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The earliest stages of hominin dispersal in Africa and Eurasia

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This chapter describes the earliest potential movements of hominins (proto-humans) within Africa, starting from almost 7 mya, and focusing on the genesis of Australopithecus *and* Homo *and the dispersal of the latter into Eurasia soon after 2 mya. The emphasis here is on the fossil record.*

Miocene origins and Pliocene dispersals

The oldest hominin specimens known at present date to the Miocene epoch of geological time (7.0 to 5.3 mya) and have been discovered in Sub-Saharan Africa, in Chad (Toros-Menalla, *Sahelanthropus tchadensis*), Kenya (Tugen Hills, *Orrorin tugenensis*), and Ethiopia (the Middle Awash region, *Ardipithecus kadabba*) – see Figure 2.1 for site locations. Although these specimens are assigned by biologists to a variety of species, they may well represent geographical variants of a single taxon. Skulls and postcranial skeletons uniformly indicate an early development of bipedalism, this being a distinctively hominin gait that might have developed as a result of environmental adaptations in more open environments. Extended rainforest areas in equatorial Africa in the Early to Middle Miocene gave way in the Late Miocene to drier, more open, and more variable habitat types in eastern Africa (Cerling et al. 1997). The above-mentioned hominin find places represent such habitats on the boundaries of forested areas (Foley & Elton 1998).

During the Pliocene (5.3 to 2.6 mya), a new species named *Ardipithecus ramidus* has been described from a wide region in eastern Africa, including the middle Awash Basin in Ethiopia as well as Lothagam and the Baringo Basin in Kenya. After 4.4 mya this species gave way to a variety of australopithecine species (*Australopithecus anamensis, A. afarensis, A. bahrelghazali*). Until 3.5 mya, these species are only known from Ethiopia, Kenya, Tanzania, and Chad, but after that time they dispersed successfully into higher latitudes and reached South Africa. The oldest hominins from South Africa

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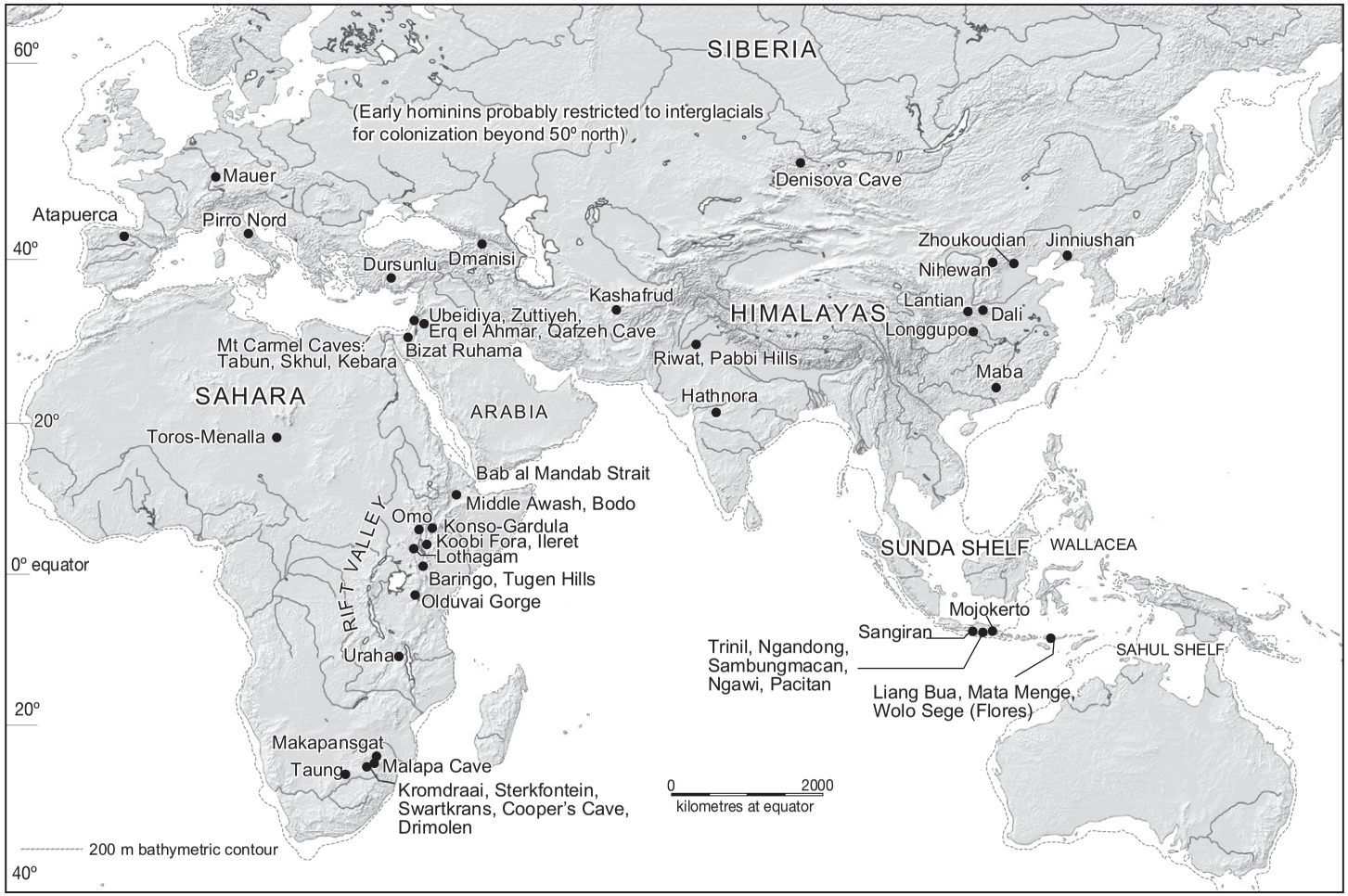

