Chapter 5

Behavioral and Environmental Background to 'Out-of-Africa I' and the Arrival of *Homo erectus* in East Asia

Richard Potts and Robin Teague

Abstract Current evidence of hominin fossils and artifacts in China and Indonesia points to the arrival and persistence of the genus *Homo* in East Asia by 1.7 million years ago (Ma). By at least 1.66 Ma, East Asian hominins had spread across a wide range of biotic and climatic zones, spanning 7°S–40°N on the basis of well-constrained age data from the Nihewan and Yuanmou basins, China, and Sangiran, Indonesia. Archeological assemblages and fragmentary hominin morphology show strong similarities with African Oldowan hominin toolmakers and early *Homo erectus*, although the taxonomic status of the oldest known Asian hominins is not yet securely established. Despite this apparent derivation of East Asian from African hominins, an initial comparison of large mammal faunas offers little evidence of 'fellow travelers', i.e., a set of African mammalian species that co-dispersed with *Homo* to East Asia. We offer three hypotheses to account for the existing data: (1) unique hominin dispersal, in which no other African mammals were involved; (2) African fellow travelers, in which *Homo* and a small number of other mammals reached western Eurasia, yet hominins dispersed independently to more distant regions; and (3) relay dispersal, in which *Homo* always dispersed as part of an ecological community but in association with a different set of mammalian species from one region to another.

Keywords Adaptability • East Asia • Geographic dispersal • *Homo erectus* • Nihewan • Paleoenvironment • Plio-Pleistocene fauna • Yuanmou

Introduction

This paper explores several datasets and their implications relevant to the spread of earliest Pleistocene hominins to eastern Asia. We first examine the African setting of stone toolmakers between ~2.6 and 1.7 million years ago (Ma), which is the era before and immediately subsequent to the first appearance datum (FAD) of hominins outside of Africa. We have assembled a range of information bearing on:

- The mobility of early human toolmakers (e.g., archeological stone source-to-site distances).
- The paleogeographic diversity of African archeological sites, which relates to constraints on the mobility of Oldowan toolmakers and when these began to be lifted.
- The adaptability of those toolmakers to habitat variability, which we consider an important factor in the eventual dispersal of African hominins to novel environments in eastern Asia.

Initial comparison of mammalian fossil data and archeological occurrences from East Africa, China, and intervening regions leads us to identify several hypotheses regarding the original timing, faunal context, and routes of the earliest dispersal out of Africa. Age constraints on the earliest Pleistocene archeological sites in China provide the oldest definitive evidence of stone toolmaking and animal processing in eastern Asia. These new findings from the Yuanmou and Nihewan basins also enable us to characterize the environments encountered by the first hominins to arrive in this region of the world, by ~1.7 Ma. We end by discussing several ramifications of early *Homo erectus*' long-distance expansion, mainly concerning the range of morphological variation in this species and its adaptability to novel habitats.

The African Context for 'Out-of-Africa I'

The mobility of Late Pliocene hominins can be assessed using at least two lines of evidence – first, skeletal morphology and, second, archeological data on rock transport distances

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and the spread of stone tools to new paleogeographic zones. Archeological data presented in this section help to assess the adaptability of African Oldowan hominins, and ultimately relates to their ability to disperse out of Africa and into novel habitats of East Asia.

Morphological Indicators of Terrestrial Mobility

A change in limb proportions evident in Plio-Pleistocene hominins is pertinent to the question of long distance dispersal. Analysis of limb bones ~2.5 Ma from the Middle Awash, Ethiopia, suggests that elongation of the femur occurred prior to shortening of the forearm in at least one lineage of late Pliocene hominins (Asfaw et al. 1999). If confirmed by further discoveries, this finding implies that an important shift in limb proportions (at least compared to *A. afarensis*) was initiated by ~2.5 Ma. *H. habilis* may also have had a human-like, elongated femur coupled with an ape-like, long forearm. According to Haeusler and McHenry's (2004) analysis of the fragmentary partial skeletons OH 62 and KNM-ER 3735 (~1.8–1.9 Ma), *H. habilis* exhibited a modern human pattern of limb shaft proportions, with an elongated hindlimb relative to *A. afarensis* and *A. africanus*, yet with similar brachial proportions to these taxa. If this finding is also borne out by future studies, the elongated hindlimb of *H. habilis* suggests similarities to *H. erectus* that may imply an anatomical commitment to terrestrial bipedality over longer distances than in early *Australopithecus*.

An even greater commitment to long distance terrestrial locomotion is suggested in the ruggedly-built innominate KNM ER-3228, thought to date to ~1.9 Ma, and is further evidenced by femora assigned to early African *H. erectus* at ~1.7 Ma (Ruff and Walker 1993) and by the overall skeletal proportions of this species (Walker and Leakey 1993).

Archeological Measures of Mobility: Lifting of Landscape Constraints

Tracing the sources of rocks found in archeological sites provides a more direct line of evidence regarding mobility. Although rock source-to-site distances offer a very limited estimate of actual home range, the development of longer transport distances may signal greater mobility associated with the dispersal of Oldowan toolmakers. The diversity of paleogeographic settings in which stone artifact sites occur is another important measure. It indicates the degree to which the ranging distances of the toolmakers were tethered to, or decoupled from, particular lithic, water, or other resources that occurred in specific depositional environments. Key observations in this regard are as follows:

- The oldest known archeological sites in the Middle Awash, ~2.6 Ma at Gona, Ethiopia, and in the Turkana Basin (West Turkana) ~2.3 Ma, were situated only tens to a few hundreds of meters away from paleo-conglomerates where the source rocks for making tools were located (Semaw et al. 2003; Kibunjia 1994; Delagnes and Roche 2005). At Turkana, archeological sites in the Late Pliocene are quite rare, and the sites are distinctly limited to places where marginal drainages intersected the axial drainage (Proto-Omo) (Rogers et al. 1994).
- Stone tools excavated from Kanjera South, ~2.1 Ma, were made of rocks obtainable from conglomerate sources up to 12 km away from the archeological sites, although most rock sources occurred within shorter distances (Plummer 2004; Braun et al. 2005; Braun 2006).
- In Bed I and lower Bed II Olduvai, ~1.85–1.77 Ma, all published sites occur within about 10 km of the most distant rock source (Kelogi gneiss). Yet all such sites and rock sources were confined to the lake margin lithofacies, which suggests a strong tethering of stone-tool activities to the lake margin zone until about 1.77 Ma (Hay 1976).
- Data for the interval 1.77–1.50 Ma, available chiefly from Bed II Olduvai and the Okote Member, East Turkana, show substantial paleogeographic diversification in the location of archeological sites for the first time in both basins. At Olduvai, hominin tool activities were situated in both the lake-margin and fluvial facies; these sites also record the first use of raw materials (e.g., Engelosin phonolite) obtainable beyond the lake margin zone (Hay 1976). At Turkana, stone tool sites occurred in the channels and on proximal and distal floodplains of the marginal drainages away from the axial river system (Rogers et al. 1994). However, the maximum transport distance of stone remains the same, with all lithic sources available within 12–15 km of the archeological sites.
- The next available East Africa dataset in the temporal sequence comes from Member 1 Olorgesailie, Kenya, ~0.99 Ma. Our detailed study of the Olorgesailie region shows that 98% of the stone tools were made from rocks obtainable within about 5 km; however, 2% were made from sources up to about 46 km away (Isaac 1977; Potts et al. 1999; Noll 2000). This fourfold increase in maximum transport distance represents a notable change in the mobility of hominin groups and the decoupling of their activities from highly localized landscape features.

Adaptability to Novel Environments

The spread of early humans to eastern Asia meant that the dispersing hominins faced new climatic and biogeographic zones. This encounter with novel landscapes and adaptive settings almost certainly placed the adaptability of those populations at a premium. The degree of adaptability of pre-existing populations of African Plio-Pleistocene hominins is thus interesting to measure, and one way to do this is by examining the persistence of archeological and fossil material across stratigraphic boundaries that mark substantial changes in environment. The lengthy stratigraphic and paleoanthropological records of the Koobi Fora and Olduvai regions are particularly helpful in this regard.

Figure 5.1 synthesizes the stratigraphic, environmental, and archeological record of the Koobi Fora region, an exercise that has benefited greatly from Craig Feibel's input (see also Brown and Feibel 1991). Our main observations are as follows:

- The Turkana basin was subject to frequent landscape remodeling due to (1) alternation between an expanded lake and widespread fluvial conditions on a precessional cycle timescale (19–23 kyr) and (2) variability in river conditions due to the effects of volcanic ash input. According to Feibel's reconstructions, a large meandering river became clogged with volcanic ash, causing the axial river system to become divided into a complex braided stream system, which eventually recovered its original meandering state (Rogers et al. 1994).
- The sporadic occurrence of archeological sites over the time period of 2.3–1.7 Ma prevents evaluation of the persistence of toolmakers across paleoenvironmental shifts.
- By the oldest part of the Okote Member, ~1.7 Ma, when environmental fluctuations were accentuated by frequent volcanic input (Feibel 1997), there is evidence that the stone toolmakers were generally able to persist through episodic disruptions of the landscape. As shown in Fig. 5.1, archeological sites greatly increase in number at this time, and the stratigraphic persistence of stone tools across intervals of major remodeling of the landscape is considerably greater than in earlier periods.

