

EARLY DISPERSALS OF *HOMO* FROM AFRICA

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■ **Abstract** The worldwide distribution of our species, *Homo sapiens*, has its roots in the early Pleistocene epoch. However, evidence has been sufficient only in the past decade to overcome the conventional wisdom that hominins had been restricted to Africa until about 800,000 years ago. Indeed, the idea that hominin dispersal was technologically mediated, and thus must correlate with changes in stone tool technology seen at the Oldowan/Acheulean transition, has proven to be a persuasive hypothesis despite persistent claims for an early Pleistocene hominin presence outside Africa. We review multiple recent lines of evidence that suggest hominin dispersals from Africa in the earliest Pleistocene, if not the latest Pliocene, correlated with the appearance of hominins typically referred to as *Homo erectus* (*sensu lato*) who carried with them an Oldowan tool technology. Changes in body plan and foraging strategy are likely to ultimately underlie these dispersals.

INTRODUCTION

Until a decade ago, most evidence suggested that hominins had been restricted to Africa (and the Levant) until about 800,000 years ago (c.f., Pope 1983, Klein 1989, Langbroek & Roebroeks 2000). Investigators thought the earliest accepted Far East and Island Southeast Asian hominin sites were between 500 and 800 ka (Pope 1983). ‘Ubeidiya, Israel represented the best evidence of 1 Ma or older hominins just outside Africa (Klein 1989, p. 204) but was widely attributed to, at best, short-term hominin forays outside Africa (Schick 1994). Thus, the earliest hominin dispersal from Africa was considered by paleoanthropologists to be relatively late in human evolution with hominins leaving Africa only with the assistance of Acheulean technology. Such a view has been dubbed the “short chronology” (e.g., Roebrooks 2001). Given the presumed timing of this dispersal, paleoanthropologists often assumed the dispersing hominin to be a late form of *Homo erectus*.

This short chronology contrasted with the opinion of many early workers in Asia who attributed the earliest hominin sites on Java to the early Pleistocene on geological grounds (e.g., von Koenigswald 1936, 1962; de Terra 1943) and to persistent, but isolated, voices that offered biogeographic, radiometric, or stratigraphic arguments for ages of 1.4 Ma or more for sites in the Levant and Indonesia (Jacob & Curtis 1971; Tchernov 1987, 1992; Franzen 1994). For most anthropologists, the data were simply too sparse and often insufficiently documented to make a strong case for early dispersals. Furthermore, the hominins in Java were too derived morphologically and too large brained to be compelling arguments of an early disperser.

In the past decade, a wealth of new data and sites have been offered supporting a “longer chronology” of hominin presence outside of Africa (e.g., Swisher et al. 1994; Larick et al. 2001; Gabunia et al. 2000a; Vekua et al. 2002). Although the precise age of the earliest occurrence varies among regions (and researchers), all regions have witnessed the accumulation of more robust evidence supporting an earlier occupation than that accepted just a decade ago. Although the precise age of many of these sites remains a controversial matter, the earliest occupation of Europe has increased to at least 800 ka, of Western Asia to 1.7 Ma, and of Indonesia to 1.6 or 1.8 Ma (Swisher et al. 1994; Carbonel et al. 1999; Gabunia et al. 2000a). Perhaps the most important, and least contested, of these sites in regard to establishing an age for the earliest African dispersals are the discoveries at Dmanisi, Republic of Georgia, dated to approximately 1.7 Ma; they are least contested both because of the combined radiometric, paleomagnetic, and biostratigraphic age estimates and because of the anatomy of the hominins discovered there.

Here we review multiple recent lines of evidence that support a longer chronology. Although scholars may quibble as to whether hominin dispersals from Africa began at 1.6 Ma or as early as 1.8 Ma, all data point to dispersal substantially prior to 800 ka, the conventional wisdom just a decade ago. These data correlate the first dispersal with the appearance of hominins typically referred to as *Homo erectus* (*sensu lato*) who carried with them an Oldowan tool technology. They do not speak to the number and longevity of these dispersals or to exactly how many forays of differential success there may have been (Dennell 2003). Nonetheless, after the late part of the early Pleistocene substantial areas of the Old World were no longer hominin-free. We discuss the possible underlying causes of such dispersal, including changes in body plan and inferred foraging strategy.

WHEN DID THEY LEAVE?: EARLY PLEISTOCENE HOMININ SITES OUTSIDE AFRICA (1.4–1.9 MA)

Throughout this text we adopt the use of a Plio-Pleistocene boundary that relatively coincides with the upper Olduvai Subchron–Matuyama Chron (Normal to Reverse) geomagnetic polarity transition, calibrated at ~1.78 Ma (e.g., Berggren et al. 1995). Therefore, the recognition of this boundary in the various regions becomes of

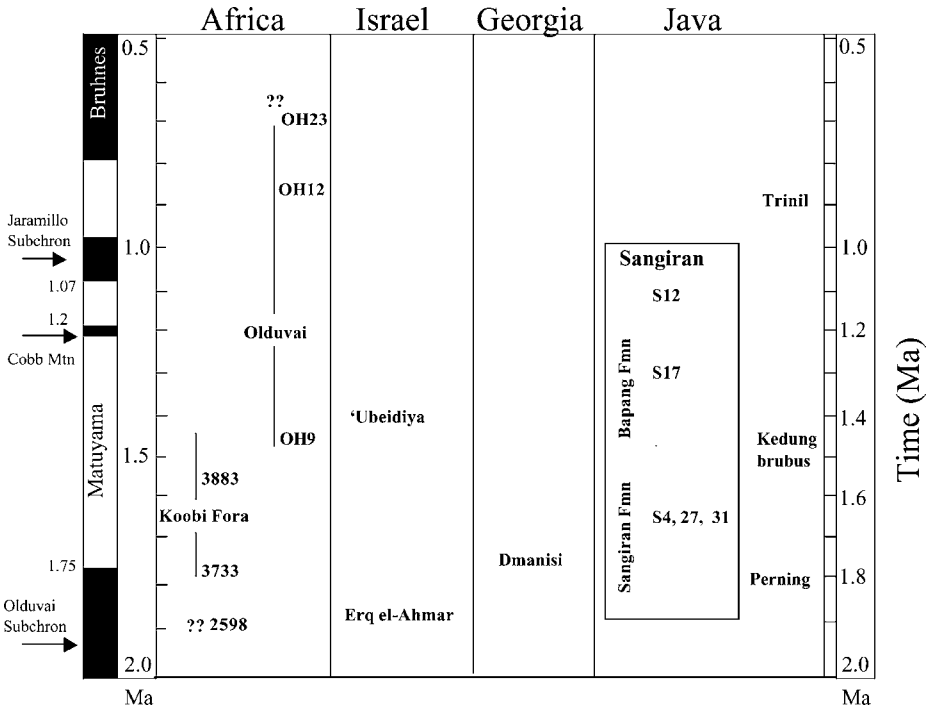


Figure 1 Temporal comparisons of hominins from early Pleistocene localities plotted by region and against the geomagnetic polarity time scale. Time is given in millions of years. Specimen numbers refer to fossil hominins.

utmost importance in the correlation and age assessment of these early hominins. Paleomagnetism, $^{40}\text{Ar}/^{39}\text{Ar}$, and Fission-Track dating, as well as faunal correlations, currently provide the best critical means of assessing age.