Figure 2.1 Important Pleistocene hominin sites in Africa and Eurasia prior to the dispersal of *Homo sapiens*. Continental shelves are delineated to −200 m. Base mapping by Education and Multimedia Services, College of Asia and the Pacific, The Australian National University.

come from cave breccias at Sterkfontein, Makapansgat and Taung, with ages between 3.5 and 2.6 mya. The gracile australopithecines from South Africa are attributed to *Australopithecus africanus*.[1] The expansion process into southern Africa was paralleled by a global warming trend between 4.5 and 3 mya (Ravelo et al. 2004). Such an enormous expansion in the distribution area of the gracile australopithecines might imply an increased level of ecological flexibility within this genus, but the ecological orientations of these groups are not yet well established and evidence for a major adaptational shift is so far lacking. However, as a result of the warmer climate conditions, the habitats to which East African australopithecines became adapted may have shifted ever further away from the equator. Although paleobotanical evidence for vegetation conditions is largely absent in the Pliocene (Jacobs et al. 2010), it can be assumed that the southern part of the East African Rift Valley might have served as a prime corridor linking eastern and southern Africa.

Paranthropus and early *Homo* in the Plio-Pleistocene

Between 3 and 2 mya, global climatic trends went into reverse, leading to lower temperatures (see Figure 2.2 for chronology and climatic cycles). Australopithecines in eastern and southern Africa were subjected to unique habitat changes. Rapid, short-term climatic shifts and increased seasonality (Trauth et al. 2005) led to the appearance of larger-toothed species that were capable of dealing with tougher food items in drier environments. This applied not only to hominins, but to other mammal taxa as well (Turner & Wood 1993). These climatic changes may have led to further hominin speciation, in that two consecutive and highly robust *Paranthropus* species (*P. aethiopicus* and *P. boisei*), along with early representatives of the genus *Homo*, appeared in East Africa. *Paranthropus* specimens dated between 2.7 and 1.4 mya occur in Ethiopia, Kenya, Tanzania, and Malawi. Molars of enormous size equipped with thick enamel provide evidence for a dietary change in *Paranthropus*, whereas early representatives of the genus *Homo* are believed to have responded to the same changes by developing methods of food preparation using stone artifacts, a more flexible strategy over the long term.

