The earliest modern humans outside Africa

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To date, the earliest modern human fossils found outside of Africa are dated to around 90,000 to 120,000 years ago at the Levantine sites of Skhul and Qafzeh. A maxilla and associated dentition recently discovered at Misliya Cave, Israel, was dated to 177,000 to 194,000 years ago, suggesting that members of the Homo sapiens clade left Africa earlier than previously thought. This finding changes our view on modern human dispersal and is consistent with recent genetic studies, which have posited the possibility of an earlier dispersal of Homo sapiens around 220,000 years ago. The Misliya maxilla is associated with full-fledged Levallois technology in the Levant, suggesting that the emergence of this technology is linked to the appearance of Homo sapiens in the region, as has been documented in Africa.

The timing and routes of modern human migration out of Africa are key issues for understanding the evolution of our own species. The fossil evidence suggests that the earliest members of the Homo sapiens clade (Jebel Irhoud, Omo, and Herto) appeared in Africa during the late Middle Pleistocene (1–4). Outside Africa, modern humans appeared much later, during the Late Pleistocene in the Levant (Qafzeh, Skhul) (5–7), and possibly in East Asia (Daxian) (8). Misliya Cave, Israel, is part of a complex of prehistoric caves along the western slopes of Mount Carmel (Fig. 1 and fig. S1). Here we report on an adult hominin left hemimaxilla (Misliya-1) (Fig. 2A) found in Square N9 of the upper part of the Early Middle Paleolithic (EMP) archaeological layer of the site (Stratigraphic Unit 6, Upper Terrace, Fig. 1 and fig. S1), associated with an Early Levantine Mousterian (Tabun D type) stone-tool assemblages (9, 10). Misliya-1 preserves much of the alveolar and zygomatic processes, part of the palate and nasal floor, and the complete left dentition from the first incisor (represented by a broken root only) to the third molar (Fig. 2A).

Three independent numerical dating methods—U-series (U-Th), combined uranium series and electron spin resonance (US-ESR) series, and thermoluminescence (TL)—carried out in three different laboratories yielded consistent results (Fig. 2B, figs. S2 and S3, and tables S1 and S3). A series of nine TL dates on burnt flints from Square L10 and N12 in the vicinity of the human fossil (Fig. 1, A and B) provided a mean age of 179 ± 48 thousand years (ky) (2σ; range = 212 to 140 ky) (II). U-Th dating of the dentine of the I2 from the maxilla and of the crust adhering directly to the maxilla yielded a minimum age of 70.2 ± 1.6 ky (2σ; table S1) and 185 ± 8.0 ky (2σ; Fig. 2B and table S2), respectively (9). The combined US-ESR dating of the enamel of the same tooth yielded a maximum age of 174 ± 20 ky (2σ).

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Dark gray: Age range for Misliya-1, based on dates obtained from the fossil (U-Th provides the minimum age and combined US-ESR the maximum age), is between 177 ky (=185 – 8 ky) to 194 ky (=174 + 20 ky). Light gray: Age range for the EMP period in the Levant (250 to 140 ky) based on the combination of TL dates obtained for Tabun Cave (13), Hayonim Cave (12), and Misliya Cave (11).

Fig. 2. Various views of the Misliya-1 hemimaxilla and overview of the dating results. (A) Lateral, occlusal, and oblique views of the hemimaxilla from Misliya Cave. Left: The virtual reconstruction; all adhering matrix was removed using virtual techniques. The enamel caps of the teeth were removed to show the dentine surfaces (which were analyzed through landmark-based methods); right: the original specimen. (B) Overview of the dating results obtained at Misliya Cave. All ages are given at a 2σ confidence level. Key: (*) The U-series age on dentine and calcitic crust on the maxilla should be considered as a minimum age estimate for Misliya-1; (**) the combined US-ESR age should be regarded as a maximum age estimate for Misliya-1; (***) average TL date based on nine samples of burnt flint obtained from nearby squares (NI2, LI0; see Fig. 1).