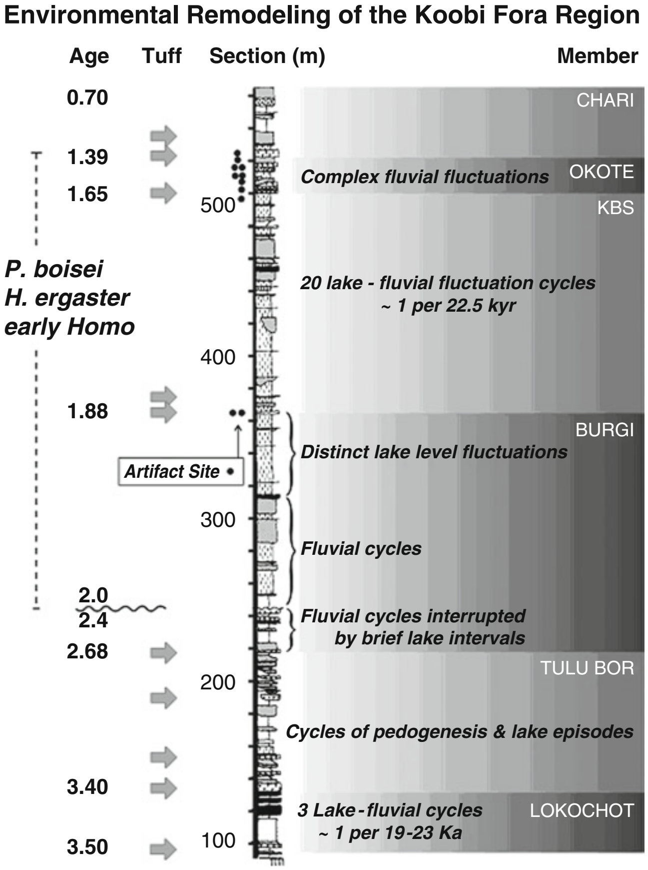

Fig. 5.1 Composite stratigraphic section of the Koobi Fora Formation, Turkana Basin, northern Kenya (based on Brown and Feibel 1991). *Arrows* indicate important tephra layers. Artifact sites are indicated by the *dots* along the *left* margin of the section, and show the stratigraphic concentration of archeological sites after ~1.7 Ma. Early hominin fossils occur throughout the section from 2.0 to 1.4 Ma. Each portion of the section is characterized by a combination of climatic and tectonically-induced environmental variability

The record from Olduvai Gorge shows the persistence of hominin toolmakers through a variety of landscape, vegetation and climatic changes (e.g., Hay 1976; Bonnefille and Riollet 1980; Cerling and Hay 1986). The stratigraphic interval from 1.9 to 1.77 Ma (Fig. 5.2) shows three significant environmental transitions: Initially wet, marshy and wooded conditions gave way to arid, open vegetation, followed by the return of moist, wooded habitats, and then followed by very dry conditions with sparse vegetation in the Lemuta Member. One major environmental shift took place every 17–37 kyr, with the Lemuta Member aridity lasting approximately 20–50 kyr (Hay 1976). Although stone tools are present throughout the sequence, the sites and lithic source rocks were evidently confined to the lake margin zone.

After this time, the broad, perennial lake intermittently broke up into a series of ponds and marshes in an arid landscape (Hay 1976). Hominin sites outside the lake margin zone occurred for the first time, indicating that toolmakers were no longer tethered to this particular environmental setting. It appears that a limited repertoire of tool activities confined to specific landscape features (evident prior to 1.77 Ma) was replaced by a more diverse array of activities able to accommodate to a less stable landscape (Potts et al. 1999).

Overall, the geographic and ecological constraints that shaped and tethered the activities of Oldowan toolmakers in East Africa apparently began to be relaxed by about the upper Olduvai-Matuyama transition at 1.78–1.77 Ma, or slightly thereafter. Evidence of the first definite appearance of hominins outside of Africa, and their spread to East Asia, now appears to be consistent with this date.

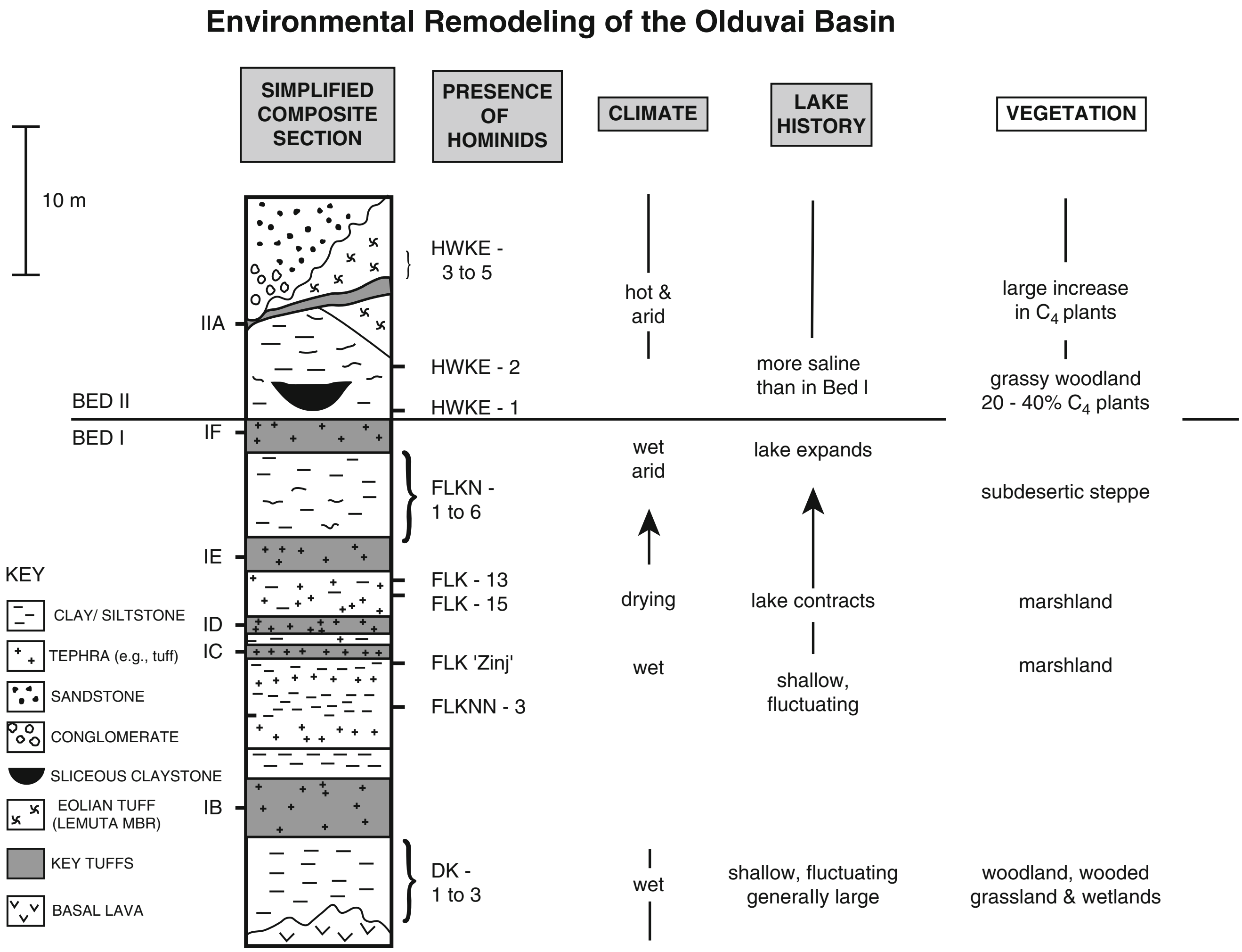

Fig. 5.2 Simplified stratigraphic section of Bed I and lower Bed II Olduvai, northern Tanzania. Also shown are the names of archeological sites, which illustrate the continuous presence of hominin toolmakers throughout the sequence, and three lines of evidence regarding environmental change

Arrival in East Asia: Evidence from Yuanmou and Nihewan, China

A team lead by Zhu Rixiang (Institute of Geology and Geophysics, Beijing) and R. Potts has undertaken a detailed re-investigation of the magnetostratigraphic ages of potentially the oldest artifacts and fossil hominins in China. This work has yielded age estimates of ~1.34 to ~1.71 Ma for the oldest archeological sites and hominin fossils in North and South China (Zhu et al. 2001, 2003, 2004, 2008).