Paranthropus represents an ecologically restricted and ecologically specialized side branch in the hominin lineage (Sponheimer et al. 2007; but for an opposing view see Wood & Strait 2004). In South Africa, paranthropine hominins appeared between 2.0 and 1.0 mya at Kromdraai, Drimolen, Coopers cave, and Swartkrans. Evidence for the presence of early *Homo* in South Africa is disputed by Kuman and Clarke (2000), although a case has more recently been made for an endemic species of *Homo* in South Africa at this time (Curnoe 2010). Following the global climate cooling between 3 and 2 mya, the gracile australopithecines in South Africa would have found their preferred habitats shifting northwards towards the equator.

There is perhaps no other segment of the hominin lineage over which there is such taxonomic debate as that which incorporates the origin of the genus *Homo*. Historically, the taxon was first described from Olduvai Gorge in Tanzania, and termed *Homo habilis* in terms of morphology and the presence of stone artifacts. Coeval hominins

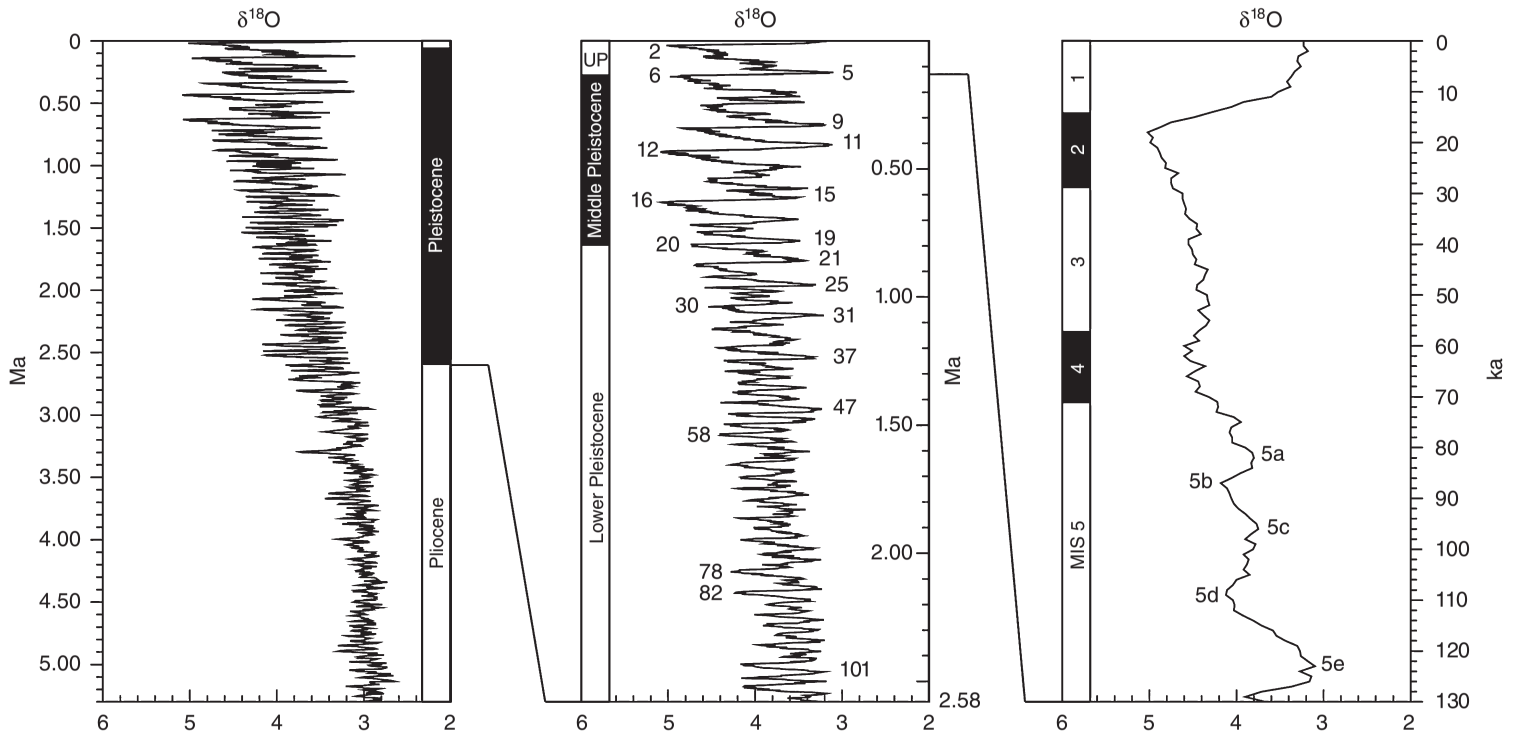

Figure 2.2 $\delta^{18}O$ isotope records at increasing resolutions for the last 5.3 myr (left), the Pleistocene and Holocene (2.58–0.0 myr, center), and the Upper Pleistocene and Holocene (130–0 kyr, right). The ratios between the oxygen isotopes $\delta^{18}O$ and $\delta^{16}O$ in marine cores reflect trends in the global temperature record. Higher temperatures are shown as excursions to the right, lower temperatures to the left. The oscillations are used to divide the record in the two right hand diagrams into marine isotope stages (MIS). Interglacials are identified by uneven MIS numbers (the Holocene is MIS 1), glacials by even numbers.

Data source: Lisiecki & Raymo 2005.

with more robust dentitions and less primitive postcranial skeletons have since been discovered in Kenya (Koobi Fora), Ethiopia (Omo), and Malawi (Uraha), and a new taxon has been suggested for these, namely *Homo rudolfensis* (Wood 1992). If both species are valid, one of them should represent an extinct evolutionary side branch. The other will have given rise to all subsequent *Homo* species.

