Title: When did *Homo sapiens* first leave Africa?

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Acknowledgments:

Chris Stringer and Julia Galway-Witham's work is supported by the Calleva Foundation and the Human Origins Research Fund

Our species *Homo sapiens* is characterised by skeletal features that can be recognised in African fossils dating back more than 150 thousand years (ka), which include a globular braincase, browridges that are divided into central and side portions, a flat and retracted midface, a chin on the lower jaw, and a narrow pelvis. Fossils showing many of these diagnostic characteristics have been excavated from the Ethiopian sites of Omo Kibish and Herto, dated at about 195 and 160 ka, respectively (*1*). Possible evidence of more primitive members of the species are known from sites such as Jebel Irhoud (Morocco) and Florisbad (South Africa), dated at about 315 and 259 ka, respectively (*1*). In spite of this relatively early appearance of members of our lineage in Africa, *H. sapiens* fossils are only first known outside of Africa around 90-120 ka, from the Israeli sites of Skhul and Qafzeh. It is generally believed that these samples represent the first excursion of our species outside its African homeland, during a humid climatic phase in northern Africa and western Asia. However, new evidence from the site of Misliya Cave, Israel (*2*) suggests that our species had already left Africa by about 180 ka.

Misliya Cave lies on Mount Carmel in Israel, and has been excavated over the last century. It shows successive periods of hominin occupation with Lower and Middle Palaeolithic tools, the use of fire, and the exploitation of a diverse fauna. Given Misliya's position at a crucial crossroads between Africa and Eurasia, the latest discoveries have enormous potential for our understanding of early populations of *Homo sapiens* in western Asia.

The newly excavated material is represented by a partial upper jaw (Misliya-1), which includes some of the bone surrounding the tooth sockets, part of the cheekbone, the roof of the mouth, the bottom of the nasal cavity, and a complete upper dentition from the left side. A 3D statistical analysis of shape indicates that the specimen is very similar to later *Homo sapiens* fossils, falling within the known range of variation with respect to both size and shape. Furthermore, Misliya-1 is clearly dissimilar to Neanderthals and earlier hominin species, lacking their unique diagnostic features, such as a low and broad tooth crown or a disproportionately reduced chewing surface relative to the base of the crown. Hershkovitz *et al.* (*2*) note Misliya-1's similarities to the later Skhul and Qafzeh fossils, though Misliya-1 does exhibit a reduction in the size of one of its tooth cusps relative to the other fossils. While individual traits associated with the morphology exhibited in Misliya-1 are sometimes observed in other hominin taxa, the *combination* of traits is characteristically that of *Homo sapiens*.

Stone tools were excavated from the same stratigraphic layer as Misliya-1 showing the use of Levallois technology, a complex method of tool preparation involving a prepared core. This

technology has also been identified from nearby Tabun Cave between about 190-260 ka, but the material at Misliya represents the earliest known association of this industry with modern human fossils in the region. Recently, Jebel Irhoud (Morocco) also yielded Levallois tools associated with putative early *Homo sapiens* fossils, suggesting that the emergence of this tool technology may be linked with the appearance and dispersal of our species in both Africa and western Asia.

Fossil and archaeological specimens from Misliya were dated using multiple methods applied to the types of material available. Uranium-Thorium and combined Uranium series and Electron Spin Resonance series techniques directly dated the fossil using samples of the tooth dentine and enamel, respectively; Uranium-Thorium dating tested the age of the sediment adhering to the upper jaw; and Thermoluminescence measured the age of the burned tools that had been located close to the fossil. Collectively, the results of these three dating methods estimate the age of Misliya-1 and its associated artefacts at around 177-194 ka.

The pattern of human occupation in western Asia in the period prior to the Misliya specimen is still unclear. Fragmentary fossils are known from the Israeli caves of Qesem and Zuttiyeh, the former consisting of isolated teeth dated to around 400 ka, the latter represented by a partial skull, perhaps of similar antiquity. Both show primitive traits, and some that are found in Neanderthals or *H. sapiens* (*3, 4*). Archaeological evidence for occupation of the region spans the time between these fossils and Misliya, but the record is not well dated, meaning that it is currently impossible to tell whether human presence was essentially continuous, or much more episodic. Palaeoclimatic reconstructions using speleothems, deep sea cores and palaeoenvironmental data suggest that Marine Isotope Stage (MIS) 7 (~244-190 ka) contained several humid phases, one or more of which could have facilitated the spread of *H. sapiens* into the region (*5*). But there were severe periods of aridity before and after MIS 7, meaning that the region was probably more often a 'boulevard of broken dreams' than a stable haven for early humans (*6*). Direct local evolutionary continuity between the population represented by the Misliya fossil and the subsequent Skhul and Qafzeh peoples thus seems unlikely, but could the Misliya population have extended further into Eurasia, encountering Neanderthals, thus leading to gene flow between these two lineages of humans? The main phases of genetic introgression from Neanderthals into *H. sapiens* are estimated to have occurred between ~50-60 ka (*7*), but genetic analyses of Neanderthal fossils from Denisova Cave and Hohlenstein-Stadel indicate at least one earlier phase of introgression, from *H. sapiens* into Neanderthals. However, age estimates for this event are ~219-460 ka, suggesting that it predated the Misliya fossil (*8*). This means that the *H. sapiens* fossils from Misliya, Skhul and Qafzeh could actually represent relatively late excursions of our species from Africa, and that during earlier humid phases, western Asia could have attracted more primitive members of the lineages of *H. sapiens* and *H. neanderthalensis*, providing repeated opportunities for exchanges of genes and technologies.
Beyond western Asia, the evidence for early dispersals of *H. sapiens* prior to ~120 ka is currently weak, with age estimates for the fragmentary Chinese fossils from Zhiren and Daoxian Caves only ranging between about 80-113 ka (*9*). The Misliya find is important in establishing an earlier dispersal of *H. sapiens* from Africa into western Asia, but it also highlights how little we still know about the early occupants of the region, nearly a century after the first discoveries from the caves of Zuttiyeh, Skhul, Qafzeh and Tabun.