Currently, the primary skeletal evidence for early Pleistocene hominins outside Africa comes from a single locality in the Republic of Georgia (~1.7 Ma) and from a series of localities in Indonesia (~1.6–1.8 Ma; Figure 1). Archaeological evidence and nonspecific hominin remains are also found in the Near East at 'Ubeidiya (~1.4 Ma) and archaeological remains alone at Erq el-Ahmar (~1.8–1.9 Ma).

Eurasia and the Neareast

Hominins were discovered by archaeologists in 1991 from a 16-m² area below a medieval village in Dmanisi, Republic of Georgia. Since 1991, four hominin crania and other hominin remains were retrieved from infillings, probably caused by soil piping, within the Pleistocene sediments (Gabunia et al. 2002a). Abundant faunal and archaeological remains were also retrieved from the infillings, overlying and underlying sediments.

Hominin fossils from Dmanisi are dated to ~ 1.7 Ma on the basis of various lines of evidence (Gabunia et al. 2000a,b). A maximum age of 1.78 Ma for the Dmanisi fossils is provided by the 1.8 Ma $^{40}\text{Ar}/^{39}\text{Ar}$ dates on the underlying Masavera Basalt and by the occurrence of the upper boundary (N-R) of the Olduvai Subchron as determined from paleomagnetism of the basalt and overlying fossil-bearing sediments. Inferred depositional rates of sediment and soil formation suggest deposition of the hominin-bearing strata quickly following cooling of the basalt flow. The reverse geomagnetic polarity of the hominin-bearing units directly above the 1.78-Ma Olduvai–Matuyama Boundary indicates a likely age range in the lower part of the mid-Matuyama chron. Although the site lacks an upper, radiometrically determined age limit, the presence of the rodents *Mimomys ostromosensis* and *M. tornensis* constrains the age of the site to the basal part of the mid-Matuyama between ~ 1.6 Ma and 1.78 Ma.

In Israel, the central Jordan valley is composed of a series of geological formations, two of which (Erq el-Ahmar and ‘Ubeidiya) have yielded traces of hominins or hominin activity in the early Pleistocene (Bar-Yosef & Goren-Inbar 1993, Ron & Levi 2001). Both formations are underlain by the Cover Basalt that yielded K-Ar age estimates of 2.0 Ma or greater for its upper levels (Siedner & Horowitz 1974). The stratigraphically lowest of the Israeli hominin occupation levels, containing core and flake tools, occurs in the Erq el-Ahmar Formation in sediments of normal geomagnetic polarity. Given the age of the Cover Basalt, the presence of sediments of both normal and reverse polarity in the Erq el-Ahmar Formation, and the presence of an early Pleistocene fauna, the normal sediments in which the hominin tools are found are interpreted by geochronologists as representing the Olduvai Subchron (Ron & Levi 2001), dated elsewhere to 1.77–1.95 Ma (Berggren et al. 1995).

The 150-m ‘Ubeidiya Formation has been the subject of systematic fieldwork for several decades (see Bar-Yosef & Goren-Inbar 1993). Strata of the ‘Ubeidiya Formation stand nearly vertical and have yielded fossil faunas, abundant stone tool remains indicative of multiple occupations, and small fragments of hominin cranial vault bone and tooth. Initial age estimates suggested ages of 0.8–1.0 Ma based on pollen correlations (Horowitz 1989) and 1.8–2.0 Ma (Repenning & Fejfar 1982) based on outdated classifications of the fauna (Bar-Yosef & Goren-Inbar 1993). However, the ‘Ubeidiya fauna lacks several extinct mollusk species present at Erq el-Ahmar (Tchernov 1987), suggesting a younger age for the ‘Ubeidiya Formation. Systematic biostratigraphic analyses and comparisons with other Old World faunas suggest that the hominins and archaeology date to ~ 1.4 Ma (Tchernov 1987, 1992).

Far East

Although investigators propose the oldest occupation of China to have occurred as early as 1.8 Ma (Huang et al. 1995), the mandible fragment from Longgupo is argued to be nonhominin and the associations of the isolated incisor have been questioned by some scholars (Schwartz & Tattersall 1996; Wolpoff 1999, p. 466;

Wu 1999). The first certain hominins from mainland Asia do not appear until about 1.15 Ma in Southern China at Gongwangling (Lantian; An et al. 1990) and are not discussed further here.

In contrast to these isolated occurrences, island Southeast Asia yields a relative abundance of fossil hominins with a record that is fairly continuous from the early- to middle Pleistocene. Hominins first appear ~ 1.8 Ma at Peking (Mojokerto) on Java, and shortly thereafter in the Sangiran Dome region (~ 1.66 Ma; Swisher et al. 1994), where there appears to have been a mostly continuous hominin presence up to about the Brunhes-Matuyama boundary (Figure 1; Table 1; Swisher et al. 1994, 1997; Larick et al. 2001).

The Sangiran area provides the most robust evidence for early dispersal into Indonesia because the ages are based on $^{40}\text{Ar}/^{39}\text{Ar}$ analyses on a series of tuffs located throughout the Sangiran section with multiple hominin fossils intercalated among them (Table 1). Fossil hominins occur in both the Sangiran (Pucangan) Formation and the overlying Bapang (Kabuh) Formation; however, the identity of the earliest dispersers rests with the hominins from the uppermost Sangiran Formation. The oldest hominin calvaria at Sangiran (e.g., Sangiran 4, 27, and 31) are associated with ages of > 1.6 Ma on the basis of dates for tuffs of 1.66 Ma for the upper part of the Sangiran Formation and 1.58 Ma for the base of the Bapang (Kabuh) Formation (C. Swisher, unpublished data; Swisher et al. 1994, Antón & Swisher 2000). Fluorine analysis supports a derivation of Sangiran 4 from either the lower Bapang (Grenzbank zone) or upper part of the Sangiran (Pucangan) Formation (Matsu'ura 1982). Most sediments within the Sangiran (Pucangan) formation are of reverse geomagnetic polarity that, in conjunction with the chronology, have been attributed to the middle part of the Matuyama chron (Swisher et al. 1994). Preservation differences between fossils from the oldest strata (Sangiran Formation black clays that badly deform and telescope included bones) and younger, overlying strata (Bapang Formation cross-bedded sandstones that do not present deformed bones) indicate that hominins certainly are associated with the Sangiran Formation and thus with ages in excess of 1.6 Ma. Similar preservation of both Sangiran 27 and 31 supports their reported position in the upper Sangiran Formation, contrary to recent inferences by Larick and colleagues (2001).

