



News and Views

The Denisova hominin need not be an out of Africa story

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The recent retrieval of a complete mitochondrial (mt) DNA sequence from a 48–30 ka human bone from Denisova (Siberia) (Krause et al., 2010) is a remarkable achievement fully deserving international acclaim. Without wishing to detract from this feat, however, we wish to challenge their conclusion that the Denisova hominin “derives from a hominin migration out of Africa [ca. 1.0 Ma] distinct from that of the ancestors of Neanderthals and of modern humans” (Krause et al., 2010: 894). In addition, we challenge their assumption that the ancestors of the Neanderthals left Africa between 500–300 ka. In our view, alternative interpretations of the evidence are available and should be considered.

Did the Denisova hominin derive from “a hominin migration out of Africa [ca. 1.0 Ma] distinct from that of the ancestors of Neanderthals and of modern humans” (Krause et al., 2010: 894)?

In support of Krause et al. (2010), there is evidence of hominin dispersals from Africa after the first documented appearance of *Homo erectus* ca. 1.75 Ma and before 0.5 Ma. Mammalian dispersals from Africa were much easier in the Early Pleistocene than during the Middle Pleistocene (see below) and several are recorded. Examples from the early part of the Early Pleistocene include the presence of several African taxa at Dmanisi, Georgia, ca. 1.75 Ma (Gabunia et al., 2000); ‘Ubeidiya, Israel, ca. 1.4–1.0 Ma (Tchernov, 1987); the An Nefud desert, Saudi Arabia (Thomas et al., 1998);

Giraffa camelopardis at Latamne, Syria, from the late Early Pleistocene (Guérin et al., 1993) (depending on whether or not the gravels underlying the Acheulean horizon at this site are regarded as late Early Pleistocene in age); and the African suid *Kalpochoerus* at Evron, Israel, ca. 1.0 Ma (Tchernov et al., 1994). *Theropithecus*, *Palaeoloxodon antiquus*, *Panthera leo*, and *Panthera pardus* were other mammals that left Africa in the Early Pleistocene (Martínez-Navarro and Rabinovich, in press). There is also archaeological evidence of at least two hominin dispersals before 0.7 Ma. The first is marked by the appearance of an early Acheulean bifacial technology at ‘Ubeidiya, Israel, ca. 1.4–1.5 Ma (Bar-Yosef and Goren-Inbar, 1993), and the second is marked by the appearance of African types of cleavers at Gesher Benot Ya’aqov (GBY), Israel, ca. 780 ka (Saragusti and Goren-Inbar, 2001). Both of these dispersals appear to have been very localised within Asia, as there is no unequivocal evidence of Acheulean assemblages outside the Levant until ca. 500–600 ka, when they are found in Europe and India.

Although hominins could therefore have dispersed from Africa ca. 1.0 Ma, as suggested by Krause et al. (2010), we also need to bear in mind both the small number of relevant African finds from the late Early Pleistocene and the virtual absence of fossil skeletal evidence from the 5,500 miles of continental Eurasia (i.e., excluding Java) between Spain and China (a gap equivalent to the distance from London to Johannesburg). In Africa, the crania from Buia (0.9 Ma) and Daka (ca. 1 Ma) are the most relevant to understanding whatever might have been happening in Asia. Neither are straightforward examples of African *H. erectus*; the Daka cranium has been classified as *H. erectus* (Asfaw et al., 2008), although Manzi et al. (2003) suggested that it should be excluded from what is generally described as *H. erectus* s.s. A preliminary assessment of the Buia cranium (preliminary because matrix obscured the left side of the cranium) indicated a mixture of *H. erectus* and *Homo sapiens* traits, and its specific allocation still remains uncertain (Abbate et al., 1998). Neither specimen has obvious counterparts in Asia. Within Eurasia, the fossil hominin evidence from Southwest Asia – the cross-roads between Africa and Europe, but also the “black hole of palaeoanthropology” (Dennell, 2009:192) – between 1.5–0.5 Ma is limited to a few incisors from ‘Ubeidiya, one of which has been identified as *H. erectus* (Belmaker et al., 2002). The earliest European hominin evidence is the mandible from the Sima del Elefante (ca. 1.3 Ma) (Carbonell et al., 2008) and an assemblage of >150 specimens from the Gran Dolina TD6 level, ca. 0.8–1.0 Ma (Falgoutès et al., 1999; Berger et al., 2008) that is attributed to *Homo*