One way around this problem is to suggest that *Homo habilis* in East Africa was the successor of *Australopithecus africanus* that migrated northwards from South Africa around 2 mya, whereas *H. rudolfensis* was a separate lineage, restricted to eastern Africa, that slightly antedated *habilis* and persisted there until 1.9 mya. At Uraha in Malawi, *H. rudolfensis* was associated with an essentially East African fauna (Bromage et al. 1995), demonstrating that this specimen was not part of the northward expansion from southern Africa that gave rise to the evolution of *habilis*. It will be possible to test this scenario by providing comparative ecological preferences for *Australopithecus africanus* and both of the *Homo* species. *A. africanus* and *H. habilis* should possess comparatively wide ecological adaptations because they occur in a wide corridor between eastern and southern Africa, from the equator into higher latitudes. In contrast, *H. rudolfensis* appears to have been restricted to equatorial and tropical environments.

Early Pleistocene corridors between Africa and Eurasia

After 2 mya, representatives of an Early Pleistocene *Homo* species (attributed either to *Homo erectus* or *H. ergaster*, the latter being an East African geographical variant of *H. erectus*) evolved from early *Homo* ancestors. Unlike their predecessors, these hominin species were extremely mobile. The oldest fossil evidence for them, with an age of 1.9 mya, comes from Kenya (Koobi Fora). Within the next 100 millennia, *H. ergaster/erectus* spread across a huge area incorporating Tanzania (Olduvai), South Africa (Swartkrans), and beyond the African continent to Georgia (Dmanisi). *H. ergaster/erectus* had a comparatively large cranial capacity of more than 800 cubic cm and essentially modern body proportions, with comparatively long legs. This species apparently overcame many of the ecological barriers that were still operative for *Paranthropus* and *H. habilis* (Antón 2003).

