and a scapula that may possess derived characters of the species (Walker and Leakey, 1993c). In particular, the axillary border of the scapula is concave laterally, and the scapular spine overhangs the supraspinous fossa. Both characters may be derived for *H. erectus*.

Although the upper limb is shortened relative to body size compared to earlier hominins, the humerus itself is still relatively long compared with

TABLE 7. Comparison of postcranial characters among specimens of certain taxa¹

	<i>Australopithecus</i> sp.	<i>H. habilis</i> OH 62	<i>H. erectus</i> WT 15000	<i>H. erectus</i> Zhoukoudian	<i>H. neanderthalensis</i>	<i>H. sapiens</i>
Innominate						
Strong acetabulo- cristal buttress	0	?	X	?	X	0
Narrow pelves	0	?	X	?	0	0
Torsion of ischial tuberosity	0	?	X	?	X	0
Femora						
Elongated	0	0	X	X	X	X
Large articular surfaces	0	?	X	?	X	X
Long necks	X	X	X	X	0	0
Platymeric (subtrochanteric and midshaft)	0	?0	X	X	X	V/0
Thick cortices	0	?0	X	X	X	0
Tibia						
Double meniscal attach	0	?	X	?	X	V/X
Ulna						
Low coronoid to olecranon	X	X	X	?	X	0

¹ X, present; 0, absent; V, variable; ?, condition unknown.

modern humans. Together with the ulna of KNM-WT 15000, they suggest a relatively long upper limb with elongated distal limb segments in this specimen (Ruff and Walker, 1993). While the KNM-WT 15000 ulna may be relatively long due to the specimen's subadult age, the high brachial index nonetheless may be interpreted to suggest a tropically adapted body form. Although requiring further study, *H. erectus* ulnae appear to be characterized, as are other archaic *Homo* specimens and hominins in general, by low coronoid processes relative to olecranon height (Churchill et al., 1996) and by relatively thick cortices. The Kapthurin (KNM-BK 66) and KNM-WT 15000 ulnae share relatively long lengths, slender shafts, and generally weak muscle markings. Both have strong supinator crests, while the Kapthurin specimen, a full adult, has much better developed brachialis and pronator quadratus muscle attachments. The interosseous crest of KNM-WT 15000 is positioned relatively anteriorly (i.e., in the neutral position), although this is likely idiosyncratic. The brachialis muscle attachment is also somewhat more distally placed on these and KNM-ER 803, in which the muscle markings are more pronounced generally. The small fragments of the radius of KNM-ER 803 provide little insight here. The KNM-ER 1808 ulna is heavily affected by periosteal bone deposition and is not considered (Leakey and Walker, 1985).

The hand elements are in large part unremarkable, although a projection on the medial surface of distal metacarpal one ("intersesamoid beak" sensu Trinkaus and Long, 1990) was suggested to be shared only by KNM-WT 15000 and Swartkrans 84, and therefore to be a unique derived feature of *H. erectus* (Susman, 1988). Walker and Leakey (1993c) disagreed with this attribution, questioning even the hominin status of the KNM-WT 15000 metacar-

pal, whereas Trinkaus and Long (1990) questioned the uniqueness of the "intersesamoid beak" itself.

The pelvic girdle, lower limb, and foot. The earliest possible *H. erectus* innominate, KNM-ER 3228, shares with definitive *H. erectus* innominates a number of similarities in size and shape (Rose, 1984; Rightmire, 1993). These include the great lateral flare of the ilium and the absolutely large size, resulting in a pelvic inlet breadth estimate of 100 for KNM-WT 15000 (at adulthood, 115 mm; Ruff and Walker, 1993). However, biacetabular and bi-iliac breadths, as reconstructed for KNM-WT 15000, are relatively narrow compared with limb length (Ruff and Walker, 1993). The auricular surface is relatively small, the ischial tuberosity is oriented posterolaterally, and the gluteal surface of the ilium (particularly the gluteus medius muscle attachment) is deep (Day, 1971; Rose, 1984). Except for the subadult, these innominates also possess strong buttressing of the ilium, both in the form of an iliac pillar (acetabular-cristal buttressing) and in a horizontal buttress between the acetabulum and ischial spine. While KNM-WT 15000 is not as strongly buttressed as the adults, its reasonably strong definition for its age suggests that had he reached maturity, it may have matched the pattern seen in adults (Ruff and Walker, 1993). Much more recent innominates, such as Arago XLIV from France, show similar morphology, limiting the usefulness of these features as taxonomic indicators (Rose, 1984). All of these fossils suggest increased body size in *H. erectus* (sensu lato) relative to earlier hominins (Rightmire, 1993).

Definitive *H. erectus* femora associated with crania from Koobi Fora share potentially derived characters with contemporaneous isolated femora from East (KNM-ER 736 and 737; Bou VP 1/175, 2/15,

and 19/63) and South Africa, and with later femora from Olduvai Gorge (OH 28) referred to *H. erectus* (Walker and Leakey, 1993c; Gilbert et al., 2000). Because the femur from Geshen Benot Ya'aqov (GBY 1) may be intrusive into this locality, it is not considered here (personal communication from Bar-Yosef, 2003). However, morphometric analysis shows that GBY 1 groups with other early Pleistocene *Homo* on the basis of general robusticity (Trinkaus et al., 1999). Potentially derived characters shared by African *H. erectus* femora and modern humans are their elongation and the large estimates of body size they yield, both of which may be derived in *H. erectus* relative to *H. habilis*. If OH 62 and KNM-ER 3735 are good proxies for *H. habilis*, then the platymeria seen in KNM-WT 15000 and the other *H. erectus* specimens mentioned above may also be derived for *H. erectus*. Although it should be mentioned that breadths are more functionally influenced than lengths and proportions (Ruff, 2003).

Other characteristics shared by African *H. erectus* femora appear to be primitive characters that are derived only for hominins generally (such as their long femoral necks) or for the genus *Homo*. Characters present in *H. erectus* that are probably derived for the genus include relatively large articular surfaces for limb size as compared with those of australopithecines, low femoral neck angles, thick shaft cortices resulting in extreme medullary stenosis, and a relatively distally positioned least width of the shaft (Table 7; Day, 1984; Trinkaus, 1984; Wolpoff, 1999; Pearson, 2000). *H. erectus* femora likewise show a deep trochlear groove and high lateral lip of their patellar groove, as do KNM-ER 1472 and particularly KNM-ER 1481A (Tardieu, 1998, 1999).

Definitive African *H. erectus* tibiae, like those of other members of early *Homo*, exhibit double attachments for the lateral meniscus, as opposed to the single attachments seen in australopithecines (Tardieu, 1998, 1999; but regarding ranges of variation in this character, see Dugan and Holliday, unpublished data). The tibiae are relatively long compared to femoral length, together yielding crural indices indicating a tropical body form (Ruff and Walker, 1993). The fibulae of KNM-WT 15000 exhibit a bowing which is, however, likely to be idiosyncratic, since the adult fibulae (KNM-ER 1808) do not exhibit such curvature.

At present, the foot is represented by several metatarsals and phalanges and the talus of KNM-ER 803 (Table 5). The third metatarsals KNM-ER 803 and Dmanisi 2021 differ in size and most substantially in their lateral facets, that of Dmanisi being ovoid (as is typical for MT3), whereas that of KNM-ER 803 is triangular and more similar in shape to that of the lateral facet of a fourth metatarsal in modern humans. The Dmanisi third metatarsal is quite small and provides the only current postcranial estimate of body size in the Georgian hominins (Table 6). Based on a maximal length of about 60 mm and regression equations derived

from modern human analogs, a stature estimate of 1.48 m (SE = 65.4 mm) places the Dmanisi hominin at the small end of the female range for early African *H. erectus* (Gabunia et al., 2000c).