In the following several paragraphs, we address in detail the challenges raised to this "long chronology." However, for the benefit of readers less familiar with geochronological techniques, we first "cut to the chase" by summarizing the major issues here. Challenges to the long chronology in Indonesia have been raised on the basis of biostratigraphic evidence, fission track ages, and paleomagnetic inference. Each of these indicators has specific issues detailed below. The Sangiran faunas are largely endemic to Java, thus offering little or no independent age information through correlation with Asian mainland faunas. Magnetostratigraphies on Java are of short duration and cannot be unambiguously correlated to the Geomagnetic Polarity Time Scale (GPTS). Thus, both the biostratigraphic and paleomagnetic calibrations are based on fission track dates from the Java sections themselves.

Arguably, the most convincing of the fission-track ages are those on Australasian tektites from Sangiran, dated reliably elsewhere to 790 ka. However, the stratigraphic positioning of these tektites, although once argued to be well-known, has been uncertain since the beginning of paleontological investigations at Sangiran. The tektite age thus offers no independent age calibration for either the biostratigraphy or the magnetostratigraphy. Thus the best age information for the Sangiran section comes from a series of stratigraphically consistent stratigraphic $^{40}\text{Ar}/^{39}\text{Ar}$ on primary volcanic layers and cross-correlated with previous microfossil age estimates.

Two recent critiques challenge all or part of these chronologies (Langbroek & Roebrooks 2000, Semah et al. 2000). Langbroek & Roebrooks (2000) suggest that all Javan hominin sites are younger than 1.0 Ma (see also Pope 1983). This critique relies heavily on the apparent stratigraphic position of Australasian tektites in the middle part of the Bapang Formation, the occurrence of the Jaramillo in the upper part of the Sangiran Formation, and the Brunhes–Matuyama boundary in the overlying Bapang Formation.

Although the age of the Australasian tektites is known with great accuracy on the basis of dates elsewhere (at 790 ka), their stratigraphic provenience at Sangiran is uncertain. Historically von Koenigswald and others thought the tektites came from sediment above the Bapang Formation. Arguments for a lower stratigraphic position, within the Bapang Formation, are largely based on the occurrence of a single, purportedly *in situ*, tektite found during trenching. The questionable stratigraphic placement of this tektite is noted by Antón (2002) and discussed by Larick et al. (2001), whose ages are also inconsistent with the proposed stratigraphic placement of the tektite and whose Indonesian coauthors, participants in the original field recovery of the tektite, have primary knowledge of the tektite's stratigraphic position (or lack thereof). It is relevant to note here that no *in situ* tektites have been recovered at Sangiran despite an increase in recent, systematic excavations in the middle part of the Bapang Formation (see Larick et al. 2001), as well as active searches dating back as early as von Koenigswald. It is of consequence that the age estimates assigned to the faunal sequences are also in part based on the stratigraphic placement of this tektite (see below).

The Langbroek critique also relies in part on older paleomagnetic data based entirely on alternating field (AF) rather than thermal demagnetization techniques (Semah 1982; Shimizu et al. 1985 in Watanabe & Kadar 1985). AF demagnetization cannot remove secondary magnetic overprints caused by secondary mineralizations, such as the formation of goethite. Consequently, it is difficult to trust normal, transitional, or intermediate polarities measured by AF demagnetization in sediments, such as those at Sangiran and Mojokerto, that are highly weathered and secondarily mineralized (see Hyodo 2001). Mixed or intermediate directions are considered the result of incomplete demagnetization and characterization of magnetic components residing in primary and secondary carriers. These types of data cannot be used to justify the occurrence of the Jaramillo in the Sangiran Formation. Similar problems may explain the preponderance of normal polarity directions in

the upper part of the Sangiran section, as these strata increasingly show evidence of secondary oxidized mineralizations (Hyodo 2001). In these circumstances, such as those at Sangiran, calibration by radiometric dating provides the most robust means of evaluating these paleomagnetic measurements and correlating them to standard geologic time scales.

Unfortunately, the Langbroek critique ignores well-behaved $^{40}\text{Ar}/^{39}\text{Ar}$ analyses from multiple studies throughout the Sangiran section that are temporally consistent with their relative stratigraphic positions (Swisher 1997, Larick et al. 2001). Arguments for the reworking of volcanic materials from older deposits as a means to explain $^{40}\text{Ar}/^{39}\text{Ar}$ dates that some workers consider too old (e.g., Sémah et al. 2000; Hyodo 2002) cannot be justified given the excellent agreement between the dates and their relative stratigraphic position, as well as their occurrence in multiple sections throughout the Sangiran dome. These data are further supported by diatom and foraminiferal data from the Sangiran Formation that indicate an early Pleistocene age for the earliest hominin-bearing sediments on Java (Orchiston & Siesser 1978, 1982; Ninkovitch et al. 1982).

In another paleomagnetic and dating critique of the Sangiran Formation, Sémah and colleagues (2000) argue that the lowest part of the Sangiran Formation can be no older than ~ 1.7 Ma, on the basis of the geomagnetic polarity and $^{40}\text{Ar}/^{39}\text{Ar}$ age of the Lower Lahar of the Sangiran Formation (Table 1). In and of itself this conclusion does not necessarily conflict with the radiometric chronologies noted above. However, several inconsistencies exist in their data that make their interpretation difficult to understand. Sémah and colleagues report $^{40}\text{Ar}/^{39}\text{Ar}$ incremental heating of hornblendes from the Lower Lahar at Cenglik that resulted in a U-shaped release pattern, with a minimum saddle of 2.37 ± 0.06 Ma and an isochron age of 1.97 ± 0.06 Ma. A step-heating experiment on a single grain from the same site yielded a minimum age of 1.77 ± 0.08 Ma. They reject the bulk incremental heating age because the U-shaped spectra is considered indicative of excess argon; likewise the isochron age of 1.97 ± 0.06 Ma is rejected, although it should account for the excess argon, if present. Sémah and colleagues also obtained dates of 1.68 ± 0.02 Ma and 1.66 ± 0.04 Ma on the basis of the total fusion of two single hornblende crystals from the lahar at the locality of Puren. According to their study, these analyses indicate that the lahar hornblendes are of a single, homogeneous population and that the older ages of the bulk sample are due to excess argon. Sémah and colleagues thus consider the best age for the Lower Lahar to be an average of the two single-grain dates from Puren ($1.66 + 0.04$ Ma) and the minimum age of 1.77 ± 0.08 Ma from Cengklik.

Although the younger total fusion dates may be reliable, as argued by Sémah and colleagues, they are difficult to evaluate. It is equally plausible that these data incorporate an amount of alteration, excess ^{36}Ar , or even ^{40}Ar loss that, if uncorrected, would result in ages that are too young. Without incremental heating of these hornblendes there is no way to be certain; however, their report of a $^{40}\text{Ar}/^{36}\text{Ar}$ isochron intercept of 274 (less than the expected 295 $^{40}\text{Ar}/^{36}\text{Ar}$) for these data supports the idea that the single-grain ages may be too young.