In Africa, the period between 3 and 2 mya witnessed considerable taxonomic diversification, whereas in the following million years this taxonomic diversity gradually vanished to leave only the genus *Homo* in Africa by 1 mya. The global cooling trend continued, and there is some evidence that continental climates in eastern and southern Africa were characterized by increasing aridity (Feaking & de Menocal 2010), as well as by increasing seasonality and rapid shifts in humidity (Trauth et al. 2005). By 1 mya, extinctions had eliminated all hominin species in Africa apart from the descendants of *Homo ergaster/erectus*. In eastern Africa, *Homo habilis* and *Paranthropus boisei* became extinct by 1.4 mya, the youngest specimens being described from Ileret in the East Turkana region of Kenya and from Konso-Gardula in Ethiopia. In southern Africa, *H. habilis* survived until 1.5 mya at Sterkfontein, *P. robustus* possibly until 1 mya at Swartkrans. Climatic change, in conjunction with competition with an ecologically

more flexible *Homo* taxon, certainly influenced extinction rates amongst Early Pleistocene hominins.

The oldest direct evidence for hominin fossils in Eurasia comes from Dmanisi in Georgia, dated to 1.77 mya (Lordkipanidze et al. 2007). Over 50 hominin specimens have been discovered here, representing at least seven individuals. The spectrum of finds also includes fauna and artifacts. Initially described as small-brained *Homo ergaster*, the hominins were later attributed to a new species, *H. georgicus*. Artifacts associated with the Dmanisi hominins represent an Oldowan pebble-tool and flake industry. With respect to anatomy, the Dmanisi hominin sample is not sufficiently homogenous to fit a single taxonomic designation, and a large-scale dispersal of an early *Homo* taxon preceding *H. ergaster/erectus* is possible.

A West Asian corridor through the Levant links eastern Africa and the Caucasus. Several studies have recently examined the question of whether a hominin dispersal through here between 2.0 and 1.8 mya is reflected by other large mammal dispersals along the same corridor. However, the large mammal fauna described from Dmanisi has an essentially Eurasian character and lacks elements of clear African provenance. Although African large mammals occasionally entered Eurasia, no particular dispersal events can be recognized at this time. The Dmanisi hominins apparently arrived on their own without fellow travelers (O'Regan et al. 2011).

Dispersals into eastern Asia

The earliest direct evidence for a hominin presence in eastern Asia comes from central Java, where Lower Pleistocene hominins from Sangiran, with an age of more than 1.5 mya, have been assigned to *Homo erectus* (see chapter 6). The first hominins in Java are comparatively robust. The *Homo erectus* type specimen from Trinil represents a more evolved stage and could possess an age of more than 1 mya (Larick et al. 2001). *H. erectus* persisted and evolved in Java until the Upper Pleistocene. Immigrations into Java were limited by the alternating drowning and exposure of the Sunda Shelf, linking the Southeast Asian mainland with the Greater Sunda islands. Hominin occurrences are linked to the emergence and consolidation of an Early to Middle Pleistocene fauna characterized by the occurrence of the proboscidean genus *Stegodon*. This fauna indicates habitats which were more open and less forested than at present.

For the wide area between East Africa, the Caucasus, and Java, fossil evidence for the earliest hominins is absent. Relations between the Dmanisi and Javan hominins are not straightforward, given the small size of the Dmanisi individuals – those from Java are particularly large and robust. The hominins from Java may thus result from an independent dispersal out of Africa, perhaps across the mouth of the Red Sea and through the Arabian peninsula. With his "Savannahstan" hypothesis, Robin Dennell (2010) provides a model for hominin dispersal out of Africa and into Asia that reflects patterns of climate change and corresponding environmental shifts. Dennell postulates a uniform type of grassland environment that stretched from northern Africa to central Asia around two million years ago, and this could have supported hominin

dispersals out of Africa. However, both the uniformity of the environment and the suggested close link between hominins and grasslands are contentious.