As summarized in Fig. 5.3, the sites of Xihoudu, Gongwangling, and Donggutuo are dated between ~1.3 and 1.1 Ma, and reflect solid evidence of hominin toolmakers in North China during that interval. Dates from the older sediments of the Nihewan basin extend the known time range of hominin stone tools and animal-processing activities in North China back to ~1.36 Ma at the Xiaochangliang site, and ~1.34–1.66 Ma for four archeological levels at the site of Majuangou. Recent work at Yuanmou, South China, has resulted in the oldest estimated ages for definite stone artifacts and hominin fossils (two upper central incisors) in China, at ~1.71–1.70 Ma. The claim of older hominin evidence from Longgupo, China, is based on published fossils (Huang et al. 1995) that are increasingly viewed as an ape possibly related to *Lufengpithecus*, which is known from the Late Miocene of South China (e.g., Schwartz and Tattersall 1996; Wu 2000; Ciochon 2010). Stone artifacts have also been recovered from Longgupo (see Hou and Zhao 2010).

Yuanmou Basin Hominin Fossils and Stone Tools

The upper central incisors of what is probably a single individual of *H. erectus* and four quartzite artifacts were

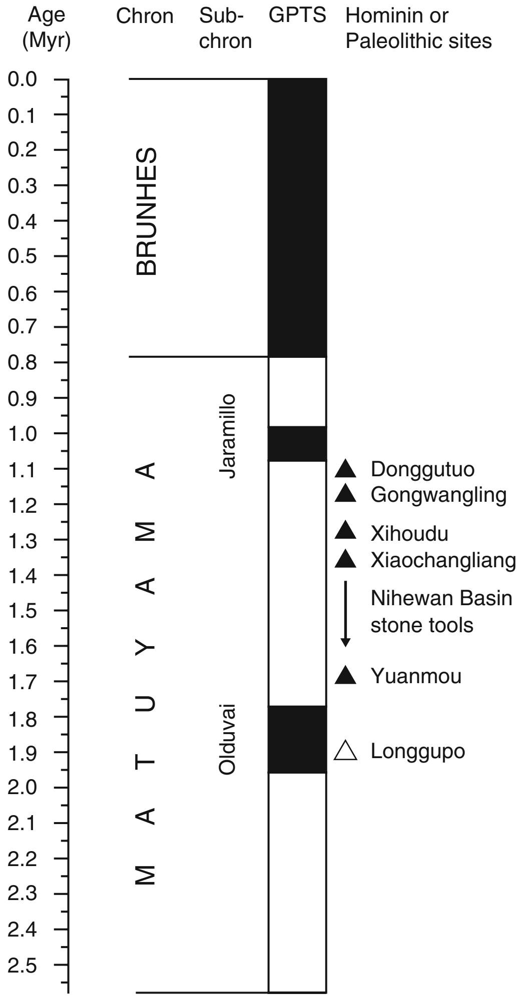

Fig. 5.3 Age estimates for the oldest Chinese paleoanthropological sites, adapted from Zhu et al. (2003). *Filled triangles* indicate sites with tight age constraints; *open triangle* (Longgupo) indicates an uncertain age constraint or the uncertain hominin status of the remains. Further excavations at Xihoudu are needed to re-examine whether its purported stone tools do indeed reflect repetitive, purposeful conchoidal fracture consistent with Oldowan capabilities

recovered in situ in silty-clay sediments within a 4-m-high hill of Member 4 sediments of the Yuanmou Formation (Hu 1973; Wen 1978; Yuan et al. 1984). The assignment of the teeth to hominins, specifically *H. erectus*, is based on observations of multiple investigators (e.g., Hu 1973; Wu and Poirier 1995; Zhu et al. 2008) that the Yuanmou incisors are essentially identical in metrical and qualitative characteristics to later *H. erectus* I^1s from Zhoukoudian. The Yuanmou I^1s also strongly resemble those of KNM-WT 15000 (1.6 million-year-old *H. ergaster*, West Turkana, Kenya) in overall and detailed morphology, including the degree of lingual cervical crown swelling, development of the central pillar (both Yuanmou I^1 crowns, only on the left I^1 of WT 15000), and the degree of enamel wrinkling. The Yuanmou incisors, furthermore, are dissimilar to the I^1 crowns of all extant great apes, especially in the lack of a cervical cingulum, the degree of expansion of the lingual cervical surface, and the overall splaying (or rounded arch) typical in the great apes. In the only definitive fossil ape comparisons possible at present, the mesiodistal and labiolingual dimensions (Yuanmou left I^1: 11.4 and 8.1 mm; right I^1: 11.5 and 8.6 mm) of the Yuanmou incisors fall outside the 95% confidence intervals estimated from the large sample of I^1 crowns of *Lufengpithecus*, a late Miocene ape known from the Yuanmou basin (Liu et al. 2000; Wood and Xu 1991; Zhu et al. 2008).

Based on more recent interpretation of the hominoid gnathic remains from Longgupo (see above), it is valid to wonder whether one or more lineages of poorly documented Plio-Pleistocene, East Asian apes converged in their dental crown morphology with that of early *Homo* in Africa (Wang et al. 2007; Ciochon 2010). The strong match of the Yuanmou incisors with those of even later *H. erectus* – coupled with the presence of artifacts in fine-grained, *in situ* context and indicative of precise stone-on-stone percussion, competent use of striking platform angles, and the production of multiple, overlapping flake scars typical of African Oldowan and slightly later Chinese archeological assemblages (Majuangou, Nihewan basin [Zhu et al. 2004]) – together present reasonably distinct evidence of hominin presence.

A previous publication claimed that the Yuanmou finds had occurred in a magnetostratigraphically normal interval that was likely the Brunhes, implying an age of <790–780 ka for the hominin material (Hyodo et al. 2002). Although it is impossible to determine from the information provided in his publication, the detailed field records show that Hyodo's magnetostratigraphic study sampled the upper 88 m of Yuanmou Member 4 in only six sampling levels, and these samples were from a section that ranged from several kilometers to 600 m away from the discovery site of the hominin fossils and artifacts (Zhu et al. 2008).

The Yuanmou work led by Zhu and Potts from 2003 to 2005 has yielded a far more detailed magnetostratigraphic record, which encompasses parallel sections throughout the entire Yuanmou sequence, including three sections surrounding the original fossiliferous hillside (which was destroyed in the process of excavation). The stratigraphic interval of the hominin finds were 12.7–14.2 m above the upper boundary of the Olduvai subchron, and the entire section of Member 4 represents a continuously aggrading floodplain. Using the range of sedimentation rates for these deposits of 29.1 cm kyr^{-1} to 21.3 cm kyr^{-1} (a relatively consistent rate estimated from various portions of the record between geopolarity boundaries), we estimated that the age of the hominin-bearing stratigraphic interval is ~1.71–1.70 Ma, with ~1.7 Ma as the best approximation of the hominin remains (Zhu et al. 2008). We have made a considerable effort to determine exactly which of the diverse mammalian fossil material is from Yuanmou Member 4, a rich assemblage derived from the same hill as the hominin material. The fauna is entirely consistent with a late Pliocene to early Pleistocene age, and the Yuanmou fauna is constrained to an age of roughly 1.8–1.6 Ma.

On the basis of the combined fossil, archeological, and paleomagnetic evidence, therefore, the teeth and artifacts found together in Member 4 of the Yuanmou Formation comprise, for now, the oldest documented record of associated *Homo* and hominin stone tools in East Asia. Although further survey is needed, it appears that stone artifacts at Yuanmou are rare. In contrast to the situation in the Nihewan basin (see below), the dearth of artifacts at Yuanmou suggests that the toolmakers there depended very little on stone tools or deposited them while merely "passing through" an ephemeral stopping point, rather than "settling in" a region for a substantial period of time.

The age estimate for the Yuanmou teeth and artifacts is only ~50–70 kyr younger than the Dmanisi material, assuming that the latter currently represents, at a maximum age of 1.75–1.77 Ma (Rightmire et al. 2006), the oldest undeniable evidence of hominins outside the African continent. Taking these dates at face value as the first appearance datums (FADs) in western Eurasia and East Asia, and given the direct distance between Dmanisi and Yuanmou of about 6,000 km, a minimum (and highly underestimated) average rate of spread across Asia would have been roughly 1.7–2.4 km per generation (20 years). By comparison, a recent paper considers a "diffusion wave" of "something more than 3 km per generation" as a model for the rapid spread of modern humans during the late Pleistocene (Eswaran et al. 2005).