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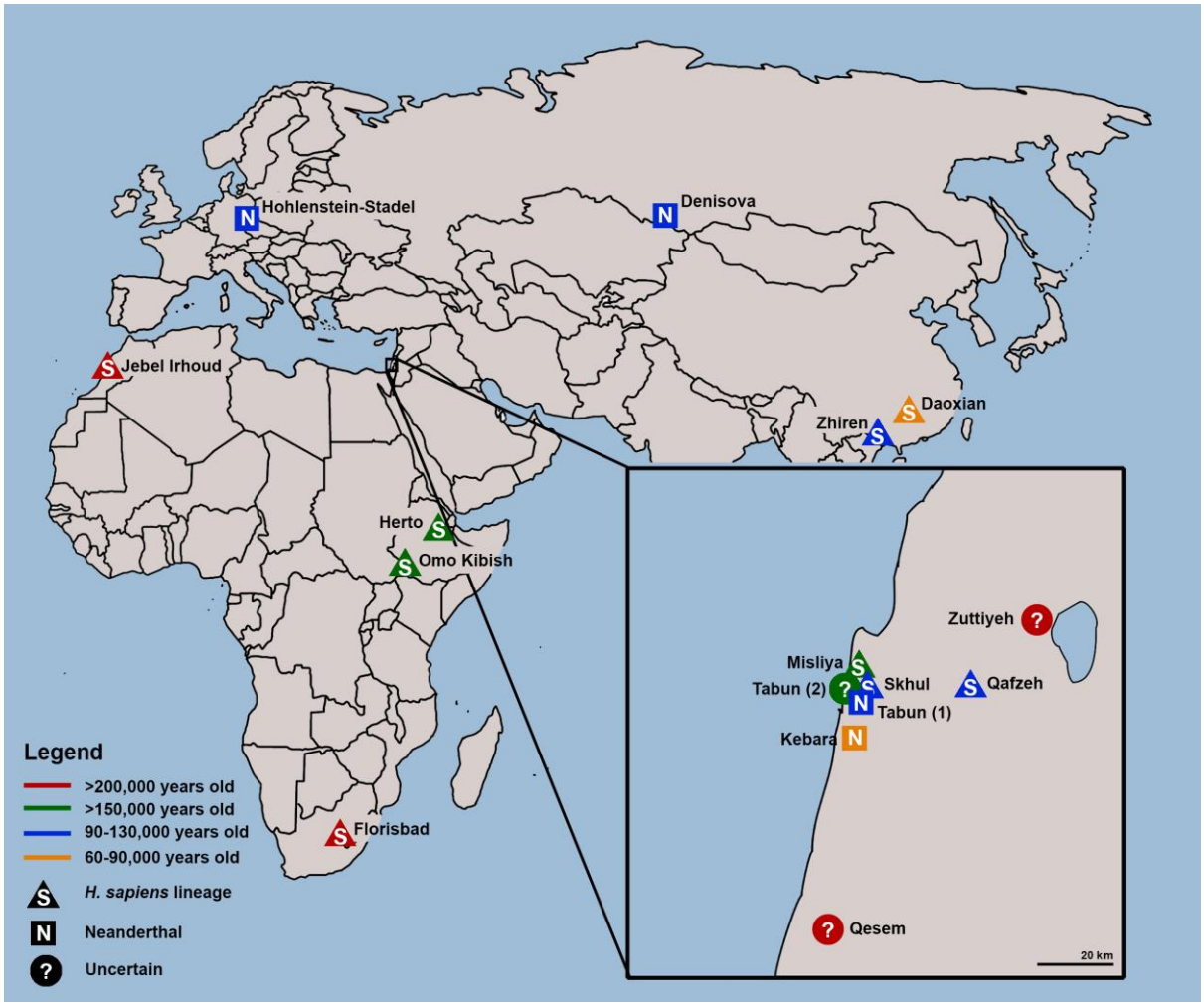
Hohlenstein-Stadel
Denisova
Jebel Irhoud
Daoxian
Zhiren
Herto
Omo Kibish
Florisbad
Zuttiyeh
Misliya
Tabun (2)
Skhul
Qafzeh
Tabun (1)
Kebara
Qesem
20 km
Legend
>200,000 years old
>150,000 years old
90-130,000 years old
60-90,000 years old
H. sapiens lineage
Neanderthal
Uncertain