For the bulk incremental heating experiment, the isochron should account for excess argon if present, making the isochron age of 1.97 ± 0.06 Ma an equally plausible age for the lahar. Alternatively the presence of older hornblende grains of similar composition could explain the results of the bulk experiment. Lahars are notorious for reworking older materials, a feature which makes them less-than-ideal candidates for radiometric dating. Essentially, we find these data too few and insufficient to reliably assess the age of the Lower Lahar.

Nonetheless, even if we accept the arguments by Sémah et al. for a $^{40}\text{Ar}/^{39}\text{Ar}$ age of 1.67 Ma for the lahar, it is difficult to rectify such an age with their geomagnetic polarity data. Sémah and colleagues (2001, as well as in their earlier work) state that the Lower Lahar gives different polarities at the two localities where measurements were made: normal for Cengklik and reverse for Puren. This finding then argues that the Lower Lahar straddles the upper Olduvai–Matuyama boundary, being of Olduvai age at Cengklik and Matuyama age at Puren. Two problems exist with this conclusion. First, it is highly unlikely, given the rapid emplacement of lahars, that the Lower Lahar, which all workers agree represents a single unit, records more than a single, true geomagnetic polarity. Given that geomagnetic polarity transitions are thought to encompass hundreds or thousands of years, whereas the deposition of lahars is more catastrophic, occurring in hours and days compared with years, it is more likely that spurious directions or secondary geomagnetic normal (present field) overprints have been incompletely removed during the laboratory demagnetization processes of these samples. Thus Sémah and colleagues have not adequately resolved the geomagnetic polarity of the lahar at the time of deposition from secondary magnetization directions. In support of this conclusion, Hyodo (2001) reports only reverse polarity in the lahar.

However, even if we assume that Sémah and colleagues correctly measured the upper Olduvai–Matuyama boundary, the age of this boundary, and thus the lahar, must be 1.78 Ma (Berggren et al. 1995), making their preferred $^{40}\text{Ar}/^{39}\text{Ar}$ age of 1.67 Ma for the Lower Lahar too young. Unpublished $^{40}\text{Ar}/^{39}\text{Ar}$ ages on two primary tuffs in the Sangiran Formation above the Lower Lahar give stratigraphically consistent ages of 1.7 Ma and 1.9 Ma, implying that the true age of the Lahar may be significantly older than that suggested by Sémah and others (Table 1) (C. Swisher, unpublished data). A preliminary $^{40}\text{Ar}/^{39}\text{Ar}$ age for the Lower Lahar of 2.08 Ma (C. Swisher, unpublished data) and a $^{40}\text{Ar}/^{39}\text{Ar}$ age of 1.9 ± 0.2 Ma reported by Bettis et al. (2004) further contradict age and implications for the Lower Lahar as drawn by Sémah and colleagues (2001).

Although these issues need to be addressed, an Olduvai–Matuyama boundary age (or, for that matter, an older age) for the Lower Lahar is not inconsistent with the findings of Swisher (1994, 1997) or Larick and coworkers (2001), or, for that matter, with Sémah's own normal polarity data.

For many years, biostratigraphic chronologies have been used to suggest that the first hominin colonization of Java occurred no more than 1.0–1.3 Ma (e.g., Leinders et al. 1985, de Vos & Sondaar 1994, Sondaar et al. 1996). These authors agree that the earliest hominins at Sangiran occur in the upper Sangiran (Pucangan) Formation

along with a limited fauna known as the Ci Saat fauna (see below). However, there are no reliable calibration points of a similar fauna elsewhere in Indonesia or on the Asian mainland, thus the fauna themselves do not offer an independent means of precise age assessment but ultimately must rely on radiometric dates on Java. The radiometric calibrations used for the biostratigraphy are based on the placement of the tektites and fission track ages (e.g., Suzuki et al. 1985 in Watanabe & Kadar 1985), the problems with which we have discussed above.

Dennell's (2003) recent review of the Indonesian age data likens the controversy between biostratigraphic and radiometric ages in Java to that over the KBS tuff at Koobi Fora Kenya and implies that the biostratigraphic indicators and previous paleomagnetic analyses, which have been used to argue for a hominin presence no older than 1.3 Ma, should be the more robust dataset and are the most consistent with the absence of early, mainland-Asian hominins. However, Dennell (2003) bases this conclusion on (a) the radiometric work of Sémah, which at best gives a lower age limit to the hominins not inconsistent with the $^{40}\text{Ar}/^{39}\text{Ar}$ chronologies of Larick et al. (2001) and Swisher et al. (1994); (b) the paleomagnetic work of Hyodo et al. (2002) that, independent of radiometric or other chronology, cannot indicate which period one is in, and that uses the biostratigraphy (which uses the tektite placement) and the suspect placement of the tektite as their radiometric calibration (Hyodo 2001, Hyodo et al. 2002); and (c) the biostratigraphic chronologies that use the same radiometric calibration that is in part dated by the tektite of uncertain provenience. All these lines of data are suspect. More important, all the above studies agree that the earliest hominins at Sangiran are from the Black clays of the Sangiran Formation and that none of them is inconsistent with the earliest hominins at Sangiran being greater than 1.0 Ma and probably 1.3 Ma.

Collectively, we conclude that the entire hominin-bearing section at Sangiran is greater than 1.0 Ma, a great departure from the accepted view just a decade ago. Further, a strong case can be made that the oldest of the Sangiran hominins is at least older than 1.5 Ma [i.e., the age for the base of the Bapang given by Larick et al. (2001), which unconformably overlies the Sangiran] and is likely older than 1.6 Ma. We find fault with the existing paleomagnetic, fission-track dating and biostratigraphies supporting a young age for Sangiran. One should note, however, that acceptance of this young chronology would require not simply reworking the volcanic elements of sediments at Sangiran but a systematic error in all $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Sangiran tuffs. Although anything is possible, $^{40}\text{Ar}/^{39}\text{Ar}$ dating currently provides us with the most accurate and reliable means of age calibration as witnessed by a plethora of such dated hominin sites in East Africa.

