Uranium series dates from Qesem Cave, Israel, and the end of the Lower Palaeolithic

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Israel is part of a geographical 'out of Africa' corridor for human dispersals. An important event in these dispersals was the possible arrival of anatomically modern humans in the Levant during the late Middle Pleistocene[1–3]. In the Levant the Lower Palaeolithic ends with the Acheulo-Yabrudian complex, characterized by technological developments[4,5], including the introduction of technological innovations such as the systematic production of blades and the disappearance of hand-axes. These reflect new human perceptions and capabilities in lithic technology and tool function[6]. Qesem Cave, discovered in 2000, has a rich, well-preserved Acheulo-Yabrudian deposit holding great promise for providing new insights into the period. Here we report the dates of this deposit obtained by uranium isotopic series on associated speleothems and their implications. The results shed light on the temporal range of the Acheulo-Yabrudian and the end of the Lower Palaeolithic, suggesting a long cultural phase between the Lower Palaeolithic Acheulian and the Middle Palaeolithic Mousterian phases, starting before 382 kyr ago and ending at about 200 kyr ago.

Qesem Cave is situated 12 km east of Tel-Aviv, 90 m above sea level (32° 11′ latitude, 34° 98′ longitude). The cave's ceiling has been removed by natural erosion and recent construction work. Some of the cave deposits were damaged, but enough were preserved to justify a long-term field project. The cave was formed in Turonian limestone in the western foothills of the backbone mountain ridge of Israel under phreatic conditions[7], and after later regional uplift it was dewatered and truncated by subaerial erosion. It has undergone several stages of natural and human-induced deposition, as well as subsidence and collapse. Natural deposits include calcite speleothems, bedrock collapse debris and clay fill, possibly originating from the overlying terra rossa soil. Speleothem deposition apparently occurred in this cave only before the last glacial cycle, probably because of a shift in the flow and dissolution processes of epikarstic water that followed the destruction of the roof. However, active speleothem deposition does occur in the region today, as it did during the last glacial and interglacial periods[8,9].

The 2001 salvage excavation exposed a stratigraphic sequence about 7.5 m deep that contained distinct archaeological horizons. Each of these yielded lithic assemblages in fresh condition and abundant faunal remains, all attributed to the Acheulo-Yabrudian complex of the terminal Lower Palaeolithic[1,4,5]. The archaeological horizons showed differences in lithic technology and typology. Some are dominated by blades and blade-tools (Fig. 1a), whereas in others blades are rare or absent. Thick side-scrapers, the 'fossil directeure' of Yabrudian industries (Fig. 1b), appear throughout the stratigraphic sequence. Hand-axes, the characteristic Acheulian tool type (Fig. 1c), appear in small numbers both at the top and at the bottom of the sequence, but not in every assemblage. The different lithic assemblages were found interspersed within the stratigraphic sequence, much like those in layer E at Tabun Cave and Yabrud I[10–13]. At the base of the cave, above bedrock, typical Acheulo-Yabrudian tool types are rare. Chopping tools and spheroids, typical of Acheulian industries, were found in these assemblages. It seems that the earliest occupation at Qesem predates the Acheulo-Yabrudian.

The chronology of the upper layers of Qesem Cave is based on speleothems from the eastern section of the cave. These were sampled with a cutting disk and their ^{230}Th–^{234}U dates were measured by thermal ionization mass spectrometry (TIMS) at the uranium-series laboratory of Bergen University (Table 1). After conventional chemical preparation, mass abundances of natural U and Th isotopes were measured against a mixed ^{236}U–^{233}U–^{229}Th spike[14]. Ages were calculated with the aid of the TIMS–Age 4U2U program[15] and corrected for thorium detrital content, assuming an initial $^{230}Th/^{232}Th$ ratio of 1.5 (ref. 16). Field relations indicate that the ages were in correct stratigraphic order (Fig. 2). We identified two main stages of speleothem deposition. The first, a massive (about 25 cm thick) flowstone deposit, is dated by five ages (in kyr): 382 ± 37, 300 ± 13, 218 ± 15, 218 ± 16 and 207 ± 12. This flowstone covers the lower Acheulo-Yabrudian layers. A detached part of the flowstone, dated to 254 ± 37 kyr ago, was redeposited in an archaeological breccia deposit, indicating that the breccia is younger. A break in speleothem deposition occurred between about 207 and 152 kyr ago. Within this period the latest human occupation of the cave might have taken place, indicated by thin archaeological sediment directly above the massive flowstone. A second, short period of speleothem deposition took place about 152 kyr ago, represented by two ages of a calcite crust a few millimetres thick, and small stalactites, dated to 152 ± 3 and 152 ± 7 kyr ago. The crust and the stalactites were deposited over the archaeological sediments and can therefore serve as a terminus of human occupation. The major Acheulo-Yabrudian occupations