Two problems exist with any such a calculation for the initial spread of hominins to East Asia. The first is that the hominin FAD error margins for western Eurasia and East Asia must be very large given the very few sites that help constrain the first appearances in these regions. In the case of western Eurasia, Dmanisi is the only relevant site so far, while in eastern Asia, the sites are few even though Yuanmou, Nihewan (Majuangou), and Sangiran all converge on a date of roughly 1.7 Ma. Dennell and Roebroeks (2005; Dennell 2010) caution that there is little firm evidence to show that the hominin dispersal out of Africa occurred at 1.9–1.7 Ma and that an earlier dispersal, possibly involving a species of hominin other than *Homo erectus* or *Homo ergaster*, is possible. The real problem, in fact, is that criteria for signaling a significant geographic expansion have not yet been adequately defined. Such criteria have never been addressed in a statistical sense by Dennell and Roebroeks, or by those who claim that a single, isolated discovery site represents a true first appearance by hominins in a new region of the world. Given the serendipitous nature of discovery and taphonomic factors such as sedimentary burial, fossilization, and erosion, the study of hominin biogeography may be better served by focusing not on isolated discovery sites and dates, but rather on evidence of successful colonization. The oldest appearance of stone tools or hominin fossils in a prolonged stratigraphic sequence of hominin sites, as is evident in Nihewan and Sangiran beginning by 1.66 Ma, may be considered to reflect success in infiltrating a new region. Such evidence signals a far more significant biogeographic and ecological event than is indicated by an isolated discovery in one stratum.

The second problem is that the notion of a direct spread from west to east, as if hominin populations knew where they were going, is flawed. Although dispersal can be defined as the unidirectional movement of an individual away from its birth place (Bullock et al. 2002), long-distance dispersal as part of the evolutionary history of a lineage is generally thought to involve numerous stochastic movements (Hubbell 2001; Nathan 2006). The resulting process of movement, thus, makes the calculation of a lineage's dispersal rate in a single direction based on two endpoints rather misleading.

Nihewan Basin Archeological Sites

The sparse hominin record from Yuanmou contrasts considerably from that in the Nihewan basin. In the Nihewan, the oldest archeological occurrence, Majuangou III, is stratigraphically located 10 m above the upper boundary of the Olduvai subchron, and is one of four stone tool levels uncovered at Majuangou between the Olduvai and the Jaramillo subchrons. Based on a highly consistent average rate of deposition in two parallel sections of predominantly lacustrine sediments, the interpolated ages of the four levels are 1.32, 1.55, 1.64, and 1.66 Ma (Zhu et al. 2004).

The significance of the Majuangou and Xiaochangliang archeological sites is as follows:

- The stone tool assemblages are consistent with African Oldowan technology, both in terms of tool types and approaches to stone flaking. Each of the Nihewan assemblages is readily divided into flakes, flaked pieces, and hammerstones; the flaked pieces can be placed into artifact categories such as chopper, scraper, and polyhedron that are distinctive of African Plio-Pleistocene stone tool assemblages. The main differences between the Nihewan artifacts and the Oldowan of East Africa can be explained by differences in the initial form of the raw material. The Nihewan cores were chipped from angular fragments of Triassic basement rock, and thus differ from typical choppers and other core forms of the East African Oldowan, which are generally made from rounded cobbles.
- Fractured animal bones damaged by stone tools are precisely associated with the stone tools at Majuangou III (MJG-III). Although some faunal remains occur in each of

the archeological levels at Majuangou and Xiaochangliang, mammalian bones ranging in size from deer to elephant are abundant at MJG-III and correspond spatially and stratigraphically exactly to the distribution of the stone artifacts. The animal remains accumulated at the site include horse *Equus sanmeniensis*, deer *Cervus* sp., elephant *Elephas* sp., bovid *Gazella* sp., and rhinoceros *Coelodonta antiquitatis*. Both the artifacts and faunal remains occur in fine-grained silty clay associated with preserved aquatic plants, which together indicate a low-energy lake margin or marsh environment. Most importantly, the animal bones show evidence of tool percussion marks indicative of marrow extraction. Surface marks are also very abundant; while some of these are very likely butchery marks, the overwhelming proportion appear to have been caused by animal trampling, which hinders the definitive recognition of cut marks. Nonetheless, evidence of marrow processing, the exact association with stone tools, and the body size and taxonomic diversity of mammals transported to the site, all represent strong similarities to the early archeological record of East Africa. The Nihewan toolmakers gained access to animal tissues in ways that suggest continuities with the Late Pliocene and Early Pleistocene Oldowan hominins of Africa.

- The stratigraphic recurrence of stone artifacts suggests frequent or continuous occupation of the Nihewan basin. In contrast to the one layer of hominin remains currently known so far in the Yuanmou Basin, the stone tools present in multiple stratigraphic horizons at Majuangou – corresponding to intervals of lake-margin sediments in a mostly lacustrine sequence – suggest that the Nihewan was an area of consistent hominin occupation for a long period. The density of archeological remains within sites and their stratigraphic recurrence are in accord with an archeological signal of groups "settling in" rather than merely "passing through" an area.
- The Nihewan basin is situated at ~40°N latitude, approximately equivalent to Dmanisi, but is nearly adjacent to a permanent area of aridity, the desert sources that supply wind-blown loess to the Loess Plateau. Furthermore, the latest age estimates for archeological sites in the Nihewan and elsewhere in North China indicate a persistence of hominins in this region from ~1.66 to 1.1 Ma, a span of ~500 kyr. This begs the question of how, beginning at ~1.66 Ma, hominins with an Oldowan technology could withstand the seasonal and longer-term oscillations in climate that must have operated in this location. The presence of a permanent lake in the basin may have had a critical ameliorating influence, serving to buffer seasonal and larger-scale fluctuations in plant and animal resources. A study of the fossil pollen sequence in the Nihewan lake sediments is planned to assess vegetational change over time.

Biogeographic Context of Out-of-Africa Dispersal

On the basis of faunal data, there were two periods of potentially marked dispersal of large mammals from Africa during the Late Pliocene and Early Pleistocene. These dispersal events are constrained to ~2.6–2.5 Ma and shortly after 2.0 Ma. Both correspond to periods of faunal turnover (Martínez-Navarro 2010; Vrba 1995). Faunal turnover in Africa and Eurasia around 2.6 Ma was associated with the onset of colder temperatures and loess deposition, and the extinction of warm-adapted taxa in the Eurasian temperate zone (Kukla and An 1989; Liu 1985; Azzaroli 1995). In this section we briefly examine the possible first appearance of African taxa in other regions immediately east of the African continent during the Plio-Pleistocene and the implications regarding potential dispersal routes.

Levant

After 1.77 Ma (upper boundary of the Olduvai subchron), African taxa are found at Dmanisi and 'Ubeidiya. It is commonly assumed that dispersal out of Africa into Eurasia took place across the Sinai Peninsula into the Levant or across the straits of Bab-el-Mandeb into the Arabian Peninsula, although the latter idea has received criticism (Derricourt 2005). East African species are found at 'Ubeidiya, along with species derived from several other biogeographic regions (Tchernov 1987, 1992). Belmaker (2006, 2010), concludes on the basis of multivariate comparison that the Levant fauna had less of an African character than previously assumed and was more similar to Mediterranean woodland faunas. Belmaker further notes that the African taxa present at 'Ubeidiya are represented by few specimens. A further reservation about the role of the Levant as a departure zone for other points in Eurasia concerns the barriers surrounding the region, which is bordered by the Taurus-Zagros mountains, and by deserts of the Arabian peninsula. Despite the mixture of biogeographic faunal elements, it appears that few faunal elements from the Ethiopian region penetrated these mountains. African species such as *Equus* cf. *tabeti*, *Pelorovis oldowayensis*, and *Oryx* cf. *gazella* are found in the Levant, but have not been found elsewhere in northern Eurasia (Martínez-Navarro 2010).

Bab-el-Mandeb

Some faunal exchange between Africa and southwestern Arabia is also proposed to have taken place at the straits of Bab-el-Mandeb (Tchernov 1992; Turner 1999). Undated

Acheulean archeological sites with low artifact densities have been identified near the straits of Bab-el-Mandeb (Petraglia 2003). Kinematic reconstruction of the Afar region suggests, however, that connectivity between the Afar triangle and the Arabian plate was lost after 6.2 Ma, although the land between remained subaerial until approximately 4.5 – 3.2 Ma (Redfield et al. 2003). Geochemical analysis of deuterium concentrations, indicative of a connection between the Red Sea and the Gulf of Aden during the latest Miocene to Early Pliocene (Friedman and Hardcastle 1974), supports Redfield et al.'s (2003) conclusion that the land bridge disappeared in the Pliocene or had become only an intermittent feature. Although glacial conditions caused the lowering of sea level several times during the last 500,000 years (Rohling et al. 1998), the low stands of earlier times in that region are not yet known. Evaporite formation, which would occur when salt became concentrated in the Red Sea due to the formation of a land barrier, is not known to have occurred since the Miocene (Fernandes et al. 2006; Orszag-Sperber et al. 2001). Derricourt (2005) argues that a dispersal involving sea crossing, as required of a route involving the Bab-el-Mandeb straits, was unlikely prior to the technological capabilities of Late Pleistocene humans.