Continental Asia. The upper limb. The clavicle from Zhoukoudian is relatively long compared to the African clavicles, well-marked, but slender (Weidenreich, 1941). The shaft is flattened supero-inferiorly, and the curvature is similar to that of modern humans. Day (1986) questioned the hominin affinities of this fragment, although recent casts suggest that it is within the anatomical range of hominin clavicles.

The humerus is known from three specimens, one of which (Humerus II) retains most of the shaft, allowing estimates of total length (Table 6; Weidenreich, 1941). Humerus I provides only a fragment of the distal end, and Humerus III a portion of the midshaft. Compared with African *H. erectus* humeri, Humerus II is less broad near the midshaft, but equally long, and exhibits the typically thick cortical walls and reduced medullary cavity seen in African *H. erectus* fossils.

The Asian *H. erectus* hand is known from a single lunate bone that is, in most respects, similar to modern human lunates. However, it appears quite small and relatively broad for its length (Weidenreich, 1941).

The lower limb. The Zhoukoudian assemblage includes the fragmentary remains of seven femora, mostly shaft fragments, with anteroposteriorly flattened subtrochanteric and midshaft regions, a strong crista medialis and lateralis, and thick cortical bone, particularly at midshaft (Weidenreich, 1941). The more complete shafts are of moderate length (Table 6). Because a significantly narrower shaft fragment (Femur II) is also present, Weidenreich (1941) interpreted the larger Femora I and IV as male. By doing so, he predicted a relatively small stature for the population, since these "male" femora are not particularly long, and female size would be proportionately smaller.

The Zhoukoudian tibia is a partial distal shaft (Tibia I, PA65) discovered in 1951 (Wu and Poirier, 1995). Tibia I is of similar robusticity as the Ngandong B tibia and the Kenyan tibiae (Table 6).

Indonesia. The pelvic girdle and lower limb. An innominate fragment (Ngandong 17) was recovered during the 1970s excavations at Ngandong, but is undescribed (Widiasmoro, 1976; Jacob, 1984).

The femora from Java are enigmatic. The femora from Sangiran are as yet incompletely published (Sangiran 29 and 30; Kresna 10 and 11; Grimaud-Hervé et al., 1994; Widiyanto, 2001), although one is reported to be "not as flattened as the Zhoukoudian femora" (Grimaud-Hervé et al., 1994; Wolpoff, 1999, p. 465). The femora from Trinil (Trinil I–IV; VI is nonhominin) are of questionable taxonomic associa-

tion (Day and Molleson, 1973). The Trinil femora do not exhibit the primitive characteristics, such as platmeria, the strong crista medialis and lateralis, and thick cortical walls, seen in either the African or Chinese *H. erectus* femora (Wolpoff, 1999, p. 465). Despite the original assertions by Dubois (1926a, b, 1932, 1934, 1935, 1937), anatomical analyses in fact suggest no appreciable differences between the Trinil femora and modern human femora (Weidenreich, 1941). In addition, the association between the Trinil femora and calotte, which is the holotype of *H. erectus*, cannot be established (Day and Molleson, 1973, p. 152). While fluorine analyses appear to restrict the femora to the region of Trinil, they cannot specifically identify the calotte and femora to the same bed. It is thus not prudent to draw conclusions regarding the postcranial morphology of *H. erectus* from the Trinil femora.

In contrast, the context of the late Pleistocene Ngandong tibiae and their association with the *H. erectus* calvaria from the site are clear (Openoorth, 1932, 1937; Santa Luca, 1980). The two tibiae differ greatly in overall robusticity, suggesting to some that Tibia A (Ngandong 9 or 13)¹ may be that of a male (Weidenreich, 1951). Natural breaks on Tibia A show thick cortical surfaces, particularly of the anterior crest, as is seen in other *H. erectus* postcrania. Likewise, the cross-sectional geometry of both tibiae, when scaled against either element length or estimates of body weight, exhibit the elevated robusticity seen in other early and archaic *Homo* (Trinkaus et al., 1999). The smaller Tibia B (Ngandong 10 or 14) is complete enough to estimate a total length of about 380 mm, suggesting a relatively tall stature for the smaller of the two (Table 6). Neither tibia differs markedly from those described for *H. erectus* elsewhere. However, neither specimen retains enough of the proximal end to assess whether they possess single or double meniscal attachments. Alternatively, the Sambungmacan tibia (SM2), which is argued to be of Middle Pleistocene age, is also more gracile and arguably more similar to modern humans than are the Ngandong tibiae (e.g., Baba and Aziz, 1992). This specimen is also a significantly smaller, more rolled fragment, and is of uncertain provenience.

Implications of postcranial anatomy

The differences in body size and postcranial anatomy between early *H. erectus* and members of *Australopithecus*, and possibly earlier species of the genus *Homo*, are likely indicative of two interrelated phenomena: increased diet quality and increased locomotor efficiency (see below; Leonard and Robert-

son, 1994; Aiello and Wells, 2002; Antón et al., 2002). Alternatively, the generalized robusticity and retention of primitive characters from early *Homo* through archaic *H. sapiens* has been argued to be a reflection of the overall similarity (and stasis) of the pattern of locomotor activity from early genus *Homo* until the advent of anatomically modern humans (e.g., Rose, 1984; Trinkaus, 1984). Whether this pattern of locomotor activity originates with *H. erectus* or earlier *Homo* depends on which species the early, large postcranial elements represent. Arguably, however, the earliest *Homo* femora and those of *H. erectus* differ from later archaic *H. sapiens* on the basis of their more consistent AP flattening along the entire length of the shaft (Weidenreich, 1941; Day, 1971; Kennedy, 1983a, 1983b). There is also a well-documented trend in *Homo* through the Pleistocene of declining shaft robusticity, but not articular size, when aspects of body proportions are held constant (e.g., Trinkaus et al., 1999). This decline is usually considered indicative of decreasing mechanical stresses, particularly axial loading, on the lower limb (e.g., Ruff et al., 1993; Ruff, 1995; Pearson, 2000).

IMPLICATIONS FOR TAXONOMY

Species, subspecies, demes, and allotaxa

The anatomical patterns and variations reviewed above have implications for taxonomic questions. How scientists parse variation into taxa is, however, an undertaking fraught with paradigmatic issues that in part dictate the outcome (see Tattersall, 2000; Foley, 2001). The famous splitter vs. lumping dichotomy is rife in *H. erectus*, and alternative species hypodigms abound (e.g., Stringer, 1984; Wood, 1991a; Rightmire, 1993; Schwartz and Tattersall, 2000; Asfaw et al., 2002). In addition, the conflict between trying to fit a static classificatory system onto a dynamic past is, of course, irresolvable at some basic level.

Homo erectus as *Homo sapiens*

In one view, *H. erectus* and *H. sapiens* represent a single evolving lineage that originated via a cladogenetic event some 2 million years ago (e.g., Jelinek, 1981; Wolpoff et al., 1994; Tobias, 1995; Wolpoff, 1999). This view argues that *H. erectus* can be defined relative to *H. sapiens* only on the basis of plesiomorphic characters, and as such, that all fossil *Homo* from about 1.8 Ma to present should be considered *Homo sapiens*. On cladistic grounds, Hublin (1986) would concur, although he would likewise appear to accept the morphological division of *H. erectus* and *H. sapiens*, and thus his work is more relevant below. Furthermore, "transitional" populations of Middle Pleistocene *Homo* throughout the Old World support the idea of Pleistocene *Homo* as a single evolving lineage, as would evidence of gradual rather than punctuated increases in brain size (Lee and Wolpoff, 2003). Although this view does not

¹Ngandong Tibia A and B were originally cataloged as Ngandong 9 and 10 (Indriati, 2003). However, more recent catalogs assigned numbers Ngandong 13 and 14 to these tibia (Oakley et al., 1975), or Ngandong 12 and 13 (Wolpoff, 1999), or used both designations 9/10 and 13/14 (Schwartz and Tattersall, 2002).

recognize any (cladogenic) speciation events within the lineage, it does recognize a number of morphological grades that in many (but not all) ways correspond to distinctions that others make between *H. erectus*, its subspecies, and *H. sapiens*. That is, this view recognizes regional morphs that others might choose to split into species (for descriptions, see Wolpoff, 1999). However, these distinctions are not viewed as being the result of autapomorphic characters in *H. erectus*, and thus are not considered indicative of a separate species designation.