In China, hominins were present from 1.2 mya onwards, with the oldest so far identified coming from Gongwangling and Chenjiawo in Lantian district, Shaanxi province. The specimens have been attributed to *Homo erectus*. Previously discussed potential hominin specimens from Longgupo with an age of 1.9 mya have now been reassigned to a fossil ape species. It has recently been suggested that the spread of *Homo erectus* to China was associated with the high-latitude northern Chinese *Mammuthus/Coelodonta* fauna (Ciochon 2010), rather than the subtropical *Stegodon/Ailuropoda* fauna. The boundary region between both of these faunas lay in central China and shifted north and south with climatic change (Tong 2007).

Dispersals into Europe

Earliest evidence for the presence of hominins in Europe comes from Atapuerca in northern Spain, where the oldest specimen (a hominin mandible) comes from Sima del Elefante, with an age of 1.2 to 1.1 mya. Larger samples come from Gran Dolina, dated to 780 kya, and Sima de los Huesos, with an age of 600 kya. The older hominins have been attributed to *Homo antecessor*, the younger to *Homo heidelbergensis*. Prior to 1 mya, the hominin presence in Europe was restricted to the Mediterranean region, in accordance with contemporary archaeological evidence from Algeria, Morocco, France, Italy, and Israel. It is still not clear whether *Homo antecessor* arrived in Spain separately from *H. heidelbergensis*. However, Leroy and her colleagues (2011) assume that ancient hominins could only have survived in Europe during transitions from glacial to interglacial periods, with full glacials being too cold for them and the interglacial to glacial transitions too heavily forested. Faunal data presented by Kahlke and his colleagues (2011) confirm mild temperatures and a low degree of seasonality at early hominin sites in Europe, but the region north of the Alps was not colonized by *Homo heidelbergensis* until 800 kya (Parfitt et al. 2010), and evidence from here prior to 150 kya is limited to warm interglacial periods.

Conclusions

The undisputed evidence for early hominin dispersals prior to the emergence of *Homo sapiens* can be summarized in three brief statements. The hominin lineage originated from the African continent. Early representatives of the genus *Homo* left the African continent and colonized Eurasia. According to current evidence from fossil discoveries and stone artifacts, this first "out of Africa" dispersal happened around 1.8 mya. These brief statements set the stage for many regional expansions and retreats, which depended to some extent on the multiple ways in which hominins related to their respective habitats. For instance, detailed reconstructions of African habitats have revealed previously unrecognized dispersals of early hominins within that continent.

Links, corridors, and barriers between environments in eastern and southern Africa are beginning to emerge, and provide exciting perspectives for further research. The initial out-of-Africa event around 1.8 mya represents an enormous expansion over the prior hominin distribution, involving migrations that somehow circumvented sea straits and mountain chains and reached latitudes up to 45°N in Asia. This latitudinal barrier was only overcome much later by *Homo sapiens*.

SEE ALSO: 3 Hominin migrations before *Homo sapiens*: Out of Africa – how many times?; 6 Pleistocene migrations in the Southeast Asian archipelagos

Note

1 To which should be added the recently announced *A. sediba* from Malapa cave near Sterkfontein, dated to just under 2 mya (Pickering et al. 2011). (Ed.)

References and further reading

Antón, S. C. (2003) Natural history of *Homo erectus*. *Yearbook of Physical Anthropology* 122 Suppl. 37, 126–170.

Bromage, T. G., Schrenk, F., & Zonnefeld, F. W. (1995) Paleoanthropology of the Malawi Rift: an early hominid mandible from the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* 28, 37–57.

Cerling, T. E., Harris, J. M., MacFadden, B. J., et al. (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389, 153–158.

Ciochon, R. L. (2010) Divorcing hominins from the *Stegodon-Ailuropoda* fauna: new views on the antiquity of hominins in Asia. In Fleagle, Shea, Grine, et al. (2010), pp. 111–126.

Curnoe, D. (2010) A review of early *Homo* in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis*). *Homo* 61, 151–177.