WHO DID THEY LEAVE WITH? FAUNAL COMMUNITIES OF EARLY PLEISTOCENE SITES

Near East and Eurasia

Tchernov (1987, 1992) argued that by at least 1.4 Ma, hominins were regular members of the faunal migrations that occurred when African ecological conditions

expanded into the Levant. Whether movement within one's ecological niche rather than expansion outside of it can be considered a "true" dispersal event is debatable (Klein 1999). However, hominins were one of only a few African taxa to pass into the Levantine fauna, although a strong Ethiopian component was still retained in the 'Ubeidiya fauna (Table 2). The faunal assemblage at Dmanisi retains less

TABLE 2 Large mammal fauna from Early Pleistocene Hominin Sites

Dmanisi, Georgia Units A and B (Gabunia et al. 2000b)	'Ubeidiya, Israel Fi member (Tchernov 1987)	Sangiran Dome, Java Sangiran Formation— Upper Black Clays (Aziz 2001)
<i>Ursus etruscus</i>	<i>Ursus etruscus</i>	<i>Stegodon elephantoides</i>
<i>Canis etruscus</i>	<i>Canis cf. arnensis</i>	<i>Bubalus palaeokerabau</i>
<i>Martes sp.</i>	<i>Canis sp.</i>	<i>Bibos palaeosondaicus</i>
<i>Megantereon megantereon</i>	<i>Vulpes sp.</i>	<i>Homo erectus</i>
<i>Homotherium crenatidens</i>	<i>Lutra sp.</i>	
<i>Panthera gombaszoegensis</i>	<i>Vormela cf. peregusna</i>	From Equivalent aged Faunas elsewhere on Java (de Vos 1995, Sondaar et al. 1996)
<i>Pachycrocuta perrieri</i>	<i>Megantereon cf. cutridens</i>	<i>Panthera sp.</i>
<i>Archidiskodon meridionalis</i>	<i>Panthera gombaszaegensis</i>	<i>Stegodon trigonocephalus</i>
<i>Dicerorhinus etruscus etruscus</i>	<i>Lynx sp.</i>	<i>Hexaprotodon sivalensis</i>
<i>Equus stenonsis</i>	<i>Felis sp.</i>	<i>Sus stremmi</i>
<i>Gazella borbonica</i>	<i>Crocota crocuta</i>	Cervids
<i>Soergelia sp.</i>	<i>Herpestes sp.</i>	Bovids
<i>Dmanisibos georgicus</i>	<i>Mammuthus meridionalis</i>	Boselephini
<i>Eucladocerus aff. Senezensis</i>	<i>Dicerorhinus e. etruscus</i>	
<i>Cervidae cf. Arvernoceros</i>	<i>Equus cf. tabeti</i>	
<i>Cervus perrieri</i>	<i>Equus cf. caballus</i>	
<i>Dama nesti</i>	<i>Kolpochoerus olduvaiensis</i>	
<i>Paleotragus sp.</i>	<i>Sus strozzii</i>	
<i>Homo ex. gr. erectus</i>	<i>Hippopotamus behemoth</i>	
	<i>Hippopotamus gorgops</i>	
	<i>Camelus sp.</i>	
	Giraffidae	
	<i>Praemegacerus verticornis</i>	
	Cervidae	
	<i>Bos sp.</i>	
	<i>Gazella cf. gazella</i>	
	<i>Gasellospira torticornis</i>	
	<i>Macaca sylvanus</i>	
	<i>Homo sp.</i>	

of such a component, suggesting that hominins dispersed outside their African ecological niche. Only six of the Dmanisi taxa (including the hominins) are of African origin (Gabunia et al. 2000b), suggesting that Dmanisi represents a true hominin dispersal event.

Far East

The faunas associated with early hominins of Island Southeast Asia, although not as numerous or well studied as those mentioned above, are of Sino-Malayan and Siva-Malayan extract, thus representing an extensive hominin dispersal (Table 2). Faunal remains from the lower black clays of the Sangiran (Pucangan) formation at Sangiran, probably below that of the hominins, are somewhat impoverished (aka Satir Fauna of Sondaar et al. 1996), which likely suggests insularity due to sea-level rise. The fauna from the upper black clays at Sangiran, probably coincident with the earliest hominins, have been associated with the Ci Saat Fauna of Sondaar et al. (1996). At Sangiran the upper black clays yield open habitat bovids such as *Bubalus palaeokerabau* and *Bibos palaeosondaicus* (Table 2) (Aziz 2001). The Ci Saat fauna in other Javan localities includes some indicators of land connection including *Panthera* sp. in addition to taxa requiring lesser land connection (e.g., *Stegodon trigonocephalus* and *Hexaprotodon sivalensis*, among other taxa), possibly suggesting filtered dispersal from the mainland (de Vos 1985) in the early Pleistocene. Unlike the abundant faunas from the Bapang (Kabuh) formation, interpreting the significance of the Sangiran (Pucangan) fauna is difficult because it is based on relatively few specimens known from a restricted paleoenvironment. If faunas from the lower part of Kedungbrubus and Peming are temporal equivalents, as is indicated by the $^{40}\text{Ar}/^{39}\text{Ar}$ chronologies, then this early fauna is more diverse than indicated by the fossils from the “black clays” of Sangiran.

WHAT DID THEY TAKE WITH THEM? MATERIAL CULTURE AND BEHAVIOR

The early Pleistocene archaeological record of Africa is composed of Early Stone Age assemblages of the Oldowan and Developed Oldowan typified by core and flake technology. Some investigators argue that between 1.8 and 1.5 Ma this record begins to indicate a more complicated and diverse foraging strategy with greater utilization of marginal areas including dry uplands and areas further from standing water (Cachel & Harris 1998). Likewise others suggest that at this time a differential pattern focusing on both meat and marrow acquisition is evidenced in the faunal record with hominins accessing carcasses earlier than had previously been the case (Monahan 1996). The limited number of archaeological sites of this age outside Africa do not allow for the comparison of distributional patterns. However, the stone tool assemblages of early Pleistocene Koobi Fora and Olduvai Gorge afford comparisons to the material culture used by early Pleistocene hominins outside of Africa.

Near East and West Asia

The stone tool assemblage from Dmanisi is a core and flake industry similar to the Oldowan chopping-tool industry of East Africa (Nioradze & Justus 1998; Justus & Nioradze, personal communication; Gabunia et al. 2000c). All tools are produced from local raw materials with selection of finer grained materials (quartzite and basalt) for tool manufacturing. Justus & Nioradze (personal communication) argue that the Dmanisi tools were knapped elsewhere similar to the situation at sites such as HWK.E from lower Olduvai Gorge. However, Dmanisi differs from these assemblages by lacking spheroids and, to date, any evidence for hominin butchery of other vertebrates. Similarities have been noted also between Dmanisi assemblages and those recently retrieved from lake-edge contexts at 'Ubeidiya that have been interpreted as systematic tool abandonment at the point of food procurement (Shea & Bar-Yosef 1999).

The Jordan valley sites include core and flake technology and bifaces. The Erq el-Ahmar artifacts, which are similarly aged, or slightly older, than those at Dmanisi are likewise flake and core tools. The somewhat-younger 'Ubeidiya assemblages include flake and core tools in proportions most similar to a Developed Oldowan, as well as Acheulean influences including bifaces such as handaxes and picks, particularly in the upper levels of cycle FI (Bar-Yosef, Goren-Inbar 1993). The 'Ubeidiya tools include spheroids also, which are lacking at Dmanisi.

Far East

Early stone tool assemblages are rare in Indonesia and hominins and stone tools have yet to be found in association with one another. However, archaeologists have found some stone tools in the Grenzbank (boundary between the Sangiran and Bapang Formations) and in the Bapang Formation of the Sangiran Dome (Sémah et al. 1992, Simanjuntak 2001). Stone tools have been recovered also from the Upper Pleistocene deposits at Sambungmacan (Jacob et al. 1978). These tools typically represent either flakes or flaked cores, and retouched flakes represent a very small percentage of those recovered. Thus, although little behavioral data is afforded by these finds, one can parsimoniously conclude the *H. erectus* reached Java with an Oldowan-like tool kit.