This view emanates from adherence to a strict biological species concept (BSC) that recognizes no interbreeding across species boundaries, no hybridization, and no marginal gene flow. Thus an evolving lineage, which presumably had no sequential breaks in the ability of its members to interbreed, by definition is a single species.

Homo erectus sensu lato

An alternative view recognizes *H. erectus* (sensu lato) as a widely dispersed, polytypic species distinct from *H. sapiens* that is defined by a shared cranial bauplan, but also exhibits geographically and temporally related variation (e.g., Howell, 1978; Howells, 1980; Rightmire, 1993). This argument has its roots in early comparative anatomical studies by Weidenreich (1943, p. 232) of Asian fossils that recognized the essential uniformity of morphology among the Chinese (*Sinanthropus*) and early Indonesian (*Pithecanthropus*) fossils, despite also recognizing the regional differences between them. In this view, characters that often differentiate Asian and African fossils are considered either to be primitive, structurally dissimilar, or variable within regions, and thus not taxonomically valent (Rightmire, 1979, 1998b; Hublin, 1986; Turner and Chamberlain, 1989; Bräuer, 1990, 1994; Kennedy, 1991). Although some simply argue that significant differences in morphology between regions do not exist (e.g., Asfaw et al., 2002), there are, however, clear differences in size and shape in *H. erectus* fossils that allow both metric and nonmetric phenetic sorting of specimens by geographic region (e.g., Antón, 2002a; Baba et al., 2003). This view argues that such variation is to be expected, given both the wide geographic and temporal spread of *H. erectus* fossils, but does not justify a specific status for these regional morphs. This view relies on a so-called phylogenetic species concept (PSC) that recognizes species on the basis of discrete, morphologically boundable units (or clades), with the underlying assumption that this tells us ultimately about interfertility.

Within this single species, some scientists recognized subspecies rather than African and Asian species (e.g., Campbell, 1965; Larnach and MacIntosh, 1974; Howells, 1980; Howell, 1994; Wood and Richmond, 2000). The named subspecies commonly include *H. erectus erectus* for the early Indonesian specimens, *H. e. pekinensis* for the Chinese material, and *H. e. soloensis* for the Ngandong/Sambung-

machan fossils, as well as *H. e. ergaster* for the African remains. I recently showed that while Indonesian and Chinese morphs can be distinguished both morphologically and metrically, perhaps supporting the *H. e. pekinensis* grouping, no similar subdivisions can be made within the Indonesian morph without also introducing time, although there is some evidence of size-related morphological differences (Antón, 2002a; but see Baba et al., 2003). *H. e. ergaster* is arguably both morphologically and temporally boundable, suggesting that this too may be a useful designation.

Paleodemes were proposed as useful for understanding and examining paleodiversity (Howell, 1999), and were suggested as particularly useful as operational taxonomic units (OTUs) for cladistic analysis (e.g., Asfaw et al., 2002). Demes should reflect local breeding populations of a species, i.e., the smallest reproductive population of the species (Simpson, 1961). Smaller and not as formal as subspecies, such demes typically include both a local geographic and temporal dimension, but may or may not include morphological bounds (beyond the generic level, at any rate). Demes may be particularly useful as a means of initial assessment of variation as bound in space and time, yet are dependent on further investigation of their morphological integrity to assess their applicability to other problems (Howell, 1999). Depending on their construction and use, demes can obscure as much as they illuminate, as for example was the case in the analysis of the Daka calvaria (Asfaw et al., 2002). In this case, the authors modified demes erected by Howell (1999) on chronostratigraphic, geographic, and morphological bases. Their Nariokotome deme included the ca. 1.5-Ma Koobi Fora fossils (KNM-ER 3733 and 3883) and KNM-WT 15000, but excluded the 1.47-Ma OH 9. Alternatively, their Olduvai LLH/Daka deme included the 1.47-Ma OH 9 and the ca. 1.0-Ma Daka and Buia, but excluded the significantly smaller-brained 0.78–1.2 Ma OH 12, arguably no younger than Daka and Buia than OH 9 is older (Asfaw et al., 2002). The results of their cladistic (PAUP) analyses of these OTUs divided the sample into large-brained and small-brained demes that were then interpreted to suggest a single, polytypic species of *H. erectus*, denying any significant regional grouping. Had they either included the small brain of OH 12 or removed the large brain of OH 9 (into the more closely coeval Nariokotome/Koobi Fora deme), they would have changed the average scoring of the Daka/Buia OTU from the large-brained to the small-brained, and thus affected its placement in the cladogram as well as the overall interpretation. This particular example, then, is not a robust argument for *H. erectus* as a single, polytypic species, although other such arguments exist (see Santa Luca, 1980; Rightmire, 1993).

Homo erectus* and *Homo ergaster

Whether the Asian and African morphologies should both be encompassed into *H. erectus* (sensu lato) remains debated. When little was known of the African fossil record, sinking the multiple Asian and African taxa into a single species, *H. erectus*, was logical and helpful (e.g., Mayr, 1950, 1963; LeGros Clark, 1964; Howell, 1978). As the African fossil record has become more plentiful, a greater diversity of morphological patterns has emerged that recognizes in many ways that Asian *H. erectus* is the more derived of the geographic samples. The recent addition of a number of very small individuals from Africa and Asia is relevant here, as they appear to complicate interpretations of the relations between the earliest *Homo* and *H. ergaster*, and present characters of possible Asian morphology, such as cranial keels. However, the subadult age of some of these specimens from Ileret and Dmanisi, for the moment, obscures just how relevant these may be (Leakey et al., 2003; Vekua et al., 2002).

In its simplest form, the multiple species position distinguishes early African *H. erectus* (i.e., fossils mostly from Koobi Fora and West Turkana) as *H. ergaster*, but leaves other African *H. erectus* (e.g., OH 9) and the Asian fossils within *H. erectus* (sensu stricto). Still others might erect more than two species (Schwartz and Tattersall, 2000), for example, retaining only Trinil and Sangiran fossils (i.e., the earliest and early Indonesian fossils) in *H. erectus* and erecting several new species for the later Indonesian fossils, the Chinese "*H. erectus*", Olduvai, Koobi Fora, and probably also West Turkana. This view is reached on the basis of more stringent parsing of individual variation, relying in essence on "Tattersall's rule," which is drawn in large part from the degree of morphological variation associated with good, extant, especially primate, species (Tattersall, 1993). "Tattersall's rule" suggests that given the small amount of skeletal variation in extant primate species, skeletal data alone will underestimate species diversity, and thus any skeletal difference among fossils is likely to be evidence of specific level distinction. In its most extreme, "Tattersall's rule" can result in the erection of multiple species among seemingly homogenous assemblages such as the Dmanisi crania (e.g., Schwartz, 2000). It is worth noting that "Tattersall's rule" was based initially on observations on strepsirrhines, and that levels of speciosity and skeletal variation might be expected to differ in animals of different body size and habit (e.g., Conroy, 2002, 2003). Furthermore, sister taxa to the hominins, such as the great apes, might be expected to yield a better estimate of fossil hominin species diversity. However, "Tattersall's rule" is supported at some level by new metric work on variation in extant great apes that are used as proxies for evaluating ranges of variation in fossil hominins (Ackermann, 2002), although this work

also found that general levels of variation were similar across great apes and humans.