(37x172) of the maxillary morphology (Fig. 3A) is the insertion of the zygomatic root in Misliya-1. The upper premolars display relatively simple occlusal surfaces and lack accessory marginal tubercles and buccal cingulum (Fig. 2A). The Misliya-1 premolars display the typical high and narrow crown of H. sapiens. In the occlusal view, the P4 displays a slight lingual narrowing, which is less pronounced in the P3. This contrasts with the characteristic Neandertal pattern featuring a low and broad crown and subequal buccal and lingual aspects of the crown in both upper premolars. The proportion of occlusal area (defined by the occlusal rim) is large relative to the crown base area in the upper premolars of Misliya-1, unlike in Neandertals, where the occlusal area appears compressed relative to the crown base area. This compression in Neandertal upper premolars is homologous to the relative reduction of the occlusal polygon found in Neandertal M’s (16, 17), and this latter feature is absent in Misliya-1.

The Misliya-1 maxillary teeth are within the upper size range of modern humans (table S5). Size proportions between the anterior and posterior teeth differentiate Misliya-1 from Neandertals (fig. S5). The buccolingual (BL) size ratio of the P2 to P3 in Misliya-1 (62.6) is just outside the upper limit of the range of modern humans (mean = 55.6, SD = 3.4, n = 31, range = 48.2 to 62.5), is similar to the mean of Qafzeh and Skhul (mean = 63.4, SD = 4.9, n = 9, range = 56.1 to 71.4), and well below the lower limit of the range of Neandertals (mean = 70.3, SD = 3.1, n = 33, range = 66.7 to 76.0). Therefore, Misliya-1 does not exhibit the relative expansion of the anterior dentition characteristic of Neandertals (18). Tooth root size and morphology are also within the range of modern human (fig. S4).

Two-dimensional GM analysis (9) of the M3 crown outline (Fig. 4) reveals that Misliya-1 is separate from Neandertals and other European Middle Pleistocene hominins, placing it with modern humans and near to Jebel Irhoud. It differs from Neandertals as well as from other European Middle Pleistocene fossils by not displaying the skewed rhomboidal crown outline.
and large and protruding hypocone. The relative sizes of the M\textsuperscript{1} protocone and hypocone align Misliya-1 with modern humans and differentiate it from Neandertals (table S4).

The 3D GM analysis (9) of the premolars, including the enamel-dentine junction (EDJ) occlusal area and cementum-enamel junction (CEJ) (fig. S6), shows that the Misliya-1 premolars are located in quadrants exclusively occupied by H. sapiens, with the exception of one Atapuerca Sima de los Huesos (SH) P\textsuperscript{3} (that is located in the same quadrant but far from Misliya-1) and the P\textsuperscript{3} of Amud 1. A similar analysis of the Misliya-1 M\textsuperscript{2} (Fig. 3B) places it in an area exclusively occupied by contemporary H. sapiens (and the Liujiang specimen), which are characterized by a reduction of the hypocone and a buccolingually widened (rectangular) crown base. This contrasts with what is observed in Neandertals and most other European Middle Pleistocene fossils where the hypocone is relatively more developed. The Qafzeh specimens are quite variable but uniformly display a larger hypocone than does Misliya-1. The strong reduction of the hypocone observed in M\textsuperscript{2} (table S4), M\textsuperscript{2}, and M\textsuperscript{3} of Misliya-1 is most frequently observed in H. sapiens, although it can occasionally be found in other Homo groups (17, 18).

Overall, the Misliya-1 teeth are distinct from those of the Middle Pleistocene specimens from Europe, Africa, and Asia such as Atapuerca (SH), Steinheim, Rabat, Qesem Cave, Xiaoxian, and Xujiaxao. Although some dental features seen in Misliya-1 can occasionally also be found in some of these samples, the entire suite of metric and morphological traits seen in the Misliya-1 maxillary bone and teeth is more consistent with H. sapiens than with Neandertals or other Middle Pleistocene hominin groups. Indeed, the combination of features in the incisor and canine appears to occur only in H. sapiens (19).