Arabian Peninsula

Oldowan and Acheulean artifact assemblages are found in the Arabian Peninsula (summarized by Petraglia 2003). Faunal remains are not reported to occur with these archeological assemblages, which are undated. A small faunal assemblage from the An Nafud Desert in Saudi Arabia contains a few African taxa, including *Crocuta crocuta*, *Pelorovis oldowayensis* and *Oryx* sp (Thomas et al. 1998). Significantly, these are species identified as African dispersants in the Levant also.

Many Arabian artifact sites are found in montane areas and near ancient lake beds and wadis, as well as along the Red Sea and Arabian Sea (Petraglia 2003). However, Petraglia cautions that the distribution of presently known sites is related to visibility and geomorphological conditions as much as to potential dispersal corridors. Artifacts in Oman have been interpreted as part of a route to the Zagros Mountains (Whalen et al. 2002). Petraglia (2003) hypothesizes an eastward expansion on the margins of the Zagros Mountains and over the Iranian plateau. If the artifact distribution does contain a signal about the dispersal route, it is possible that hominins expanded mainly into areas that had local raw material sources for stone toolmaking.

Indian Subcontinent and Central Asia

Information from this area is limited. From a faunal perspective, Africa and India share several species of small mammals, including gerbillids, which dispersed from Africa to India in the Late Pliocene (Patnaik and Sahni 2000). From the evidence of shared taxa, they conclude that during the Pliocene, there was a means of dispersal between Africa and India suitable for small mammals. Martínez-Navarro (2010) also notes evidence that African antelopes dispersed to the Siwaliks in the Pliocene. According to Badam (1984), by the middle and late Pleistocene, many African mammalian species occurred in India, and a faunal connection existed between India and Europe.

The ability of hominins to reach sites at the latitude of Dmanisi and the Nihewan basin (40°N) raises the possibility that hominins could have spread further east into Eurasia along a Palearctic mammalian dispersal corridor running between mountain systems, as suggested by Rolland (1997). This route would also have kept hominins close to raw material sources. A second route of dispersal to East Asia might have occurred along the southern margin of Asia. A third route, which requires strong consideration, is suggested by the likely co-occurrence of excellent source rocks for making tools, perennial fresh-water springs and water courses, and the potential to harbor a high mammalian biomass in the Purana basins of north-central India (Korisettar 2007). This region would seem to have high potential for paleoanthropological investigations related to the spread of early hominins both eastward and westward across Asia (Fig. 5.4).

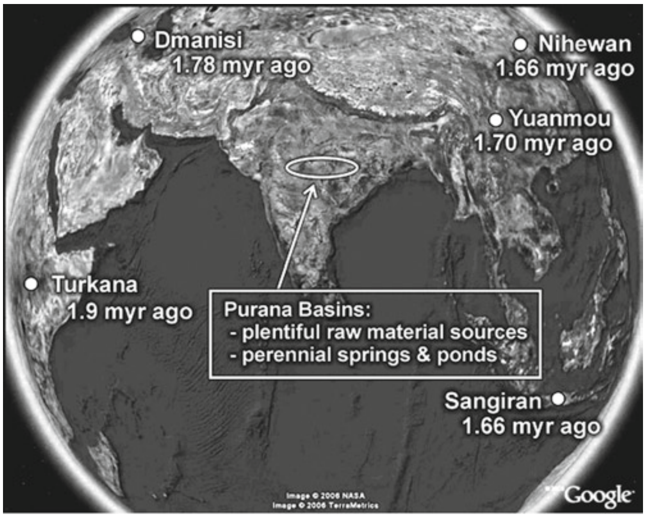

Fig. 5.4 The Purana basins of north-central India, situated between East African and East Asian sites of earliest *Homo erectus sensu lato*, are posited by Korisettar (2007) to have been areas attractive to early and middle Pleistocene hominin populations. Due to abundant food, water, and lithic sources, these basins may have also offered a viable route of population movement between the western and eastern parts of Eurasia. Google Earth image

Fellow Travelers and Three Hypotheses of Hominin Dispersal

Fellow travelers – i.e., mammalian populations that dispersed from Africa and through Eurasia at the same time as hominins – are thought to be important for understanding the environments into which hominins dispersed and the ecological circumstances of the dispersal (Turner 1984; Martínez-Navarro 2010). Table 1 presents those taxa of African origin that are found in the Levant and the known first occurrences of these taxa in other regions. We summarize here several hypotheses to account for patterns of co-occurrence of hominins and possible fellow travelers.

1. Unique dispersal hypothesis: Hominin dispersal out of Africa was a unique event, and did not involve the co-dispersal of any other African species.
2. African fellow travelers hypothesis: The out-of-Africa dispersal represented a small ecological opportunity, allowing hominins and other African taxa to reach a surrounding region. After that regional dispersal, hominin groups dispersed independently to distant regions.
3. Relay hypothesis: Hominins have always dispersed with other species; however, the movement from one region to another was associated with different animal species. For example, some African species may have participated in the initial out-of-Africa dispersal; west Asian taxa may have accompanied hominins into central or southern Asia; and species endemic to these latter regions dispersed with hominins into eastern Asia. The implication is that early human dispersers were always part of a local/regional ecological community, and their dispersal was associated with, and perhaps facilitated by, a relay of fellow travelers from one region to another.

The first hypothesis proposes a case in which only hominins could take advantage of the conditions offering a very limited dispersal opportunity. This hypothesis rules out the spread of vegetational types, such as savannas, which other African species could have followed. The implication is that hominins may have had unique capabilities compared with other animals. Given the presence of some African species at 'Ubeidiya (~1.6 to 1.2 Ma), it may be argued that early Pleistocene dispersals beyond Africa were not unique to hominins, and that other African taxa dispersed into regions of western Eurasia at roughly the same time.

The second hypothesis involves an initial regional dispersal made with fellow travelers. For example, an ecological opportunity may have allowed hominins to travel with several African species to the neighboring regions of the Levant, the Arabian Peninsula, and even as far as India. After dispersing with these African species, the hominins had adapted sufficiently to Eurasian environments that they were then able to disperse to areas such as East Asia without the benefit of fellow travelers. In regions close to Africa, hominins would appear with African species, while hominins in more remote regions would not be found with African taxa. Both *Megantereon* and *Crocuta* have been reported from many sites out of Africa, including East Asia; however, the timing of the initial dispersal of the species ancestral to the Eurasian forms is uncertain (for further discussion, see Lewis and Werdelin 2010). A great deal of further research would also be required to determine whether the timing of the dispersal of *Theropithecus* to India matches that of the arrival of hominins in that region.

The third hypothesis involves a change in the taxonomic identity and biogeographic affinities of the species dispersing with hominins. When dispersing to distant regions, such as East Asia, hominins may have dispersed with non-African species. If this were the case, the fossil record would show hominins appearing with African animals in some regions, but with exotic, non-African species in other, more distant regions. To determine whether this is a possibility in relation to East Asia, the faunas of potential intermediate regions such as the Arabian Peninsula and India must be dated and analyzed thoroughly to see whether faunal exchange occurred with distant regions such as East Asia. This evidence could also be used to understand routes of dispersal.

Preliminary evidence (Table 5.1) shows that although some African species found in the Levant are also found in some other regions, there is no clear pattern indicating a group movement of all these species to other regions, such as India or the Caucasus. Individual species did, however, succeed in colonizing other regions. The exceptions to this are the carnivores *Crocuta* and *Megantereon*, which are found in many areas. Carnivores are good dispersers, and hominins may have followed their biogeographic pattern rather than that of herbivores that did not disperse as far from Africa. However, as noted earlier, the phylogenetic relationships and timing of dispersal events of *Crocuta* and *Megantereon* in East Asia and East Africa are not certain (Lewis and Werdelin 2010).

Another possibility is that not all of the potential African fellow travelers have been identified. An overall taxonomic comparison of the faunas of East Asia and Africa (Table 5.2) shows those species that are shared. Common to both regions were representatives of the Carnivora, Proboscidea, and Equidae – i.e., those mammalian groups known to have species with excellent dispersal abilities and wide ranges. Some micromammals are also found in both regions. Micromammalian connections also occur between Africa and India, with a proposed dispersal of gerbillids from India to Africa in the Late Pliocene when fewer ecological barriers existed (Patnaik and Sahni 2000). *Equus* entered Africa from Eurasia around 2.5 Ma, and thus the genus-level similarity between East African and East Asian equids is probably

Table 5.1 These African species have been found in the Levantine site of 'Ubeidiya (Tchernov 1987; Martínez-Navarro 2004; Belmaker 2010), and are identified as potential fellow travelers for the initial hominin dispersal. Following the interregional approach discussed in the text, the other regions in which these taxa have been identified are indicated. This evidence suggests that the dispersals of *Giraffa* and *Oryx* predate current evidence for the earliest hominin dispersal to Eurasia.