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antecessor (Carbonell et al., 1995, 2008; Bermúdez de Castro et al., 1997). Putting aside discussions about its taxonomic distinctiveness (e.g., Lahr and Foley, 1998; Rightmire, 2008; Hublin, 2009; but also see Bermúdez de Castro et al., 1997, 2003; Delson et al., 2000; Mounier et al., 2009; Stringer, 2009), morphologically, the European Early Pleistocene populations currently represented by the Sierra de Atapuerca hominins are closer to Early Pleistocene hominins from Asia than those from Africa (Carbonell et al., 2005, 2008; Martínón-Torres et al., 2007). Archaeologically, the absence of any Acheulean artefacts at Atapuerca would make a Eurasian origin more likely, as hominins dispersing from the Levant after 1.4 Ma would be expected to retain an Acheulean technology. The Chinese evidence ca. 1 Ma is limited to the cranium from Lantian (Gongwangling), for which an age of 1.15 Ma is most commonly cited (An and Ho, 1989), and the two crania from Yunxian, which probably date to 0.8–1.0 Ma. Both have previously been assigned to *H. erectus* (Wu and Poirier, 1995). Work in progress indicates that the Gongwangling cranium is likely significantly older than 1.15 Ma and nearer in age to that of Dmanisi, and is thus not relevant here. With a cautionary note due to the high distortion of this fossil, the Yunxian crania may show affinities with *Homo heidelbergensis* (Stringer, 2002; Etler, 2010; see below), may or may not be derived directly from the population represented by the Gongwangling specimen, and may not be ancestral to the better known *H. erectus* population at Locality 1, Zhoukoudian.

Although hominins could therefore have dispersed from Africa ca. 1.0 Ma, as suggested by Krause et al. (2010), large-scale dispersals also occurred within Eurasia in the Early Pleistocene. Some were latitudinal: one example is the recent discovery of artefacts at Happisburgh that probably date to MIS 21 (866–814 ka) or MIS 25 (970–936 ka), and show a significant northward extension of the hominin range to 530 N into areas of coniferous forest (Parfitt et al., 2010). Another example is the earliest evidence from Central Asia, where the first appearance of hominins is evidenced by artefacts from Kuldara, dated to ca. 0.9 Ma (Ranov, 1995). In both cases, hominins were present throughout the late Early and Middle Pleistocene only during interglacials, when they expanded northwards from source populations in southerly refugia. There were likely also large-scale longitudinal mammalian dispersals across Eurasia before the Middle Pleistocene. Examples are the presence of the Indian *Hemibos* at the Cava di Brecchia, Italy, during the Early-Middle Pleistocene transition (Martínez-Navarro and Palombo, 2004), the South Asian *Stegodon* and *Elephas maximus* at Evron Quarry, Israel, ca. 1.0 Ma (Tchernov et al., 1994), and *Stegodon* at GBY, Israel, ca. 0.78 Ma (Martínez-Navarro and Palombo, 2004). One hominin dispersal that we consider likely is from SW Asia to Western Europe by 1.3 Ma, as indicated by the mandible from Sima del Elefante (Carbonell et al., 2008). There were probably also longitudinal dispersals between Central Asia and North China throughout the Early Pleistocene, when cold, dry periods were shorter and less severe than in the Middle Pleistocene, as indicated by the significantly lower rates of loess deposition in both Tajikistan and the Chinese Loess Plateau (Liu and Ding, 1998; Ding et al., 2002). Recently, several researchers have suggested the occurrence of multiple hominin dispersals and complex demographic patterns and population interactions (including interbreeding among groups) (Bermúdez de Castro et al., 2003; Hublin and Roebroeks, 2009; Dennell et al., 2010; Green et al., 2010; Krause et al., 2010). Under conditions of repeated fragmentation and recombination, part of the European Early Pleistocene population's gene pool could have developed in isolation as a separate deme and persisted in time. The mid-Middle Pleistocene dates (0.45 ± 0.05/–0.10 Ma) for Ceprano (Muttoni et al., 2009), tentatively assigned to *H. antecessor* (Manzi et al., 2001) because of its primitive morphology and lack of Neanderthal traits (see also Manzi et al.,