Middle Pleistocene fossils from southwest Asia (e.g., Qesem Cave, Zuttiyeh) are rare and display a mixture of features considered characteristic of Neandertals or modern humans, thus complicating their taxonomic assignment (20–22). Although incomplete, the Misliya-1 maxilla does not exhibit any derived skeletal or dental Neandertal features. A specific comparison with the earlier teeth from Qesem Cave (20, 21) reveals a number of differences. Specifically, the Qesem F\textsuperscript{3} shows a pronounced lingual tubercle, greater degree of labial curvature, and more pronounced shoveling, whereas the Qesem C\textsuperscript{3} shows more pronounced shoveling, a lingual tubercle, and a canine mesial ridge. All of these features are more commonly found in Neandertal anterior teeth and represent points of departure from the morphology seen in Misliya-1 teeth. In contrast, Misliya-1 resembles the later Levantine H. sapiens fossils from the sites of Skhul and Qafzeh regarding many dental features, but it also differs from them regarding the degree of hypocone reduction seen in Misliya-1.

The geographical origin, timing, and identification of the last common ancestor of Neandertals and modern humans remain controversial (23, 24). Nevertheless, the evolutionary emergence of Neandertals in Europe from their Middle Pleistocene precursors [e.g., Atapuerca (SH), Steinheim, Ehringsdorf] is better established, despite the possibility that more than one lineage coexisted in the European Middle Pleistocene (25). The geographical origin of H. sapiens is generally considered to be Africa, and the Jebel Irhoud fossils, recently dated to ~300 ky ago (2), are thought to represent an “early phase of H. sapiens evolution” ([1], p. 291). Younger fossils from the sites of Omo (~195 ky ago) and Herto (~160 ky ago) have been attributed to H. sapiens (3, 4). Nevertheless, the African fossil records reveal temporal overlaps between more “archaic” and more “modern” forms of early H. sapiens (24). These African specimens are thought to be members of the H. sapiens clade, even though some of them fall outside the range...
of variation of Holocene humans regarding certain features (3, 24, 29). Similarly, many of the teeth, which are thought to represent early H. sapiens from North Africa, retain primitive features (26).

Misliya-1 considerably pushes back the timing of the earliest migration of members of the H. sapiens clade out of Africa, well predating Qafzeh and Skhul in the Levant, and Duxiana and Liujian in China (8) and (27); but see (29)).

Archaeologically, the EMP layers of Misliya cave document the emergence of novel technological concepts in the Levant, including full-fledged Levallois technology and laminar technology (29). Similar technological concepts have been documented at contemporary and earlier Middle Stone Age sites in Africa, i.e., the Maghreb (Jebel Irhoud), eastern Africa (Gademotta and Kulkulliet formations, Ethiopia, and the Kaphurin Formation, Kenya), and southern Africa (Kathni Pan) (2, 30–34).

To date, Misliya-1 appears to represent the earliest fossil evidence of the migration of members of the H. sapiens clade out of Africa. It therefore opens the door to the possibility that H. sapiens dispersal from Africa could have occurred earlier than previously thought (probably before 200 ky ago), as has been recently suggested based on genetic evidence (30).

REFERENCES AND NOTES

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Earliest modern humans out of Africa

Recent paleoanthropological studies have suggested that modern humans migrated from Africa as early as the beginning of the Late Pleistocene, 120,000 years ago. Hershkovitz et al. now suggest that early modern humans were already present outside of Africa more than 55,000 years earlier (see the Perspective by Stringer and Galway-Witham). During excavations of sediments at Mount Carmel, Israel, they found a fossil of a mouth part, a left hemimandible, with almost complete dentition. The sediments contain a series of well-defined hearths and a rich stone-based industry, as well as abundant animal remains. Analysis of the human remains, and dating of the site and the fossil itself, indicate a likely age of at least 177,000 years for the fossil—making it the oldest member of the Homo sapiens clade found outside Africa.

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