	Equus cf. *tabeti*	*Pelorovis oldowayensis*	*Oryx* cf. *gazella*	*Kolpochoerus*	*Giraffa sp.*	*Hippopotamus*	*Theropithecus*	*Crocuta crocuta*	*Megantereon*	References
Arabia		*Pelorovis* sp. (Early Pleistocene)	*Oryx* sp. (Early Pleistocene)					*Crocuta crocuta* (Early Pleistocene)		Thomas et al. 1998
India			*Oryx sivalensis* (2.6 Ma)				*T. delsoni* (Mirzapur, 1.0 Ma)	*Crocuta* sp. (Pinjor Formation?)	*Megantereon falconeri* (Siwaliks, upper Pliocene)	Martínez-Navarro 2004, 2010; Gupta and Sahni 1981; Delson 1993; Pickford 1993; Lewis and Werdelin 2010
Europe						*H. antiquus* (Venta Micena, 1.5 Ma)	(Pirro Nord, 1.5 Ma)	(Gran Dolina, Atapuerca, 0.8 Ma)	*M. whitei* (Venta Micena, 1.6 Ma)	Martínez-Navarro 2004, 2010; Rook et al. 2004; Alberdi and Ruiz-Bustos 1985; Martínez-Navarro et al. 2004; García 2003
Caucasus					(Kvabebi 2.5Ma)	(Akhalkalaki, 0.98–0.78 Ma)		*Crocuta sinensis* (Akhalkalaki, 0.98–0.78 Ma)	*Megantereon* sp.(Dmanisi)	Vekua 1972, in Martínez-Navarro 2010; Tappen et al. 2002; Gabunia et al. 2000
North Africa	(Ain Hanech)	*Pelorovis* sp. (Ain Hanech, 1.8 Ma)	*Oryx* sp. (Ain Hanech, 1.8 Ma)	*K. phacochoeroides* (2.5 Ma)	*G. pomeli* (Ain Hanech, 1.8 Ma)	*H. amphibious* (Ain Hanech, 1.8 Ma)	*T. atlanticus* (2.5 Ma)	*C. dbaa* (2.5 Ma)		Arambourg 1970; Martínez-Navarro 2004; Geraads 1993; Alemseged and Geraads 1998; Geraads 1997
Far East Asian mainland	*Equus* sp; relationship to *Equus* cf. *tabeti* unknown							*Crocuta honanensis* (Longdan, Late Pliocene)	*Megantereon* sp. (Haiyan Fm., Yushe Basin, 2.5–1.9 Ma); *Megantereon nihowanensis* (Longdan, Late Pliocene)	Flynn 2002; Flynn et al. 1991; Qiu et al. 2004

Table 5.2 Chinese early Pleistocene hominin and archeological sites are listed, along with evidence of dating, and genera that are found in both Africa and East Asia. Asterisks indicate taxa that are only found in North Africa. The Pliocene site of Ahl al Oughlam is provided for comparison as a richly fossiliferous site that does not have evidence of hominins.

Site	Hominin Evidence	Date	Method	Number mammal species	Genera also found in Africa	References
Xiaochangliang, Nihewan Basin, North China	Artifacts	1.36 Ma	Paleomagnetic stratigraphy	11	*Equus, Gazella, Hipparion, Hyaena*	Tang et al. 1995; Zhu et al. 2003
Majuanguo, Nihewan Basin, North China	Artifacts; tool-modified bone	Sequence dated 1.34 to 1.66 Ma	Paleomagnetic stratigraphy	6	*Elephas, Equus, Gazella, Pachycrocuta*	Zhu et al. 2004
Gongwangling, Lantian North China	*Homo erectus* cranium	1.15 Ma	Paleomagnetic stratigraphy	43	*Canis, Equus, Felis, Gerbillus, Hyaena, Hystrix, Megantereon, Micromys, Panthera, Stegodon, Ursus*?	An and Ho 1989; An et al. 1990; Zhu et al. 2003
Yuanmou South China	Hominin incisors; stone artifacts (n=4)	1.7 Ma	Paleomagnetic stratigraphy; biochronology	35	*Canis, Equus, Gazella, Megantereon, Pachycrocuta, Panthera, Stegodon, Vulpes*	Zhu et al., in review; Han and Xu 1 985
Jianshi (Longgudong Cave), South China	Hominin teeth; artifacts	Early Pleistocene	Biochronology	87	*Crocidura, Equus, Homotherium, Pachycrocuta, Micromys, Rhinolophus, Ursus*?	Zheng 2004
Xihoudu, North China	Stone artifacts	1.27 Ma	Paleomagnetic stratigraphy	22	*Elephas, Equus, Gazella, Hipparion, Hyaena, Stegodon*	Zhu et al. 2003
Gigantopithecus Cave, Liucheng, South China (Juyuandong)	No clear evidence of hominin fossils or artifacts	Early Pleistocene	Biochronology	40	*Equus, Felis, Herpestes delibis, Hyaena (Pachycrocuta?), Hystrix, Megantereon, Micromys, Panthera pardus, Viverra*	Han and Xu 1985; Zhang 1985
Renzidong, Fanchang, Anhui (Renzi Cave) eastern China	Purported hominin artifacts	Late Pliocene	Biochronology	67	*Equus, Felis, Hipposideros, Homotherium, Hystrix, Megantereon, Micromys, Nyctereutes, Pachycrocuta, Rhinolophus, Ursus*?	Jin et al. 2000
Longgupo Cave (Wushan), South China	Purported hominin teeth Stone artifacts	Fossils/artifacts in a normal magnetozone, possibly 1.95–1.77 Ma	Biochronology; paleomagnetic stratigraphy; ESR	68 (genera)	*Equus, Felis, Hipposideros, Homotherium, Hystrix, Nyctereutes, Pachycrocuta, Rhinolophus, Ursus*?	Huang et al. 1995
Zhoukoudian 1, North China	Hominin remains Stone artifacts	500–200 kyr	Geological, faunal, pollen correlation with glacial chronology	89	*Canis, Crocidura, Crocuta crocuta, Equus, Felis, Gazella, Gerbillus, Homotherium, Hystrix, Lepus, Lutra, Macaca, Megantereon, Micromys, Miniopterus schreibersi, Mus, Nyctereutes, Pachycrocuta, Panthera pardus, Rhinolophus, *Spiroceros, Ursus?, Vulpes*	Dong et al. 2000; Aigner 1986; Wu 1985
Mohui cave, Bubing Basin, South China	Hominoid teeth (hominin status uncertain)	Plio-Pleistocene	Biochronology	30	*Felis, Hystrix, Macaca, Stegodon, Ursus?*	Wang et al. 2007
Dmanisi, Caucasus	Hominin remains, artifacts	1.8 Ma	K-Ar; ^{40}Ar/^{39}Ar	36	Shared with Africa *Canis, Equus, Gazella, Gerbillus, Homotherium, Megantereon, Mungos, Pachycrocuta, Panthera, Ursus?* Shared with China *Apodemus, Archidiskodon, Canis, Cervus, Dama, Dicerorhinus, Equus, Eucladoceros, Gazella, Gerbillus, Homotherium, Hypolagus, Kowalskia, Lynx, Marmota, Martes, Megantereon, Mimomys, Ochotona, Pachycrocuta, Panthera, Sorex, Sus, Ursus*	Gabunia et al. 2000, 2001

(continued)

Table 5.2 (continued)

Site	Hominin Evidence	Date	Method	Number mammal species	Genera also found in Africa	References
Ahl al Oughlam, North Africa	None	2.5 Ma	Biochronology	52	Shared with Sub-Saharan Africa *Acinonyx, Anancus, Beatragus, Camelus, Canis, Ceratotherium, Chasmaporthetes, Crocuta, Dinofelis, Elephas, Felis, Gazella, Genetta, Gerbillus, Herpestes, Hipparion, Homotherium, Hyaenictitherium? (only in very old sites), Kobus, Kolpochoerus, Lepus, Lutra, Mellivora, Mus, Nyctereutes, Panthera, Parmularius, Praomys, Serengetilagus, Sivatherium, Suncus, Theropithecus, Tragelaphus, Ursus?, Viverra* Shared with China *Camelus, Canis, Chasmaporthetes, Crocuta, Elephas, Erinaceus, Felis, Gazella, Gerbillus, Herpestes, Hipparion, Homotherium, Hystrix, Lepus, Lutra, Lynx, Macaca, Mus, Nyctereutes, Panthera, Ursus, Viverra*	Geraads, 1993, 1994, 1995, 1997; Geraads and Amani 1998; Geraads and Metz-Muller 1999; Alemseged and Geraads 1998