Most scientists who separate African and Asian *H. erectus* into two species consider the significance of the morphological characters that distinguish these morphs to be of greater importance and the distinctions to be more complete than do those that recognize only one species (e.g., Stringer, 1984). Most argue that cranial superstructures, such as metopic and sagittal keels and angular tori, are autapomorphies that differentiate Asian *H. erectus* from early African forms (Delson et al., 1977; Andrews, 1984; Stringer, 1984; Wood and Collard, 1999). In addition, other differences that separate *H. ergaster* and *H. erectus* are those related to degree of expression of traits, including more robust supraorbital tori, thicker cranial vaults, and low, highly angulated crania in the latter (e.g., Gabunia et al., 2000a). New fossils with additional facial remains suggest that facial and dental characters may also differentiate the two groups at a specific level. Both the significance and existence of these characters has been periodically questioned, as for example by Bräuer and Mbua (1992), who suggested that many features are primitive. And new discoveries from Dmanisi (D2700 in particular; Vekua et al., 2002) and Koobi Fora (KNM-ER 42700; Leakey et al., 2003) may be obscuring these differences.

Allotaxa and *Homo erectus* (sensu lato)

It should be clear from the foregoing discussion that these arguments have failed to reach a consensus in no small part because of definitional constraints. It should also be clear that the alternative, strict species definitions (BSC and PSC) reflect only very little of the complexity known to exist in the extant world, and that as such, the argument is largely semantic rather than substantive (see Jolly, 2001). The substantive arguments, in fact, revolve around issues of trait heritability and plasticity, genetic vs. epigenetic underpinnings, and variability and trait correlation relative to age, sex, and size. While these are important issues to resolve, the species question may be both less important and less biologically relevant, especially given what we know of extant animal behavior.

I find the most useful approach to the taxonomy of *H. erectus* to be that proposed recently by Jolly (2001), who recognized both the complexity of species boundaries in living organisms and that the fossil record is magnitudes too incomplete to test alternative interpretations (if indeed it ever could). Jolly (2001) suggested avoiding arguments over definitionally induced differences in favor of recognizing geographically replacing allotaxa. Such a move recognizes the likelihood that morphological difference may arise among allotaxa, but allows for hybridization between them. This aptly reflects the situation in *H. erectus* sensu lato, in which evident regional variation exists in cranial morphology and yet in which a total morphological pattern is shared across

regions (see above). The species question becomes irrelevant to biologically more interesting questions of energetics, local adaptation, life history, dispersal, development, and group interaction at boundaries.

IMPLICATIONS FOR BIOLOGY

Energetics, nutrition, and dispersal

While there is a long history of trying to infer the diet of fossil hominins, modeling the energetic requirements of ancient hominins recently provided a link between the data sets of human biology and paleoanthropology (e.g., Leonard and Robertson, 2000). The energetics perspective has been particularly useful in circumscribing the bounds within which hominins must operate, eliminating biologically impossible scenarios (Sorensen and Leonard, 2001). These models are rooted in the physical evidence of the fossil record, including measures of brain size, body size, and proportions.

Brain size increase: costs, benefits, and consequences

The extent to which cranial capacity increased over time in *H. erectus* and whether this increase was gradual or abrupt is debated (e.g., Rightmire, 1981, 1985, 1986, 1993; Wolpoff, 1984; Leigh, 1992; Lee and Wolpoff, 2003). Some authors found little increase (i.e., stasis) in brain size through time in *H. erectus* (e.g., Rightmire, 1985, 1986; Eldridge, 1985), whereas others found a trend toward gradually increasing brain size (Leigh, 1992; Antón and Swisher, 2001; Lee and Wolpoff, 2003). Using time series analyses and adjusting the data of Leigh (1992) for the significantly modified geochronological time-scale of *H. erectus* (see previous and Swisher et al., 1994, 1996; Larick et al., 2001) supports a significant but gradual trend for increasing brain size through time in Asian *H. erectus*, at the rate of about 160 cc per million years (Antón and Swisher, 2001). Importantly, these results are not significantly weighted by either the oldest (Mojokerto) or youngest (Ngandong) data points. Given the relatively small number of African *H. erectus* crania, it is not possible to robustly establish rates of increase for Africa or to compare between African and Asian rates. However, introduction of the African specimens would be unlikely to affect this analysis, since the cranial capacities and ages of these specimens are similar to Asian specimens already included.

As has been widely noted, the brain is an extremely costly organ from a nutritional perspective, consuming about 16 times as much energy as does muscle by weight (Foley and Lee, 1991; Leonard and Robertson, 1992; Aiello and Wheeler, 1995; Martin, 1983, 1996). Thus sustaining trends in brain size increase requires additional energetic resources and a clear selective advantage for the organism involved. From estimates of *H. erectus* body size of about 130 pounds, Leonard and Robertson (1992)

reconstructed the proportion of resting energy required to support the brain of *H. erectus* to be about 17% of total resting energy, or some 260 kcal of a 1,500-kcal energy budget. Alternatively, an 80–85-pound australopithecine with a brain size of 450 cc would have devoted about 11% of its resting energy to the brain. Thus some strong advantage of larger brain size, presumably related to resource and mate acquisition, must have counterbalanced its costs.

These differences suggest that *H. erectus* must have had a more energy-rich diet than earlier hominins. There are several suggestions for what might constitute this energy-rich diet, from animal meat and marrow (Walker et al., 1982; Shipman and Walker, 1989; Leonard and Robertson, 2000; Antón et al., 2002) to honey (Skinner, 1991) and underground tubers (e.g., Wrangham et al., 1999). While all may have contributed as important resources, the limited evidence for fire until well after the origin of *H. erectus* (Bellomo, 1994; Brain and Sillen, 1988) reduces the viability of the “tuber as resource” argument, since these require fire to release their nutritional bounty. Similarly, honey was found to contain less vitamin A than previous models had assumed (Skinner et al., 1995). The abundant archaeological evidence for meat consumption at hominin sites (e.g., Shipman, 1986; Blumenshine et al., 1994) and the associated stone tool record (e.g., Leakey, 1971), as well as the sporadic consumption of meat by extant primate groups (Stanford, 2001) and earlier hominins (de Heinzelin et al., 1999), suggest that increasing reliance on animal resources was an important, although perhaps not an exclusive, part of this dietary shift (Shipman and Walker, 1989; Antón et al., 2001, 2002). Tapeworm phylogeny offers additional evidence that *H. erectus* consumed other animals. The molecular phylogenies of the two most closely related human-specific tapeworms (*Taenia saginata* and *T. asiatica*) suggest the species diverged sometime between 0.78 ka and 1.7 Ma (Hoberg et al., 2001). Since the species are host specific, such a divergence date is consistent with a human host (*H. erectus*) being infected, presumably by consuming the flesh of an infected animal, during this time period. Since the third human-specific tapeworm (*T. solium*) is closely related to those that are specific to other African carnivores, early humans are inferred to have sampled similar animals (and parasites) as these carnivores.

What is more, the costs of growing big brains differentially increase maternal costs in both energetic terms during pregnancy and lactation, and in terms of decreased locomotor efficiency related to broad pelvises for accommodating large-brained infants (Aiello and Key, 2002; Aiello and Wells, 2002). These costs, particularly those related to pregnancy and lactation, are suggested to require the acquisition of a high-quality diet (Martin, 1996), as well as one rich in essential fatty and amino acids (Milton, 1999). Aiello and Wheeler (1995; see also Aiello et al., 2001) argued that a decrease in the size of an-

other nutritionally expensive tissue, such as the gut, was necessary to balance the increased energetic costs of the expanding brain in both males and females. They further argued that the narrow bi-iliac breadth of the KNM-WT 15000 pelvis reflects such a decrease in gut size in early *H. erectus*, in support of their “expensive tissue hypothesis.” It is unlikely that any one of these issues is operating in isolation, but rather that a complex web of costs and benefits worked together to allow the expansion of the brain as well as the body at the origin of *H. erectus*.