2010), could support this scenario. Within this frame, 1.0 Ma DNA from Denisova could be another example of lineage persistence in time. Interestingly, the Yunxian evidence has recently been cited as an “ideal candidate” for the ancestor of both the Denisova hominin and *H. heidelbergensis* in both Europe and Africa, and thus it may also imply a large-scale dispersal westwards after 1.0 Ma (Etler, 2010). Therefore, whilst a dispersal event out of Africa may have occurred ca. 1.0 Ma, dispersal events within Eurasia seem at least as likely. As there is no ancient DNA evidence from Eurasian populations of *H. antecessor*, *H. heidelbergensis*, and East Asian *H. erectus*, it is thus a massive assumption that the source of the Denisova mtDNA was necessarily African.

Did *H. heidelbergensis* leave Africa ca. 500–300 ka?

A popular scenario is that *H. heidelbergensis* originated in Africa; some groups left ca. 500 ka, dispersed into Europe and possibly India (Cameron et al., 2004), and thereby introduced an Acheulean bifacial technology into these regions (e.g., Klein, 2009). Some have even claimed that *H. heidelbergensis* dispersed as far east as China (e.g., Stringer, 1990, 1992; Rightmire, 2001).

There are several reasons for expressing caution over this scenario. First, archaeologically, there is no need to postulate an immediate African origin for the Acheulean in Europe or India ca. 500 ka, as an Acheulean hand-axe and cleaver tradition with clear African affinities is evidenced at GBY, Israel, ca. 780 ka. The Levant is a far more likely starting point for the Acheulean of Europe and India after 500–600 ka than an East African one. There is also no clear evidence that later Levallois technologies in Eurasia were African in origin (*contra* Foley and Lahr, 1997), and not independent, indigenous developments within those areas where Acheulean bifacial technologies were used (Tuffreau, 1995). Second, the ambiguities and limitations of the Middle Pleistocene hominin record preclude firm inferences about these events. One of the few statements that specialists who deal with the Middle Pleistocene hominin record might agree upon is that there is very little agreement over the origin, definition, and thereby, extent of *H. heidelbergensis*. Again, we need to be mindful of the current limitations of the fossil hominin record of continental Asia west of Central China, which remains extremely poor between 1.0–0.4 Ma: from SW Asia, there are only two cranial fragments, one from Kocabaş, Turkey (Kappelman et al., 2007), and one from Nadaouiyeh, El Khowm, Syria (Le Tensorer et al., 2006), both tentatively attributed to *H. erectus*; nothing from India and Central Asia, and only a few teeth of *H. erectus* from mainland SE Asia, from Tham Khuyen, Vietnam (Ciochon et al., 1996). In Europe, the fossil hominin record between 1.0–0.5 Ma is limited to that from Atapuerca (i.e., the TD6 *H. antecessor* material, and possibly the hominin assemblage from Sima de los Huesos, but only if the date of ≥0.6 Ma [Bischoff et al., 2007] is accepted: we are aware that the latter remains controversial [see Endicott et al., 2010]), possibly the type specimen from Mauer, for which ages of 0.5 Ma or 0.6 Ma are the most commonly cited; and the tibia fragment and three incisors from Boxgrove (Roberts et al., 1994; Hillson et al., 2010). However, we now have to exclude the recently redated cranium from Ceprano (Muttoni et al., 2009), which now appears to have no known counterpart in the fossil record (Manzi et al., 2010).