Artiodactyla, Bovidae: *Beatragus*, *Gazella*; *Kobus*, *Parmularius*, *Spiroceros*, *Tragelaphus*; Camelidae: *Camelus*; Cervidae: *Cervus*, *Dama*, *Eucladoceros*; Giraffidae: *Sivatherium*
Suidae: *Kolpochoerus*, *Sus*
Carnivora, Canidae: *Canis*; *Nyctereutes*, *Vulpes*; Felidae: *Acinonyx*, *Dinofelis*, *Felis*, *Homotherium*, *Lynx*, *Megantereon*, *Panthera*
Hyaenidae: *Chasmaporthetes*, *Crocuta*, *Hyaena*, *Hyaenictitherium*, *Pachycrocuta*; Mustelidae: *Lutra*, *Martes*, *Mellivora*
Ursidae: *Ursus*; Viverridae: *Genetta*, *Herpestes*, *Mungos*, *Viverra*
Chiroptera, Hipposideridae: *Hipposideros*; Rhinolophidae: *Rhinolophus*; Vespertilionidae: *Miniopterus*
Insectivora, Soricidae: *Crocidura*, *Sorex*, *Suncus*; Erinaceidae: *Erinaceus*
Lagomorpha, Leporidae: *Hypolagus*, *Lepus*, *Serengetilagus*
Perissodactyla, Equidae: *Equus*, *Hipparion*; Rhinocerotidae: *Ceratotherium*, *Dicerorhinus*
Primates, Cercopithecidae: *Macaca*, *Theropithecus*
Proboscidea, Elephantidae: *Archidiskodon*, *Elephas*; Gomphotheriidae: *Anancus*; Stegodontidae: *Stegodon*
Rodentia, Arvicolidae: *Mimomys*; Hystricidae: *Hystrix*; Muridae: *Apodemus*, *Gerbillus*, *Kowalskia*, *Micromys*, *Mus*; *Praomys*; Sciuridae: *Marmota*

ancient. *Equus* cf. *tabeti* found at 'Ubeidiya has also been found at Koobi Fora, and is related to the African equid *E. oldowayensis* (Eisenmann 1983). The shared genera *Hipparion, Camelus*, and *Gazella* also represent ancient similarities rather than a dispersal event associated with *H. erectus*. Movements, taxonomic similarities, and interconnectivity among the regions need further investigation. At present, none of the three hypotheses summarized here receives overwhelming support.

Environmental Contexts of the Oldest Hominins in East Asia

The oldest hominin evidence in China converges on the oldest age estimates for hominin fossils from Java in Southeast Asia (Swisher et al. 1994; Larick et al. 2001; Antón and Swisher 2004; Zaim 2010). By at least ~1.66 Ma, East Asian hominins had dispersed over a latitudinal range from 7°S to 40°N, and across habitats ranging from tropical woodland/forest to seasonally cool grassland. In this section we summarize the diversity of East Asian fauna, vegetation, and climate dynamics that formed part of the context of the oldest known Asian dispersal of hominins.

Distinctive Faunas and Regional Diversity

Early Pleistocene hominins arriving in East Asia encountered a novel array of mammalian species relative to East Africa. East Asian faunas were taxonomically diverse, combining species from the Palearctic and Oriental realms and from North America. One potentially important difference between the two faunal communities was the presence of a diverse bovid community in East Africa while East Asia was characterized by woodland and forest cervids that were unknown in Pleistocene sub-Saharan Africa.

After a period of high faunal similarity between China and Europe (at the genus and species levels) prior to 2.5 Ma (Tedford 1995), North China became separated from other Eurasian temperate faunas due to uplift, climatic changes, and the expansion of a desert-steppe belt across the southern region of Inner Mongolia (Zhang 1988). During the Pleistocene, the faunas of North and South China also became increasingly divergent, apparently due to climatic differences between the regions and uplift of the Tibetan Plateau and Qinling Mountains (Xu 1988; Zhang 1988; Cao 1994).

North and South China are divided by the Yangtze River and the Qinling Mountains, which pose a formidable barrier to faunal interchange. Early Pleistocene sites of southern China are generally assigned to tropical or subtropical forest habitats, whereas northern Chinese sites supported a steppe and grassland fauna that included forest elements during the Early Pleistocene (Han and Xu 1985). The northern forests included floral species such as *Quercus*, *Ulmus* and *Carpinus* (Cao 1994). Sites in the Nihewan basin, North China, include taxa that reflect a variety of habitats, including woodland, grassland and arid environments. Examples of open country and steppe taxa include gazelles, *Proboscidipparion sinense*, *Equus, Myospalax tingi* and camelids, while cervids may indicate the presence of woodland (Zhang 1988; Qiu et al. 2004; Cao 1994; Geist 1998).

A transitional zone between North and South China existed between the middle and lower Yangtze River, the Qinling Mountains and the Huai River. The early Pleistocene site of Gongwangling, which is in the transitional zone, contains several southern taxa in its faunal assemblage, possibly reflecting the ability of these animals to expand their ranges northward during favorable climatic conditions. Gongwangling also contains montane and forest indicators, such as *Capricornis sumatraensis, Myospalax fontanieri* and *Elaphodus cephalophus*, which are found at higher elevations, and *Scaptochirus moschatus*, *Ailuropoda* and *Stegodon*, which are found in forests (Zhang 1988; Nowak 1999).

Early Pleistocene sites of South China are characterized by forest indicators, such as *Stegodon* and *Ailuropoda*. The fauna and paleobotanical remains associated with the Yuanmou hominin fossils suggest that this basin hosted a diverse mosaic of habitats. Twenty-one of 35 mammalian taxa (for example, *Equus yunnanensis*) belong to families, genera, or species typical of an open grassland environment. Bushland habitat is also suggested by the presence of *Rhizomys* sp., *Sus* sp., *Nestoritherium* sp. and *Viverricula malaccensis fossilis*, whereas fossils of *Megantereon nihowanensis*, *Stegodon elephantoides* and *Stegodon* sp. are considered indicative of forest. Numerous mollusks indicate a low-energy lakeshore or marsh setting, and the occurrence of *Cyriuus caspio* and *Testudo* sp. is characteristic of a perennial open aquatic environment (Zhu et al. 2008). Fossil pollen was also recovered in the sedimentary layer bearing the *H. erectus* fossils and artifacts at Yuanmou. The pollen samples are dominated by *Pinus* (33.3%), *Alnus* (13%) and herbaceous vegetation (40%) (Pu and Qian 1977; Qian and Zhou 1991), indicative of locally extensive herbaceous cover and patches of forest surrounding the ancient lake or swamp. The faunal assemblage and pollen from the hominin site thus imply that the diverse habitats encountered by the Yuanmou hominins included open grassland, bushland, forest, marsh and fresh water – i.e., vegetation not at all typical of that assumed to characterize the Early Pleistocene of southern China (Ciochon 2010; see Wang et al. 2007).

Climate Dynamics

Environmental proxies derived from coring of the South China Sea (e.g., $\delta^{18}O$, K/Si and Ba/Al ratios) and the analysis of Loess Plateau sediments (e.g., Fe isotope ratio, magnetic susceptibility) provide a lot of information about East Asian climate history. A substantial shift in elemental ratios in sediments younger than 3.0 Ma resulted from stronger seasonality in East Asia, which appears to have been caused by a change in atmospheric circulation due to uplift of the Himalayan-Tibetan complex. Tectonic changes after 3.2 Ma are likely to have led to an intensified Siberian high-pressure system that resulted in colder, drier, and less stable climate conditions after 2.65 Ma (Wehausen and Brumsack 2002; Müller et al. 2001). Onset of the loess-paleosol sequence of the Loess Plateau at ~2.6 Ma is related to the intensification of the winter monsoon.

One commonality in the climate histories of East Africa and East Asia, therefore, is insolation-driven monsoon variability, with a major low-latitude influence. Low-latitude insolation variability appears to have asserted major control on the pace and intensity of climate oscillation. Beyond this, however, the details of climate change in East Asia, the zonation of habitats, and the expansion/contraction of habitats in response to climate variability were the result of tectonic features, pressure systems, and monsoon wind intensities unique to that region of the world.

Magnetic susceptibility data from the Loess Plateau (Guo Zhengtang, personal communication) and planktonic foraminifera $\delta^{18}O$ from the South China Sea (Steven Clemens, personal communication) show that relatively low-amplitude climate oscillation characterized the period from at least 2.0 to ~1.2 Ma, which was followed by substantial increases in oscillation amplitude at ~1.2 Ma and 550 ka. In other words, the first appearance of hominin populations in East Asia occurred during a period of relatively low climate variability.