Body size and proportions

The larger size of postcranial fossils of *H. erectus* relative to those of earlier hominins indicates that increased body size characterizes the species from its inception (Table 6). However, a variety of methods have been used for deriving precise estimates of body size and proportions in extinct hominins (e.g., McHenry, 1992, 1994; Ruff and Walker, 1993; Aiello and Wood, 1994; Kappelman, 1996; McHenry and Coffing, 2000). Each relies on some level of estimation or inference, and most rely on regression equations derived from living populations to estimate the stature of a hominin *not of that population*. We are all aware of the dangers inherent in such estimations, given both the assumption of the statistical inference and, in particular, the possibilities of different body proportions across taxa. However, with these caveats duly noted, estimates of body mass of *H. erectus* were attempted, using various postcranial (McHenry, 1992, 1994) and cranial (Aiello and Wood, 1994; Gauld, 1996) dimensions. Leaving aside estimates developed from the cranium, which tend not to work as effectively as those derived from the postcrania, particularly for larger-brained hominins (Delson et al., 2000; Stubblefield, 2002), stature is estimated to range between 148–185 cm for known *H. erectus* specimens with related body mass estimates of between 46–68 kg, if all geographic areas are included (Table 6). The adult projections for KNM-WT 15000 represent the large end of this range. In contrast, very approximate body-mass estimates for *H. habilis* (*sensu lato*), based on associated postcranial and cranial remains, suggest a weight of less than 30 kg for a presumed female (OH 62; Johanson et al., 1987) and about 46 kg for a presumed male (KNM-ER 3735; Leakey et al., 1989), overlapping the australopithecine size range. Cranial estimates range from 27–45 kg (Aiello and Wood, 1994; Kappelman, 1996). The larger end of this range (149 cm/47 kg) may be further substantiated if certain Koobi Fora postcrania (e.g., KNM-ER 1472 and 1481) are also included in *H. habilis*.

As is well-known, body size and shape (linearity) are significantly influenced by climate (Katzmarzyk and Leonard, 1998; Stinson, 2000; Ruff, 2002), and there is evidence of this in the postcrania of *H. erectus*. Unfortunately, pelvic breadth, a stronger indicator of latitudinal variation (Ruff, 2002), is not

available for most *H. erectus*. However, stature estimates do vary by region (Table 6). African *H. erectus* yield stature estimates between 160–180 cm (Nariokotome excluded), whereas Asian remains yield estimates between 150–160 cm. In addition, the more tropical Indonesian fossils are somewhat taller (~160 cm) than the more northerly located Zhoukoudian and Dmanisi samples (~150 cm), although sample sizes are extremely small. The KNM-WT 15000 subadult provides additional insight into both stature and thorax breadth, and suggests a quite linear, tropically adapted form (Ruff and Walker, 1993).

Ohman et al. (in press) suggested that stature estimates based on femoral length overestimate the height of KNM-WT 15000 because of the relatively small size of the vertebral column height compared to femoral length. They suggested that considering axial size yields an estimate closer to 147 cm *at death* vs. the 159 cm estimated from femoral length. Such a prediction would remove the projections of adult size for Nariokotome from the extreme end of the range of *H. erectus* variation, but does not radically shift the adult range, since KNM-ER 736 yields an estimate only 5 cm shorter than the adult estimate for Nariokotome. If the proportions between the axial and appendicular skeleton of Nariokotome are typical for *H. erectus*, all stature estimates might be similarly reduced. Arguments that KNM-WT 15000 may present pathological skeletal changes, particularly of the vertebral column (Latimer and Ohman, 2001), suggest that his body proportions are not likely to be universal to *H. erectus*. However, if he is typical of other *H. erectus*, it is likely these proportions would also be shared by earlier hominins as well, unless differential elongation of the femur, only secondarily followed by proportional thorax elongation, is the pattern followed during body-size increase in *Homo*. Thus, even if KNM-WT 15000's proportions are typical for other *H. erectus*, this may have no, or little, influence on the argument of relative size *between taxa*.

Although there is some uncertainty in these estimates, due both to methods and to sample composition, these data suggest that body-size increase is an important shift between *H. erectus* (*sensu lato*) and *H. habilis* (*sensu lato*). Whether this shift is strongly punctuated remains to be resolved, as does the related question of whether the range of variation in body sizes is greater in earlier than in later *H. erectus* populations. Nonetheless, the larger average body size of *H. erectus* is well-established, and has multiple implications for life history and ranging (see below). Body-size increase itself is generally considered a response to shifting climate patterns from moister to drier (more xeric) conditions and more patchily distributed resources in East Africa around and slightly before the origin of *H. erectus* (e.g., Antón et al., 2002; Aiello and Key, 2002).

Sex dimorphism, diet, and social implications

Based on these estimates of body size and correlative estimates of sex-based robusticity, we can estimate the degree of sexual dimorphism in *H. erectus* (McHenry, 1992; Leonard and Robertson, 1997; McHenry and Coffing, 2000; Ruff, 2002). It should be noted that changing samples or the sex estimates of particular fossils can significantly influence results (see Ruff, 2002). *H. erectus* females appear to increase more in size relative to earlier *Australopithecus* (and possibly *Homo*) females than do males. Thus sexual dimorphism is decreased in *H. erectus*, and energetic demands for *H. erectus* females are differentially increased (e.g., Aiello and Key, 2002). These estimates are made for East African *H. erectus*, and it should be noted that the Swartkrans remains were recently argued to display more postcranial dimorphism than is the case in East Africa (Susman et al., 2001). Although taxonomic arguments continue regarding the South African remains, if they prove to be *H. erectus*, differences in sexual dimorphism between regions would require explanation, and may provide insight into the several possible reasons for decreasing dimorphism in East Africa. In addition, recent discoveries from Dmanisi, Georgia and Ileret, Kenya represent individuals of very small size but clear *H. erectus* affinities, possibly suggesting that size variation (and sexual dimorphism?) in early *H. erectus* is greater than previously appreciated.

Decreasing levels of dimorphism due to differentially increasing female body size are likely to be related to the previously discussed demands placed on female energetics by the requirements of gestating and lactating a large-brained offspring. Larger mothers can deliver absolutely more energy to their offspring at relatively smaller cost to themselves (Charnov and Berrigan, 1993). Differential female size increase may additionally be related to the differential energetic benefits accrued to females during walking when the lower limb is lengthened (Leonard and Robertson, 1996). This benefit is in part related to the fact that limb lengthening relatively reduces the mechanical cost of a broad pelvis by reducing the degree of femoral angulation necessary to bring the knee under the center of gravity. Both advantages are of course somewhat counterbalanced by the increased energy requirements of large body size itself, and thus both indirectly support the previously discussed idea that *H. erectus* required a dietary shift to high-quality food items to maintain both large body and brain size. However, it should be noted that a balanced energy budget, not necessarily an energy efficient budget, is what is required for survival.

Some workers further argued that body size and energetic shifts at the origin of *H. erectus* suggest that social shifts, as well as dietary shifts, would have been necessary for *H. erectus* females to meet their energy and childbirth requirements (Rosen-

berg and Trevathan, 1996; O'Connell et al., 1999; Aiello and Key, 2002. But see Ruff, 1995 re: brain size limits and pelvic shape.). These range from suggesting that, unlike other primates, assistance in childbirth is necessitated in *Homo* by an enlarged brain size and pelvic constraints of bipedality (Rosenberg and Trevathan, 1996), to scenarios entailing longer-term assistance throughout child-rearing. These latter scenarios envision cultural changes that provide for the survival of greater numbers of infants per *H. erectus* female by the enlistment of a set of helpers. These scenarios include the "grandmothering" hypothesis, which implicates a relatively long postmenopausal role of female caregiving in *H. erectus* society (O'Connell et al., 1999) and the shortening of interbirth intervals, and the assistance of both male and female helpers, including provisioning and cooperative care (Aiello and Key, 2002). Neither is easily testable in the fossil record. Arguably, the grandmothering hypothesis could be supported, albeit not exclusively, by finding aged (i.e., postmenopausal) fossils of *H. erectus*. However, the difficulties of providing accurate age estimates for adult skeletal remains in humans (e.g., Meindl and Lovejoy, 1985; Buikstra and Ubelaker, 1994), and the possibility of differences in patterns of aging between these taxa, leave this a remote possibility at present.