WHO LEFT AFRICA? TAXONOMY OF HOMININS OUTSIDE AFRICA

Given an earliest Pleistocene age for the first hominins outside Africa, the first hominins to leave Africa could have been any species of early *Homo* or perhaps an australopithecine. Several authors suggest that a less-derived hominin than *H. erectus*, or a more primitive version of *H. erectus*, may have been the first to disperse from Africa, and thus multiple taxa may be found in the early non-African hominin faunas (e.g., Robnson 1953; Sartono 1981, Orban-Segebarth & Procureur

1983, Howell 1994, Tyler et al. 1995, Dennell 2003). Specific assertions that an australopithecine may be present in the early assemblages cannot be supported on the basis of current dentognathic evidence (Kramer 1994). However, the question of multiple taxa of *Homo* remains more problematic (e.g., Howell 1994). Thus, the morphological attributes of the earliest non-African hominins are of critical interest.

East African localities at Koobi Fora, Kenya, and Olduvai Gorge, Tanzania, provide the most abundant sources of early *Homo* skeletal material that may provide a source of dispersing hominins and appropriate comparisons for early Pleistocene hominins on other continents. Olduvai Gorge has yielded a number of early Pleistocene *Homo* fossils from Beds I and II (e.g., Leakey et al. 1964, Leakey 1971, Tobias 1991, Blumenshine et al. 2003). However, only one *H. erectus* specimen, Olduvai Hominid (OH) 9 from upper Bed II, dates to the early Pleistocene (≥ 1.47 Ma based on single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ age determinations for the overlying tuff III-1; Manega 1993). Alternatively, numerous *H. erectus* fossils from the Turkana Basin, Kenya, range from possibly as much as 1.9 Ma to younger than 1.45 Ma (Wood 1991a, Brown & McDougall 1993, Walker & Leakey 1993, Leakey et al. 2003). The most remarkable of these are the relatively complete crania (KNM-ER 3733, 3883, and 42,700 at 1.78, 1.6, and 1.55 Ma, respectively) and the KNM-WT 15000 skeleton from West Turkana (~ 1.5 Ma). Earlier fragmentary Koobi Fora cranial remains, including the occipital fragment KNM-ER 2598 (1.88–1.9 Ma) and KNM-ER 3732 (1.89 Ma), and large-bodied postcranial remains (e.g., KNM-ER 3228 at 1.95 Ma) hint at an even earlier presence of *H. erectus*.

Early African members of *H. erectus* (e.g., KNM-ER 3733, 3883, KNM-WT 15000, and OH 9) are separable from earlier members of genus *Homo* on the basis of characteristics of the cranium including development of a supraorbital torus and posttoral gutter, an occipital torus (restricted in the African fossils to the middle third of the occipital), more angular cranial vaults, and occasionally cranial keeling along the sagittal (or metopic) suture (Table 3; Antón 2003). Early *H. erectus* also have somewhat enlarged cranial capacities; larger body sizes, based on postcranial remains; and elongated lower limbs (Table 4; McHenry and Coffing, 2000). However, it is relevant to note that recent discoveries at Ileret, Kenya, appear to extend the lower end of the size range of *H. erectus* (Leakey et al. 2003).

Hominins from Georgia

The Dmanisi material is particularly similar to African members of the species *H. erectus* (Gabunia & Vekua 1994; Rosas et al., 1998; Gabunia et al. 2000a,b; Vekua et al. 2002), and particularly to those from Kenya. Specific similarities include especially facial and dental characteristics (Antón 2003). However, the small cranial capacities (e.g., < 700 cc) of recent discoveries (D2700) have again raised the specter of a pre-erectus disperser (Dennell 2003). These fossils, along with the 1.5 Ma KNM-ER 42700 from Ileret, question the relationship between

TABLE 3 Comparisons of some traits in earliest *H. erectus* and nonerectus *Homo*. SAG, sagittal; SOT, supraorbital torus; SO, supraorbital; MMR, mesial marginal ridge

	Vault	Face	Dentition	Postcrania
Early Non-erectus <i>Homo</i>	500–700 cc vault rounded, keeling absent, thin-walled, mastoids in nuchal plane	No or small SOT No or restricted SO gutter	Broad molars Multi-rooted premolars	130–149 cm tall Variably platymeric
EARLIEST <i>H. erectus</i> East Africa (1.5–1.8 Ma, or more)	700–1067 cc Low and angular in sag view Broad posteriorly Moderate or no keeling Moderately thick walls	Moderate to large SOT Straight SO gutter Broad pyriform ap. Flat infraorbital Paranasal pillars Narrow extramolar sulcus Variable corpus height	Narrow, long molars No accessory cusps Low MMRs Multi/single-rooted premolars	147–173 cm tall platymeric femur (midshaft & higher) Thick cortical bone Acetabulocrystal buttress strong
Georgia (~1.7 Ma)	650–780 cc Low and angular in sag view Broad posteriorly Incipient or no keeling Moderately thick walls	Moderate SOT Straight SO gutter Broad pyriform ap Flat infraorbital Paranasal pillars Narrow extramolar sulcus	Broad, long molars Accessory cusps Low MMRs Single-rooted premolars	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 ap. Convex infraorbital No paranasal pillars Tall mandibular corpus	Broad, long molars (very large) Accessory cusps High MMRs Multi/single-rooted premolars	?

TABLE 4 Long bone lengths, stature, and body-weight estimates^a

Specimen	GeolAge Ma	Length (mm)	Midshaft AP (mm)	Midshaft ML (mm)	Stature (cm)	Weight (kg)
Femora		Bicondylar				
Early <i>Homo</i> Koobi Fora						
KNM-ER 1472	1.89	400	25.1	26.4	149	47
KNM-ER 1481	1.89	395	22.4	25.6	147	46
KNM-ER 3728	1.89	390	20.1	24.7	145	45
African <i>Homo erectus</i>						
KNM-ER 736	1.70	500	36.1	37.7	180	62
KNM-ER 737	1.60	440	27.1	32.4	160	52
KNM-ER 1808	1.69	480	—	—	173	59
KNM-ER 15000 ^b	1.53	429 at death	24.5	24.3	159 at death	52
Third metatarsal		Maximum				
Dmanisi D2021	1.7	60	—	—	148	46

^aData are from H. McHenry (personal communication); McHenry & Coffing (2000); Walker & Leakey (1993); Gabunia et al. (2000c).