In sum, upon arrival in East Asia, early hominin populations encountered climatic and biotic regimes that differed substantially from those of East Africa. In East Asia, hominins inhabited temperate woodlands and grasslands and tropical/subtropical wooded landscapes that were under the influence of Asian monsoonal conditions and that harbored plant and animal communities unlike those of Plio-Pleistocene East Africa. Evidently, early *H. erectus* possessed the ability to adjust to these differences and also to the wide variety of climatic and biotic settings throughout its range in eastern Asia. The ecological, behavioral, and physiological means by which *H. erectus* accommodated to this breadth of environments is not yet well understood, even though such means of adaptability have been characteristic of the genus *Homo* ever since.

Discussion

The implications we draw based on this wide variety of data sets can be summarized as follows:

1. The earliest hominins in East Asia show morphological and behavioral connections with East African hominins.
    - Stone flaking: The oldest definite stone artifacts of East Asia can be described as Oldowan, and show details of percussion flaking and core form that match those of the African Oldowan.
    - Morphology: The morphology of the oldest distinctively hominin dental remains in China (from Yuanmou) – possibly the oldest known hominin fossils in all of eastern Asia – show strong similarities to the dental remains of early African *H. erectus*.
    - Acquiring large mammal carcasses: Archeological evidence from the Nihewan basin closely matches that from East African Plio-Pleistocene sites. The similarities include: access by the toolmakers to a wide variety of mammalian taxa (e.g., equids, bovids, cervids, rhinos, elephants) across a broad range of body sizes; accumulation of animal bones and stone tools in distinct concentrations; and the butchery and extraction of bone marrow from these animals.
2. Animal foods may have been a critical resource to dispersing hominin groups because plants produce potentially toxic secondary compounds, whereas animal tissues have relatively similar nutritional and digestive properties across diverse biotic zones.
    - Access to animal tissues was almost certainly instrumental in enabling hominins to enter and pass through a wide variety of habitats, harboring many unfamiliar plant species, from Africa to East Asia. Despite the taxonomic differences of the prey, techniques of animal food foraging were probably transferable across faunal communities.
    - The earliest hominin toolmakers in North China evidently persisted long-term in a seasonally cool and dry habitat; consuming animal tissues would have been an important aspect of the survival strategy in temperate latitudes.
3. The combination of current dating and mammalian faunal evidence from Dmanisi and East Asia suggests that *Homo erectus* took advantage of a general mammalian dispersal opportunity to reach western Eurasia, and was then able to overcome geographic barriers and adapt to new habitats beyond the capabilities of most other mammalian taxa. The dispersal of hominins through eastern Asia especially required an ability to adjust to a wide array of novel environments.

4. Potentially rapid, long-distance dispersal across Asia probably increased the geographic isolation and morphological variability of *H. erectus* populations.

    - Beginning ~1.7 Ma, the heightened degree of intergroup isolation may have been unprecedented to that point in human evolutionary history. East Asian *H. erectus* was isolated not only from African populations, but also from other Eurasian and East Asian populations. During the early Pleistocene, temperate woodland populations of East Asia were periodically cut off from those in Europe. There is also evidence that North and South China diverged over time in their faunal composition; the degree of isolation of hominin groups across these regions is unknown, but could have been substantial.
    - Wide geographic dispersion and small population sizes may have increased the degree of morphological variation due to genetic drift. Like species of carnivores, *Homo erectus* occurred over a wide range and may have had a low speciation rate.

5. The Asian archeological record between 1.77 and 1.66 Ma is very sparse and/or hard to detect – essentially nonexistent across vast areas of Asia – which may reflect the fast pace of dispersal of relatively small populations.

    - In contrast to the Asian record, the African archeological record between ~1.8 and 1.5 Ma is highly visible because Oldowan toolmakers recurrently visited or occupied specific regions and discrete places on the landscape. This is known as "the archeology of settling in" – prolonged habitation of a region by stone toolmakers leaves an easily-detected signal in the stratigraphic record.
    - The archeological record of Yuanmou, where only four artifacts were found in an excavation of a hillside that preserved many mammalian fossils, including two *H. erectus* teeth, is consistent with what is called "the archeology of passing through" – i.e., toolmakers moving through a region leave an archeological record that is highly dispersed in space, possibly confined to a single stratigraphic layer. (No other stone tools have been found in the Yuanmou basin.) Such a record is nearly invisible archeologically in comparison to the rich stratigraphic series of early Pleistocene Oldowan sites in certain East African basins. "The archeology of passing through" implies the dispersal of small, widely spaced groups that were not tethered to specific places on the landscape for multiple generations.
    - The oldest archeological evidence in Asia for "settling in" occurs in the Nihewan basin, beginning at least ~1.66 Ma. There we see the familiar African Oldowan evidence of multiple archeological strata reflecting a lengthy period of re-occupation. Stone-tool evidence from the Nihewan and Yuanmou basins implies that the dispersing populations reaching East Asia had maintained the ability to make stone tools from local source rocks. This idea implies that the Oldowan toolmakers of Asia, as in Africa, could adapt their stone flaking capabilities to a large variety of rock types.

6. There are several possibilities for determining possible dispersal corridors from East Africa to East Asia.

    - Oldowan hominins are likely to have dispersed into regions and moved through areas where stone raw materials were locally available, enabling them to maintain a basic toolmaking tradition. Likely dispersal routes may thus have been constrained by this factor, along with continuous access to fresh water and animal meat/marrow resources.
    - Overall faunal biogeographic patterns can be broken down regionally, and suggest which areas may have been connected by dispersal corridors. Taxa shared between widely separated locations, such as *Equus* and genera of proboscideans and carnivores, are good dispersers. Most African species found in the Levant during the early Pleistocene have so far not been found in Eurasia outside this region. Exceptions to this are *Hippopotamus* and *Theropithecus*. Early Pleistocene African taxa found in the Levant, therefore, may have spread not in response to the expansion of a specific type of habitat across Asia so much as to a more specific geographic opportunity (i.e., a favorable dispersal corridor) to spread beyond Africa.

7. The dispersal from Africa to East Asia, along with evidence regarding the climate dynamics, habitat diversity, and distinctive faunas of East Asia, all suggest that earliest Pleistocene *H. erectus* adjusted to highly-varied adaptive conditions across disparate types of environment – and had thus evolved a high degree of adaptability, with important implications for its evolutionary history.

    - Earliest Asian *H. erectus* evidently occurred from northern China to Java, occupying open and forested settings, and accommodating to a wide variety of mammalian communities and changing environmental conditions.
    - The implication is that *H. erectus* responded to disparate adaptive conditions (in time and space) by a combination of population movement and local adaptability. Given the paleoclimate evidence of alternating periods of increased-decreased moisture, warmer-cooler temperatures, and higher-lower climate variability, we may envision that *H. erectus* experienced alternating periods of population isolation and contact/mixing (as well as local extinction). That is, considerable opportunity would have occurred for phenotypic experimentation,

without any one period necessarily lasting long enough to promote the development of permanent reproductive barriers.

- *H. erectus* spread to new habitats within African basins, then took advantage of an opportunity in its initial move to western Eurasia, and did so during a time of faunal turnover. Whatever characteristics enabled this initial dispersal probably also aided *H. erectus*' survival during its spread across Asia and expansion into the diverse and dynamic environments of East Asia.

Conclusion

The African background: Between 2.5 and 1.8 Ma, shifts in East African hominin limb proportions and locomotor morphology began to occur that were related to long-distance bipedal mobility. While these changes may have presented an opportunity for hominins to engage in a greater range of mobility, they appear to precede archeological behavioral evidence signaling (a) longer distance (>12 km) transport of stone raw material, and (b) an expansion of tool activities into a wider diversity of environmental zones.

Fellow travelers: Preliminary analysis shows that the African taxa found immediately outside Africa in the Levant are not found with *H. erectus* in East Asia, with the exception of the carnivores *Megantereon* and *Crocuta*. However, these may not be the same species as those found in western Asia and in Africa. Comparison of the faunas found in the intervening regions may show corridors of faunal dispersal, and might identify non-African fellow travelers with whom hominins may have spread simultaneously into East Asia (the Relay Hypothesis).

The timing of dispersal: The faunal evidence for a broad dispersal of fellow travelers is unclear on this point. East African archeological evidence shows, however, that the expansion of hominin toolmakers into new landscapes and depositional zones began ~1.77–1.70 Ma, a period that corresponds with the oldest definite evidence of hominins outside of Africa and the spread of *H. erectus*, in particular, to East Asia.

Speed of dispersal: Based on new age estimates of the oldest stone tools and hominin fossils known so far in China, the dispersal across Asia may have been rapid, and led hominin toolmakers into biogeographic zones of different taxonomic makeup from those in Africa.

Adaptability: The oldest recorded spread of hominins across Asia apparently culminated in an ability to adapt to novel habitats and climatic regimes in East Asia. This degree of adaptability likely enabled the persistence of *H. erectus* in East Asia for a very long time prior to the arrival of *H. sapiens*.

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