Home range and dispersal

Recent work suggests that the geographic dispersal of *Homo* from Africa is intimately tied to the shifts discussed above. Dispersal from Africa began coeval with the appearance of the larger-bodied/brained *H. erectus* (sensu lato, ~1.7–1.8 Ma; Swisher et al., 1994; Gabunia and Vekua, 1995; W. Huang et al., 1995; but see Schwartz and Tattersall, 1996; Gabunia et al., 2000a, 2001; Larick et al., 2001; Vekua et al., 2002). Estimates of the rate of this dispersal, using diffusion coefficients (D) based on site locations and ages and predictions of changes in home-range size based on body-size estimates from the fossil record, suggest rapid dispersal rates for early *Homo* and highlight ecological parameters that likely promoted the dispersal (Tables 8 and 9; see Antón et al., 2001, 2002; Leonard and Robertson, 2000).

Potential correlates of this rapid spread in *H. erectus*, based on our knowledge of widely dispersed extant mammals and models of ancient dispersals, include larger home range sizes (Ehrlich, 1989), a shift in foraging behavior (Ehrlich, 1989; Shipman and Walker, 1989; Leonard and Robertson, 2000), and a somewhat slower pattern of dispersal than was the case for fossil carnivores (Antón et al., 2001, 2002). Several other lines of evidence, including the spatial patterning of sites (Jablonski et al., 2000), community analyses (Turner, 1992), and taphonomy (Blumenschine et al., 1994), also suggest that hominins and carnivores shared similar niches by at least Middle and later Pleistocene times. These correlates

TABLE 8. Estimated body weight and home range size for fossil hominid species

Species	Male Wt ¹ (kg)	Female Wt ¹ (kg)	Average Wt ¹ (kg)	HR _i -Ape ² (ha)	HR _i -Human ³ (ha)
<i>A. afarensis</i>	44.6	29.1	37.0	40	247
<i>A. africanus</i>	40.8	30.2	35.5	38	234
<i>A. robustus</i>	40.2	31.9	36.1	39	239
<i>A. boisei</i>	48.6	34.0	44.3	51	316
<i>H. habilis</i>	51.6	31.5	41.6	47	290
<i>H. erectus</i>	63.0	52.3	57.7	73	452
<i>H. sapiens</i>	65.0	54.0	59.5	76	471

¹ After McHenry (1992, 1994). Wt, weight.

² Home range estimates, assuming a diet quality equal to average for modern apes. HR_i, home range.

³ Home range estimates, assuming a diet quality at low end of range of modern tropical human foragers. HR_i, home range.

TABLE 9. D values for extant mammals and calculated D values for fossil taxa

Species	Intrinsic rate of natural increase (r)	Time to occupy (t)	Area occupied (z) ¹	Diffusion coefficient (D) ²
Recent dispersals³				
<i>Enhydra lutris</i>	0.06	Various	Various	13.5–54.7
<i>Ondatra zibethicus</i>	0.2–1.4	Various	Various	9.2–231
<i>Sciurus carolinensis</i>	0.82	Various	Various	0.4–18.5 ⁴
Ancient dispersals				
<i>Macaca sp.</i> (Europe to Asia)	0.05	1.5 Ma–10 ka	a) NA b) 2,220 c) 3,135 d) 4,525	0.00001–0.2 0.00002–0.5 0.000045–1.0
<i>Theropithecus darti</i> (to South Africa)	0.05	0.7 Ma–1 ka	a) NA b) 1,555 c) 2,200 d) 3,175	0.00002–0.1 0.00004–0.2 0.0001–0.5
<i>Homo erectus sensu lato</i> (to Indonesia)	0.01–0.015	200–10 ka	a) NA b) 3,100 c) 4,380 d) 6,324	0.006–2.4 0.01–4.8 0.02–9.9
<i>Homo erectus sensu lato</i> (to Georgia)	0.01–0.015	100–10 ka	a) NA b) 1,885 c) 2,665 d) NA	0.01–0.9 0.02–1.8

¹ Z values are calculated as square root of linear distance between localities; a) squared, b) multiplied by a transect 600 km wide, c) by a transect 1,200 km wide, or d) by a transect 2,500 km wide. NA, not applicable, areas not calculated because transect size would include unreasonably large areas (e.g., dispersal into oceans or Arctic). Most conservative comparisons consider largest area for dispersal of nonhuman primates against smallest area of dispersal for hominids.

² Diffusion coefficients calculated as $D^{1/2} = z \div (t)(2r^{1/2})$, where z = square root of area invaded, t = time over which invasion occurred in years, and r = intrinsic rate of increase of species. See Antón et al. (2002) for further methodological details. Differences between modern and ancient dispersal rates relate to 1) greater speed of dispersal in nonprimate, r-selected mammals such as squirrels, and 2) time averaging inherent in paleosamples.

³ Data from Williamson (1996).

⁴ Predicted values and observed historical spread are significantly lower than other dispersing mammals, presumably because of ecological interaction between red and grey squirrels.

of rapid dispersal are similar to the shifts inferred above from increasing energetic requirements of increasing body and brain size, although they are based on independent data sets (Antón et al., 2001, 2002). Interestingly, dispersal in extant animals, and by inference *H. erectus*, may or may not correlate with increasing population pressures (e.g., Grant, 1978; Stenseth and Lidicker, 1992).

It is relevant to note here that several authors suggested that an earlier hominin than *H. erectus*, or a more primitive version of *H. erectus*, may have been the first to disperse from Africa (e.g., Robinson, 1953c; Sartono, 1981; Orban-Segebarth and Procureur, 1983; Tyler et al., 1995). The principal new evidence for this assertion is likely to be the

subadult cranium from Dmanisi (D2700) that has been argued to be very primitive in its anatomy and similar in its face to the Koobi Fora *H. habilis*, KNM-ER 1813 (Vekua et al., 2002). Although Vekua et al. (2002) are clear in their attribution of the Dmanisi specimen to *H. erectus* (sensu lato) and not to a more primitive hominin, others have begun to make a case for a pre-erectus disperser. It should be noted, however, that while it is the case that this specimen has a very small cranial capacity (~600 cc), it also has a fairly wide cranial base but a narrow face. The sphen-occipital synchondrosis of D2700 is completely open and distantly spread, suggesting significant growth left to achieve. If a pattern of human growth can be at all accepted for *H.*

erectus, then substantial growth in the width of the lateral portions of the face, and in facial height, as well as in secondary sexual features including the supraorbital tori, is to be expected in this individual, making it a poor individual from which to argue for the facial evidence of the presence of early *Homo* outside Africa.

It would seem that increasing body size, decreasing sexual dimorphism, and increasing home-range size are responses to changing ecological conditions at the origin of *H. erectus*, and part of a web of factors that fueled the rapid expansion of *H. erectus* from Africa into Asia (Antón et al., 2002). The shift from mesic to xeric conditions provided more grasslands and wooded grasslands, with greater numbers of niches for terrestrial herbivores (~2.5–1.8 Ma; Behrensmeyer et al., 1997), which ought to have increased secondary productivity. Slightly larger-bodied and larger-brained hominins exploited this new resource, and by so doing differentially increased their own reproductive success (Shipman and Walker, 1989; Leonard and Robertson, 1997). Following dispersing herbivores provided both a food resource and a dispersing impetus. Shifts in foraging strategy, body size, and ecosystem structure (patchier resources) led to increases in home-range size, further enhancing dispersal capability over that of earlier hominins.