Because the absolute dating of key specimens attributed to *H. heidelbergensis* or *Homo rhodesiensis* is still problematic, the relative dating of specimens remains unclear: obvious examples are Kabwe and Sima de los Huesos. At present, it is not even unequivocally clear that the earliest example of *H. heidelbergensis* (if considered as an Afro-Eurasian lineage) is African rather than European or East Asian. Dentally, the Pleistocene Eurasian

specimens appear to be distinct from those from Africa (Martínón-Torres et al., 2007), although an enlarged Middle Pleistocene African sample might eventually indicate otherwise. Even in the case of the latter, similarities between European and African Middle Pleistocene hypodigms would be equally compatible with a scenario where Eurasian populations are the source for the African ones and vice versa. Cranial and postcranial evidence show similarities between African and European Middle Pleistocene fossils such as Bodo, Kabwe, Arago, and Petralona (e.g., Stringer, 1983; Churchill et al., 2000; Rightmire, 2001; Carretero et al., 2009; Harvati et al., 2010; but see also Arsuaga et al., 1997, 1999; Martínez and Arsuaga, 1997, for differences), or even between Petralona and Dali, but it is not clear whether or not these features are plesiomorphies or derived from when inter- and intra-continental contacts were more feasible before 500 ka. As examples of the range of current interpretations on offer, one can argue either that *H. heidelbergensis* originated in sub-Saharan Africa and dispersed as far as China (Stringer, 1990, 2002; Rightmire, 2001), or that it originated in China and eventually dispersed as far as sub-Saharan Africa (Etler, 2010)! Alternatively, it has been suggested that African specimens such as Bodo, Kabwe, and Ndutu should be classified as *H. rhodesiensis* (McBrearty and Brooks, 2000; Hublin, 2001), and seen as distinct from *H. heidelbergensis*, which is thus restricted to Eurasia. Consistent with that suggestion, a SW Asian origin of *H. heidelbergensis* has been proposed, possibly with some traits shared with *H. antecessor* (Martínón-Torres et al., 2006, 2007; Gómez-Robles et al., 2007; Bermúdez de Castro et al., 2008; Carbonell et al., 2008; Dennell, 2009). Here, we are not advocating any one of these scenarios but aim only to point out that there are several alternatives to the one presented by Krause et al. (2010). Based on the differences in the genetic diversity of *H. sapiens* and *H. neanderthalensis* (e.g., Orlando et al., 2006; Green et al., 2010; Krause et al., 2010), future genetic studies might contribute to this debate by analysing the theoretical genetic models behind “Africa into Eurasia” and “Eurasia into Africa” scenarios.

The third line of evidence requiring interpretive caution includes faunal data, which indicate that Africa and SW Asia were probably largely isolated by the Saharan-Arabian desert barrier between 500–300 ka. Evidence of faunal movement from Africa to Asia in the Middle Pleistocene is far more limited than for the Early Pleistocene, and this impacts directly on both the assumption that the Neanderthals' ancestors left Africa ca. 500–300 ka (Krause et al., 2010), and assessments of whether *H. heidelbergensis* should be regarded as a Eurasian or Afro-Eurasian population. Starting ca. 950 ka, NE Africa became extremely arid until at least 650 ka (Almogi-Labin, in press). The only mammals recorded at GBY ca. 0.78 Ma, that are also recorded in Africa, are *Hippopotamus amphibius*, which may be present at Kapthurin, Kenya, although the evidence is unclear (O'Regan et al., 2005), and *Bos*, which Martínez-Navarro et al. (2007, 2010; see also Martínez-Navarro and Rabinovich, in press) considered to be African in origin, and to have dispersed out of Africa at the same time as the Acheulean, which could have been as early as 1.4 Ma when the Acheulean is first recorded in the Levant. (However, Geraads (2010) considered that *Bos* originated in Asia and later dispersed into East Africa, so this line of evidence appears ambiguous). According to O'Regan et al. (2005), there is no evidence for mammalian dispersal from Africa into SW Asia in the Early-Middle Pleistocene, i.e., 780–500 ka. Between this time and the last interglacial, the only evidence of any African fauna in SW Asia is one specimen of the African hunting dog *Nyctereutes* at Hayonim in the late Middle Pleistocene (Stiner et al., 2001). The faunal assemblages <400 ka from sites such as Qesem, Tabun, Umm Qatafa, and Hayonim, etc., are Eurasian, as stated by Tchernov (1992:118), who noted that, for the