^bTo be conservative, subadult stature and body weights for KNM-WT 15,000 are used instead of the larger values projected had he lived to adulthood.

absolute size and shape-related features. Their interpretation is further complicated by the subadult age of both fossils; the sphen-occipital synchondrosis is unfused in D2700 (Vekua et al. 2002) and partially fused in KNM-ER 42700 (Leakey et al. 2003). KNM-ER 42700, despite its small size, exhibits classic *H. erectus* characters, including characters often thought to be limited to Asian *H. erectus* such as cranial keels (Leakey et al. 2003).

Alternatively, investigators have argued Dmanisi (D2700) 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). Though recognizing D2700's small size, the describers of D2700 are quite clear in their attribution of the fossil to *H. erectus* (Vekua et al. 2002); however, others have used D2700 to suggest *H. habilis* as a possible early disperser (Dennell 2003). Although the D2700 specimen is quite small, it has a wide cranial base and an open sphen-occipital synchondrosis coupled with a narrow face. These features suggest that the D2700 face had significant growth still to achieve, much of which would have been in width of the lateral face and in facial height. Thus, contra Dennell (2003), the appearance of the face in D2700 is not particularly useful in making arguments for a pre-erectus disperser. That said, the phyletic relationships among *H. erectus* and various possible nonerectus *Homo* taxa in Africa currently are quite muddled and require substantial revisitation (e.g., Stringer 1986, Wood & Collard 1999, Blumenshine et al. 2003).

As previously mentioned, the Dmanisi hominins are unexpectedly small for their cranial anatomy. On the basis of the metatarsal (D2021), the postcranial

skeleton also appears to have been relatively small in comparison with African *H. erectus* (Gabunia et al. 2000c). 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* (Table 4; Gabunia et al. 2000c) and more similar in size to the earlier, probably nonerectus, *Homo* from Koobi Fora that, owing to a lack of association with relevant cranial remains, are assigned only to *Homo* sp.

Hominins from Indonesia

Most previous work concludes that the earliest hominins in Indonesia are *H. erectus* (e.g., Rightmire 1993; Antón 1997, 2003; Grimaud-Hervé 2001). The very earliest Indonesian crania from the Sangiran (Pucangan) Formation are few in number and often badly deformed postmortem. The best preserved of these, Sangiran 4, exhibits morphology typical of Asian *H. erectus* (Table 3). Those crania dating to between 0.9 and 1.5 Ma are more numerous and less deformed and likewise exhibit morphology typical of Asian *H. erectus*. Estimates of size must rely on cranial robusticity and capacity, both of which are substantial in the earliest hominins. Cranial capacity is about 900 cc, and most of the earliest cranial and mandibular remains are, if anything, hyperrobust (Wolpoff 1999, Antón 2003). The entire Sangiran assemblage, however, shows substantial cranial size variation. Early Indonesian postcrania are currently unavailable for size estimates. Whereas some specific characters appear to unite earliest western Asian and Javan hominins, they each also show characters perhaps indicative of endemism and/or different source populations (Antón & Indriati 2002).

WHY DID THEY LEAVE? MODELS OF DISPERSAL

The early Pleistocene hominin dispersal(s) contrast the range retraction undergone by other k-selected apes throughout the Pliocene and recent times (Fleagle 1998). Thus hominins must have found a way around the usual restrictions placed on primates with their life-history variables (Cachel & Harris 1998, Jablonski et al. 2000, Antón et al. 2002). The foraging strategy associated with the Oldowan Industry and changes in body plan may have facilitated hominin dispersal (Shipman & Walker 1989, Leonard & Robertson 2000, Antón et al. 2002). Modeling the effects of these changes remains speculative but can draw from knowledge of the extant world in a number of ways.

Energetics, Body Size, and Home Range

Modeling the energetic requirements of ancient hominins begins with physical evidence of the fossil record including measures of brain size, body size, and proportions. Such models have been particularly useful in defining physiologically reasonable scenarios (Leonard & Robertson 2000, Sorensen & Leonard 2001).

TABLE 5 Estimated body weight and home range size for fossil hominins

Species	Avg Wt ^a (kg)	HR _r -Ape ^b (ha)	HR _r -Human ^b (ha)
<i>A. afarensis</i>	37.0	40	247
<i>A. africanus</i>	35.5	38	234
<i>A. robustus</i>	36.1	39	239
<i>A. boisei</i>	44.3	51	316
<i>H. habilis</i>	41.6	47	290
<i>H. erectus</i>	57.7	73	452
Large Koobi Fora early <i>Homo</i>	46.0	53	331
Dmanisi 2021	46.0	53	331
African <i>H. erectus</i> & Dmanisi	54.2	66	413
African <i>H. erectus</i> , Dmanisi, & Early Koobi Fora <i>Homo</i>	51.0	61	380
<i>H. sapiens</i>	59.5	76	471

^aAverage body weights for Australopithecines, *H. habilis*, *H. erectus*, and *H. sapiens* after McHenry (1992, 1994). Sample composition for body-weight estimates for Large Koobi Fora early *Homo*, Dmanisi 2021 African *H. erectus* and Dmanisi and African *H. erectus*, Dmanisi and Koobi Fora calculated from specimens and weights listed in Table 4.

^bHome range estimates based on the equation $\log HR = 1.36(\log \text{Weight}) + 0.009(\text{Diet Quality}) - 2.01$, as derived by Leonard & Robertson (2000). HR_r-Ape assumes a diet quality equal to the average for modern apes (DQ = 164), and for HR_r-Human a diet quality at the low end of the range of modern tropical human foragers (DQ = 252).

The postcranial fossils of *H. erectus* are, in general, relatively larger than those of earlier hominins (e.g., McHenry 1992, 1994; Ruff & Walker 1993; Aiello & Wood 1994; Kappelman 1996; McHenry & Coffing 2000) (Tables 4, 5). Stature estimates range between 148 and 185 cm for known *H. erectus* specimens with related body-mass estimates of between 46 and 68 kg if all geographic areas and times are included (Antón 2003). In contrast, estimates for *H. habilis* (*sensu lato*) overlap with *Australopithecus* with 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), although sample sizes are extremely small. Body size increase itself is often considered a response to shifts in climate from moister to drier conditions and to more patchily distributed resources in East Africa around and slightly before the origin of *H. erectus* (e.g., Aiello & Key 2002, Antón et al. 2002).

Recent work allows the estimation of home range (HR) size from body-weight and diet-quality estimates and has suggested a substantial increase in HR size between early *Homo* and *H. erectus* (Table 5) (Leonard & Robertson 2000). However, as noted, apparently the range of body sizes is greater than paleoanthropologists have appreciated in the past. Large postcranial remains appear at Koobi Fora as early as 1.95 Ma (e.g., ilium KNM-ER 3228), whereas small *H. erectus* are present at Dmanisi and at Ileret Kenya (KNM-ER 42700 at 1.55 Ma; Leakey et al. 2003).