Growth and development

Understanding the evolution of development is critical, because new adult morphologies emerge as the developmental pattern is modified. Ultimately, we may hope to address both how and why growth patterns changed, and thus illuminate the evolutionary problems to which they reflect solutions. The simple identification and assessment of subadult *H. erectus* remains have received a fair bit of attention and controversy (Black, 1931; Weidenreich, 1943; Riscutia, 1975; Mann, 1981; Storm, 1994; Antón, 1997, 1999, 2002b; Antón and Franzen, 1997). Beyond this, two issues regarding growth patterns have been addressed in *H. erectus*. The first relates to whether developmental rates were relatively fast or slow, as compared to modern humans, and thus whether shifts in developmental pattern can account for differences in cranial size and shape (Antón and Leigh, 1998, 2003). The second addresses issues of growth stages and whether *H. erectus*, like modern humans, possessed an adolescent growth spurt (B.H. Smith, 1993; Bogin and Smith, 1996; Clegg and Aiello, 1999; Tardieu, 1998, 1999; Antón, 2002b; S. Smith, 2003; Antón and Leigh, 2003). Both have been significantly influenced by the remarkably complete KNM-WT 15000 subadult skeleton (Walker and Leakey, 1993a), and each is likely to be further informed by the recent subadult remains from Dmanisi (D2700/2735 and unpublished post-cranials; Vekua et al., 2002) and Ileret (KNM-ER 42700; Leakey et al., 2003). All of these works pre-

sume that at least some portion of *H. erectus* (*sensu lato*) is ultimately ancestral to modern humans.

Developmental rates: fast or slow?

Weidenreich (1943) argued that growth was accelerated in *H. erectus*, based on ideas about the relationship between sutural fusion and dental eruption in humans and great apes, and the conventional wisdom that Asian *H. erectus* was more apelike than humanlike in its cranial development (see Antón and Franzen, 1997). That is, Weidenreich (1943) considered *H. erectus* to mature earlier (faster) than do modern humans, an idea that had important implications for how he estimated age in fossils and explains why he identified so many subadult *H. erectus* (Antón and Franzen, 1997). Black (1931) concurred that *H. erectus* matured quickly, but he felt that rate to be less accelerated than did Weidenreich (1943). More recently, B.H. Smith (1993) argued, on the basis of relative brain size models, that *H. erectus* probably reached maturity somewhat early, about age 15, and lacked an adolescent growth spurt (see below). Her work was based in large part on the KNM-WT 15000 skeleton, for which she estimated a developmental age of about 11 years, based on dental formation and eruption patterns. Dean et al. (2001), using dental microstructure, argued for an even faster rate of dental growth, more similar to that seen in the great apes and probably more coincident with the views of Black (1931), and they offered an age of about 8 years for KNM-WT 15000. Their data suggested a large range of variation for *H. erectus*, with KNM-WT 15000 having the lowest perikymata counts (92–110 for anterior teeth), well outside the human range, whereas Sangiran 4 had a count of 138 for its upper canine, placing it within their human range (of 148 ± 19) and either just within or just outside human crown formation times, depending on inferred periodicity. Nonetheless, first molar emergence times based on Sangiran 7 appeared to occur at about 4.4 years of age in *H. erectus*, somewhat earlier than modern humans. These rates, or at least whether they are relatively faster or slower than those of modern humans, may have implications for the different mechanisms for brain size increase.

Brain evolution: neoteny or sequential hypermorphosis?

As discussed above, the brain undergoes increases in size throughout the evolution of *H. erectus* (Leigh, 1992; Antón and Swisher, 2001), followed by exponential increases at the origin of modern humans (Henneberg, 1987, 2001; but see Lee and Wolpoff, 2003). In addition, vault shape also changes between *H. erectus* and *H. sapiens*, being taller and more rounded in the latter (see above). These changes in brain size and shape have often been used to suggest that *H. sapiens* is paedomorphic (juvenilized) relative to *H. erectus* (e.g., Gould 1977).

In contrast, “sequential hypermorphosis” has been argued to be responsible for the evolution of the human brain by prolonging several brain growth periods (McKinney and McNamara, 1991; McKinney, 2002; Minugh-Purvis and McNamara, 2002). Proponents of this view see prolongation of growth as resulting in a relatively large brain over the course of human evolution, rejecting paedomorphosis as a mechanism for evolutionary changes in brain size (see critiques by Godfrey et al., 1998; Shea, 2000; Antón and Leigh, 2003). Prolongation of growth periods can only produce relatively large structures if the growth rate *increases* from ancestor to descendant, or is maintained at ancestral levels. However, if anything, the data discussed above argue for a *decrease* in dental developmental growth rates in *H. sapiens* over those in *H. erectus* (Dean et al., 2001). If we can extrapolate rates across systems, which may or may not be advisable given a general lack of correlation between maturation indicators in different systems (e.g., Clegg and Aiello, 1999), this may indicate faster growth in *H. erectus* in general than in *H. sapiens*. Furthermore, although human growth data indicate extension of an early period of growth, they also indicate relative *reductions* in body-mass growth rates (Leigh, 2001). Together, these data argue against sequential hypermorphosis.

Alternatively, direct support for paedomorphosis, and specifically neoteny (juvenilized adult morphology via size/shape dissociation), of the human vault comes from a two-part heterochronic analysis of cranial size and shape in *H. erectus* and *H. sapiens* adults and subadults (Antón and Leigh, 2003). First, modern humans present an adult vault shape that, based on angular dimensions, is very similar to subadult *H. erectus* vault shape. Second, modern human adults, although much larger in size, are similar in shape to juvenile *H. erectus*, but show trends of growth that are nonparallel and nonoverlapping with those of *H. erectus*. Shape change dominates *H. erectus* cranial growth, whereas size change dominates *H. sapiens* cranial growth (e.g., Gould, 1977). This size/shape dissociation suggests that the heterochronic transformation of neoteny is at work, *in this particular system*, possibly related to the evolution of behavioral flexibility.

Paedomorphosis is often considered an adaptation that limits evolutionary specialization; thus paedomorphic vault shape is consistent with suggestions that behavioral flexibility is a “hallmark” of our evolution (Potts, 1996). Possibly, selection for paedomorphosis through neoteny represents a mechanism for sustaining high levels of neural plasticity (Antón and Leigh, 1998, 2003; Antón, 2002b). That is, if adult modern humans possess a brain that is both shaped *and* structured much like that of a juvenile *H. erectus*, then human brains might also retain juvenile attributes, such as plasticity/flexibility, well into adulthood. High levels of neural plasticity in humans are suggested by our ability to regain nor-

mal language facility even after eliminating Broca’s area (Vining et al., 1997). Of course, behavioral correlates of vault shape remain to be established in primates. Some support for such a link in carnivores comes from the finding that selection for certain behaviors appears to have also resulted in juvenilized cranial shape in adult domesticated foxes (Trut, 1991; Trut et al., 1991). This hypothesis suggests that shape change (and its underlying causes related to brain function) was the emphasis of cranial evolution in *H. sapiens*.

Alternatively, neoteny may simply reflect a conservative way to increase brain size while maintaining functional relations within the skull (Antón and Leigh, 2003). That is, the emphasis may in fact have been on size increase, with shape change being its byproduct. Because spheres can be stronger using less material than angular forms of similar size, retention of a more globular, juvenile vault shape allows maximal size increase and reduction of cranial thickness (within the limits required for active bone marrow), and reduction in the energy and resources necessary to grow thick walls. The globular, juvenile form of the modern human brain, then, may bear no relation to juvenilized function or increased neural plasticity.