mid- to late-Middle Pleistocene, “The ‘Levantine Corridor’ was a cul de sac rather than a passage way, as the Saharan belt was too firmly closed to allow free dispersal into sub-Saharan domains.”

Although dispersals from Africa into SW Asia between 400 ka and the last interglacial ca. 125 ka seem highly improbable, there is a gap in the Levantine faunal sequence between 400–500 ka. Some dispersal might therefore have occurred during this relatively brief window, although faunal movement in the Middle Pleistocene between North Africa and the Levant appears to have been extremely limited (Geraads, 2010). Additionally, we do not know the extent, timing, and duration of wet phases in the eastern Sahara, Sinai, and Negev deserts before MIS 6 that might have briefly allowed some dispersals from Africa into SW Asia. The biggest gap in the current knowledge of faunal dispersals out of Africa in the Middle Pleistocene is the Arabian Peninsula, which has no Middle Pleistocene faunal record but does have a diverse modern fauna that reflects its geographic position at the crossroads of NE and N. Africa and SW Asia. However, there are currently no indications that mammals dispersed from Africa and headed east via southern Arabia in the Middle Pleistocene. Overall, the faunal evidence argues firmly against hominin dispersals out of Africa between 500–125 ka, and only weakly in its favour between 500–800 ka.

Some researchers might assume that *H. heidelbergensis*, by reason of its large brain and a bifacial technology, had the ability to “buck the trend,” and traverse desert areas that were impassable to other mammals. Yet, the evidence seems to indicate otherwise: in northern Europe and Central Asia, hominin dispersals in the Middle Pleistocene were strongly constrained by climate and thus limited to interglacials or their moist, warm equivalents in non-glaciated regions (e.g., Ranov and Dodonov, 2003; Stringer, 2006). This also seems true of Central China (RD, pers. obs.) and probably India, where a few basin areas were the favoured, core areas of settlement (Korisettar, 2007). African hominins also appear to have operated under similar climatic constraints in the Middle Pleistocene (see Barham and Mitchell, 2008), and there seems no obvious reason to assume that they could successfully cross large areas of desert.

We suggest, therefore, that the evidence that the ancestors of Neanderthals dispersed out of Africa between 500–300 ka is, *contra* Krause et al. (2010), equivocal on chronometric and morphological grounds, and improbable on archaeological and faunal grounds. Earlier dispersals between Africa and Asia might have been possible in interglacial periods, but we suggest that the current Eurasian fossil record between Spain and China is so poor that the place of origin of *H. heidelbergensis* cannot yet be determined with confidence. As noted above, arguments can be made in favour of Africa, SW Asia, or China.

Summary

As outlined above, we urge caution over both the interpretative framework of Krause et al. (2010) and their main conclusion. The evidence that the ancestors of Neanderthals (i.e., *H. heidelbergensis*) left Africa ca. 500–300 ka is currently inconclusive, and the origin of *H. heidelbergensis* remains enigmatic. Whilst dispersals out of Africa might have occurred ca. 1.0 Ma, large-scale dispersals within Asia were also probable, and thus an Asian origin of the Denisovans cannot be excluded. These issues cannot be resolved without substantial improvements in the dating of key specimens, without an enlarged Asian fossil hominin record (particularly from SW Asia), and without a much more detailed Middle Pleistocene climatic record from SW Asia and NE Africa. Although the Denisova evidence is undoubtedly a fascinating piece in the jigsaw puzzle of human origins, it would be premature at present to determine the part of the picture to which it belongs.

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