Dennell, R. W. (2010) The colonization of "Savannahstan": issues of timing(s) and patterns of dispersal across Asia in the Late Pliocene and Early Pleistocene. In Fleagle, Shea, Grine, et al. (2010), pp. 7–30.

Feaking, S. J. & de Menocal, P. (2010) Global and African regional climate during the Cenozoic. In Werdelin & Sanders (2010), pp. 45–55.

Fleagle, J. G., Shea, J. J., Grine, F. E., et al. (2010) (eds.) *Out of Africa I*. Dordrecht: Springer.

Foley, R. A. & Elton, S. (1998) Time and energy: the ecological context for the evolution of bipedalism. In E. Strasser, J. Fleagle, A. Rosenberger, & H. McHenry (eds.), *Primate Locomotion: Recent Advances*. New York: Plenum, pp. 419–433.

Jacobs, B. F., Pan, A. D., & Scotese, C. R. (2010) A review of the Cenozoic vegetation history of Africa. In Werdelin & Sanders (2010), pp. 57–72.

Kahlke, R.-D., García, N., Kostopoulos, D. S., et al. (2011) Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews* 30, 1368–1395.

Kuman, K. & Clarke, R. J. (2000) Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution* 38, 827–847.

Larick, R., Ciochon, R. L., Zaim, Y., et al. (2001) Early Pleistocene $^{40}Ar/^{39}Ar$ ages for Bapang Formation hominins, Central Jawa, Indonesia. *Proceedings of the National Academy of Sciences* 98, 4866–4871.

Leroy, S. A. G., Arpe, K., & Mikolajewicz, U. (2011) Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. *Quaternary Science Reviews* 30, 1448–1463.

Lisiecki, L. E. & Raymo, M. E. (2005) A Plio-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanography* 20: PA1003 (online doi: 10.1029/2005PA001164).

Lordkipanidze, D., Jashashvili, T., Vekua, A., et al. (2007). Postcranial evidence from early Homo from Dmanisi, Georgia. *Nature* 449, 305–310.

O'Regan, H. J., Turner, A., Bishop, L. C., et al. (2011) Hominins without fellow travelers? First appearances and inferred dispersals of Afro-Eurasian large mammals in the Plio-Pleistocene. *Quaternary Science Reviews* 30, 1343–1352.

Parfitt, S. A., Ashton, N. M., Lewis, S. G., et al. (2010) Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* 466, 229–233.

Pickering, R., Dirks, P., Jinnah, Z., et al. (2011) *Australopithecus sediba* at 1.977 mya and implications for the origins of the genus *Homo*. *Science* 333, 1421–1423.

Ravelo, A. D., Andreasen, D., Lyle, M., et al. (2004) Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature* 429, 263–267.

Sponheimer, M., Lee-Thorp, J., & de Ruiter, D. (2007) Icarus, isotopes and Australopith diets. In P. S. Ungar (ed.), *Evolution of the Human Diet*. Oxford: Oxford University Press, pp. 132–149.

Tong, H. W. (2007) Occurrences of warm-adapted mammals in north China over the Quaternary Period and their paleoenvironmental significance. *Science in China Series D: Earth Sciences* 50(9), 1327–1340.

Trauth, M. H., Maslin, M. A., Deino, A., & Strecker, M. R. (2005) Late Cenozoic moisture history of East Africa. *Nature* 309, 2051–2053.

Turner, A. & Wood, B. (1993) Taxonomic and geographic diversity in robust australopithecines and other African Plio-Pleistocene mammals. *Journal of Human Evolution* 24, 147–168.

Werdelin, L. & Sanders, W. J. (2010) (eds.) *Cenozoic Mammals of Africa*. Berkeley: University of California Press.

Wood, B. (1992) Origin and evolution of the genus *Homo*. *Nature* 355, 783–790.

Wood, B. & Strait, D. (2004) Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution* 46(2), 119–162.