The origin of adolescence?

The adolescent growth spurt, a dramatic increase in growth due to an increase in growth velocity around the time of sexual maturity, occurs in most human groups (Bogin, 1994). The origin of this life stage could have important implications for hominin evolution, relating either to cultural complexity, since adolescence is a time when human individuals learn critical adult roles (Bogin, 1994), or to solutions for dealing with the increased metabolic demands of large body size (Leigh, 1996). Bogin (1994, 1999) argued that the human adolescent skeletal growth spurt reflects a uniquely “inserted” period of ontogeny that is entirely absent in early hominins, including *H. erectus*. On the other hand, adolescent skeletal growth spurts are reported in nonhuman primates, particularly in the face (personal communication with Leigh, 2002), and body weight spurts are also known (Leigh, 1996), indicating that such spurts may be a feature shared in a distant common ancestor rather than unique to humans.

Several authors tried to use the KNM-WT 15000 skeleton to address the issue of the origin of the adolescent growth spurt. B.H. Smith (1993) suggested that there was no growth spurt, on the basis of the disagreement between dental, postcranial, and statural developmental ages for KNM-WT 15000 (Bogin and Smith, 1996). Others suggested that the data are not inconsistent with the presence of a growth spurt (Clegg and Aiello, 1999; Tardieu, 1998; Antón, 2002b; S. Smith, 2003), but none of these studies estimated growth velocities. We reconstructed arithmetic (pseudo)velocity curves for *H. erectus* and argued, tentatively, in favor of a small

spurt in the facial skeleton (Antón and Leigh, 2003). However, the fossil data are not particularly convincing on this point, given the extremely small sample sizes. More convincing is the comparative evidence from both modern human (Antón and Leigh, 2003) and great ape (Taylor and Antón, unpublished data) skeletal samples that exhibit peak velocity values for facial growth at “adolescent” dental developmental ages. These values suggest a cranial growth spurt that is similar in timing and intensity to those recorded in longitudinal growth data on stature and body mass in humans and great apes (Leigh, 1996). However, whether these can be considered comparable growth phenomena to somatic adolescent growth spurts remains to be established.

The presence of an adolescent growth spurt has several ramifications, both proximate and ultimate. Of a more practical nature are the implications for interpreting adult size and shape from subadult remains. As discussed above and elsewhere, vault shape changes dramatically in *H. erectus*, mostly due to brain size increase before “adolescence.” However, cranial superstructure development continues even into the late subadult period (Antón, 1999, 2002b). As should also be clear from the foregoing discussion, facial size and shape changes are substantial during and after adolescence in humans: comparative skeletal data suggest increases of human facial height by more than 20% of total height at rates of increase of several millimeters per year (Goldstein, 1936; Buschang et al., 1983; Marshall and Tanner, 1986; Antón and Leigh, 2003). Thus facial morphology in subadolescent hominins (i.e., with sphen-occipital synchondrosis open) may not accurately reflect adult morphology. As a result, for example, the subadult D2700 from Dmanisi may be expected to have had a less primitive facial appearance at adulthood. The degree of this change would clearly be related to the intensity of the growth spurt. Similarly, the adult height estimates of the Nariokotome specimen will vary, depending on whether a growth spurt was or was not present in *H. erectus*, its intensity, and how far along in his growth the fossil KNM-ER 15000 was at the time of his death.

More ultimate implications relate to the biological and perhaps cultural significance of the adolescent period of development. The presence of an adolescent growth spurt may be beneficial in that it delays to older ages the metabolic costs of growing and maintaining large body size (e.g., Leigh, 1996). However, the retention of relatively smaller, preadolescent body sizes would make these hominins relatively more susceptible to predation for longer periods of time. Perhaps this may be no more significant a cost than earlier, smaller hominins had already successfully negotiated (Leigh, 1996), unless the increase in adult body size shifted the entire group into the prey range of a larger set of predators. Behavioral/cultural advantages of the adolescent growth spurt were proposed by Bogin (1994), who

saw both the spurt and its timing (early in females, late in males) as allowing a period for practice of adult economic, social, and sexual behaviors. In this view, females appear adult before being sexually mature, allowing them to practice mating strategies and caregiving without incurring offspring. Males appear juvenile even after sexual maturity, allowing them to avoid conflict with adult males while still performing socially and sexually. Thus both sexes are allowed to practice behaviors without incurring the full adult consequences if mistakes are made (Bogin, 1994).

Overview of life history and biology of *H. erectus*

H. erectus was a large-bodied, large-brained, moderately sexually dimorphic hominin whose ranging patterns were significantly enlarged over those of earlier hominins. The energetic costs of maintaining enlarged body and brain size suggest the occurrence of a shift to a higher-quality diet, some part of which likely included increased emphasis on meat and marrow acquisition. Maternal costs must have been differentially larger due to both carrying and birthing large-brained neonates. Hypotheses of changes in social structure related to these changes include “grandmothering” and the assistance of male and female “helpers,” none of which are amenable to testing through the fossil record. Data from extant dispersals and models of fossil dispersals suggest that increasing body size, greater reliance on animal food resources, and increased range size were part of an ecomorphological web of factors that facilitated the initial hominin dispersal from Africa.

Developmental rates appear to have been somewhat faster in *H. erectus* than are those of modern humans, but an adolescent growth spurt cannot be rejected. Changes in growth between *H. erectus* and *H. sapiens sapiens* include heterochronic shifts in cranial vault growth. The data support the idea that the *H. sapiens* vault is neotenic relative to *H. erectus*, and suggest either that size increase led to changes in shape, due to the increased efficiency of the shape of a sphere over more angular forms, or that behavioral flexibility and juvenilization of the brain are linked phenomena in the evolution of human skull form.

FUTURE DIRECTIONS

Howells (1980) focused on what were then the main themes concerning research on *H. erectus*: its taxonomic status and subdivision, and the pace of change in the species through time. Since then, a revised chronostratigraphic framework gives us a longer view of the species, and additional specimens allow us to emphasize the biology of the taxon. While we have not resolved the taxonomic issues, I suggest that the proposal by Jolly (2001) to move away from the species debate by using the allotaxa model is particularly relevant for *H. erectus*.

I imagine that much of the future debate will be in trying to sort out the biogeographic implications and local adaptations of any number of these allotaxa, but particularly those in island Southeast Asia, Northern China, and Africa. The fate and constituency of the African lineage around 1.0 Ma require particular attention. I argue that a total morphological pattern of cranial morphology unites regional lineages across Africa and Eastern and Southeastern Asia. However, this should not be mistaken as arguing for the absence of (in some cases marked) regional variation. Regional lineages are easily identified and persist over long time periods with moderate morphological change. For example, in Southeast Asia, a morphologically identifiable, regional lineage persists for most of the Pleistocene. I previously argued that some of this regionality may be explicable by intermittent isolation due to changes in sea-level at the onset of Northern Hemispheric glaciation (Antón, 2002a). However, it is certainly possible that small populations dispersed over large areas could produce similar regional lineages. In the interests of full disclosure here, I see the regionality expressed in *H. erectus* as completely independent of the origins of modern humans, who in my view share neither the morphological pattern of *H. erectus* nor the vestiges of the regional anatomy of that species. Some of these debates will only be moved forward by additional fossil remains, particularly in the region of the Indian subcontinent.

As the fossil assemblages grow, the other theme will be the need for systematic assessment of the covariance and significance of characters related to time and geography, but also most critically to size, sex, and particularly age variables. As always, the greater the fossil data set, the less clear the boundaries between taxa appear to be, and the more critical it becomes that we understand the structure, function, and development of the characters that appear to separate or unite our fossil groups. Understanding the function, developmental origins, and underlying variability of these features in extinct and extant primates remains an imperative task.

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