Recalculations of HR estimates, considering the recent discovery of smaller-bodied *H. erectus*, are reported in Table 5. These recalculations suggest that even if all of the largish postcrania older than 1.8 Ma are included in *H. erectus* (a step many are understandably unwilling to take; see Trinkaus 1984), average HR size is still larger in *H. erectus* than in earlier *Homo* (380 versus 290 ha, respectively). If only the Dmanisi remains are included with *H. erectus*, arguably a more reasonable position given cranial anatomy, then the differences between average *H. erectus* HR and that of earlier *Homo* are even more substantial (413 versus 290 ha, respectively).

Differences in estimated body and brain size between *H. erectus* and *Australopithecus* suggest substantially greater expenditures of total resting energy to maintain brain function in the former than in the latter (Leonard & Robertson 1992, 1994, 1996, 1997); approximately 17% of total resting energy (or about 260 Kcal) in *H. erectus* and only 11% in *Australopithecus* is devoted to brain support. These differences suggest that *H. erectus* must have had a more energy-rich diet than had earlier hominins. The smaller differences between early *Homo* and *H. erectus* as calculated above suggest similar, if less significant, foraging shifts.

Such an enriched diet might include animal meat and marrow (Walker et al. 1982, Shipman & Walker 1989, Leonard & Robertson 2000, Antón et al. 2002), honey (Skinner 1991; but see Skinner et al. 1995), or underground tubers (e.g., Wrangham et al. 1999). Underground tubers require fire to release their nutritional stores and thus may have been of limited use until well after the origin of *H. erectus*, given the scant evidence for early controlled fire (see Brain & Sillen 1988, Bellomo 1994). Alternatively, there is abundant archaeological evidence for meat consumption at hominin sites including butchered animal remains and associated stone tool assemblages (e.g., Leakey 1971, Shipman 1986, Blumenschine et al. 1994). The sporadic consumption of meat by some extant primates (Stanford 2001) and earlier hominins (de Heinzelin 1999) suggests that increasing reliance on animal resources was a feasible, although perhaps not an exclusive, means of increasing diet quality (Shipman & Walker 1989; Antón et al. 2001, 2002). Further support of meat consumption comes from tapeworm phylogenies that suggest the two most closely related, human-specific species (*Taenia saginata* and *T. asiatica*) diverged sometime between 0.78 ka and 1.7 Ma (Hoberg et al. 2001), which suggests that a human host (*H. erectus*) was infected, presumably by consuming the flesh of an infected animal, during this time period.

Ancient Dispersals

Another line of recent work suggests that the geographic dispersal of *Homo* from Africa is intimately tied to the shifts in body size and foraging strategy discussed above. Estimates of the rate of hominin dispersal have been calculated using diffusion coefficients (D) based on site locations and ages from the fossil record (Leonard & Robertson 2000; Antón et al. 2001, 2002). A subset of these estimates are reported in Table 6. D values suggest rapid dispersal rates from Africa that contrast with ancient dispersals made by other primates. By analogy, ecological parameters that could have promoted the quick hominin dispersal include larger

TABLE 6 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 ^a (z)	Diffusion coefficient ^b (D)
RECENT DISPERSALS ^c				
<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 ^c
ANCIENT DISPERSALS				
<i>Macaca</i> sp. (Europe to Asia)	0.05	1.5 Ma–10 ka	3135	0.00,002–0.5
<i>Theropithecus darti</i> (to South Africa)	0.05	0.7 Ma–10 ka	2200	0.00,004–0.2
<i>Homo erectus</i> s.l. (to Indonesia)	0.01–0.015	200–10 ka	4380	0.01–4.8
<i>Homo erectus</i> s.l. (to Georgia)	0.01–0.015	100–10 ka	2665	0.02–1.8

^aZ values are calculated as the square root of the linear distance between localities multiplied by a transect 1200 km wide.

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

^cData from Williamson (1996).

^dPredicted values and observed historical spread are significantly lower than for other dispersing mammals, presumably because of ecological interaction between red and gray squirrels.

home-range sizes (Ehrlich 1989), a shift in foraging behavior (Ehrlich 1989, Shipman & Walker 1989, Leonard & Robertson 2000), and a somewhat slower pattern of dispersal than was the case for fossil carnivores (Antón et al. 2001, 2002). These parameters are similar to the shifts inferred above from increasing energetic requirements of increasing body and brain size, although they are based on independent datasets (Antón et al. 2001, 2002).

How Many Dispersals Were There?

The title of this review implies multiple early dispersals. Over the past decade increasing evidence has accumulated to suggest that hominins began dispersing from Africa in the early Pleistocene, a case we have summarized here. However, this evidence comes from only a few localities outside Africa. The tendency is to “connect the dots” between these localities with a single arrow and thus to imply that early dispersal was a single, unidirectional, always-successful event. From these few data points we try to sort out the types of hominins, nonhominin fauna, and toolkits that left Africa, as well as to discern the probable catalysts, if not the causes, of this dispersal. But this approach may lead us a bit astray.

Given modern mammalian dispersal and migration patterns it is likely that multiple dispersals of small groups occurred periodically, that the fossil hominins we

currently know in the early Pleistocene outside of Africa come from slightly different source populations, that some of those that left stayed in localities whereas others moved further on, and that back migrations of genes or organisms were possible. It is also likely that, although the broad ecological parameters we outline, including shifts in body size and foraging strategy, were partly behind these dispersals, other less-logical or deliberate factors, such as curiosity, were involved as well. Certainly, if we look at the decision-making processes involved in modern human migrations we must also allow for any number of idiosyncratic causes leading to dispersal.

It is also plausible that the various pulses of dispersal were controlled in part by cyclic Pleistocene climate, waxing and waning between glacial and interglacial periods. Although less affected in equatorial regions, certain corridors or migratory paths may have been differentially affected owing to more northern latitude or elevation. Given the lack of sufficient hard data, these scenarios can only be speculative, being derived from temporal correlations with global Pleistocene climatic patterns. We are, however, unconvinced by Dennell's (2003) argument that the current early Pleistocene record of hominins outside Africa is any better read as "evidence of absence" (i.e., quite sporadic or episodic dispersal events) than it is as "absence of evidence" owing to insufficient investigation of early Pleistocene localities in large parts of the old world.

SUMMARY

In the past decade, a wealth of new data has supported a longer chronology of hominin presence outside Africa beginning at ~ 1.6 – 1.8 Ma (e.g., Swisher et al. 1994, Gabunia et al. 2000a, Larick et al. 2001, Vekua et al. 2002). Collectively, these data indicate an early Pleistocene date for the initial dispersal(s) from Africa of a hominin carrying a core and flake tool technology. The cranial anatomy of these hominins indicates that the source populations for these hominins were those of early African *H. erectus*. Although the resolution of the fossil record of the early ex-African sites could be interpreted as a single wave of dispersal, the anatomy of the hominin fossils outside of Africa and dispersing patterns of extant animals are suggestive of several source populations of *H. erectus* migrating at slightly different times. Nonetheless, increasing body size and home range size are likely responses to changing ecological conditions at the origin of *H. erectus* and are perhaps part of a web of "eco-morphological" factors that fueled the rapid expansion of *H. erectus* from Africa into Asia in the early Pleistocene.

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