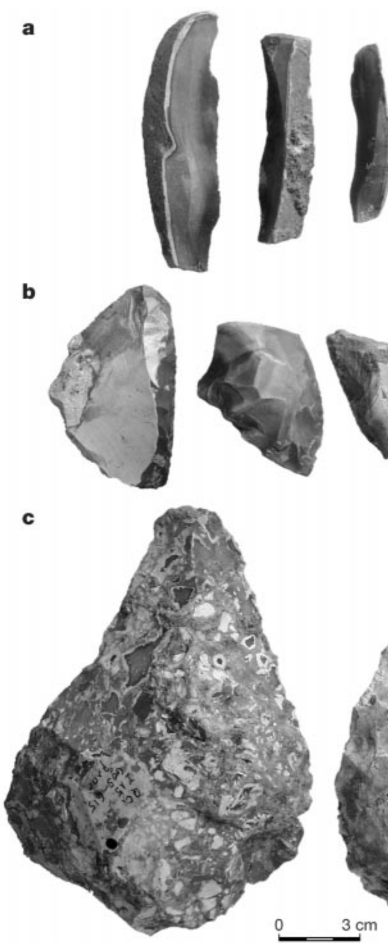

Figure 1 Flint tools from Qesem Cave. **a**, Backed blades; **b**, side-scrapers; **c**, hand-axes.

Table 1 **Isotopic data and ages of speleothems in Qesem Cave**

Sample	^{238}U (p.p.m.)	$^{230}Th/^{234}U$	$^{234}U/^{238}U$	$^{230}Th/^{232}Th$	Initial $^{234}U/^{238}U$	Age (kyr)	Corrected age (kyr)
507 (Q5)	0.36	0.7711 ± 0.0146	1.0266 ± 0.0074	19.51 ± 0.58	1.0417 ± 0.0075	$158.52^{+750}_{-6.96}$	$151.97^{+7.55}_{-7.02}$
501 (Q11-1)	0.78	0.8864 ± 0.0116	1.0869 ± 0.0324	61.96 ± 1.28	1.1624 ± 0.0346	$220.73^{+15.11}_{-12.53}$	$218.52^{+15.11}_{-12.53}$
502 (Q10-1)	0.29	0.9284 ± 0.0212	1.0829 ± 0.0300	23.58 ± 0.37	1.1732 ± 0.0325	$259.98^{+37.06}_{-26.34}$	$253.88^{+37.07}_{-26.34}$
503 (Q3B1)	1.74	0.8698 ± 0.0130	1.0907 ± 0.0183	149.90 ± 1.31	1.1636 ± 0.0195	$208.10^{+12.02}_{-10.56}$	$207.21^{+12.02}_{-10.56}$
504 (Q2)	0.33	0.7624 ± 0.0054	1.0409 ± 0.0143	94.51 ± 0.75	1.0633 ± 0.0146	$153.73^{+3.29}_{-3.12}$	$152.43^{+3.29}_{-3.12}$
528 (Q10-2)	0.18	0.8890 ± 0.0171	1.0543 ± 0.0047	13.98 ± 0.36	1.1037 ± 0.0049	$228.06^{+16.53}_{-14.30}$	$217.65^{+16.61}_{-14.38}$
526 (Q3D1)	0.24	0.9534 ± 0.0065	1.0470 ± 0.0034	24.45 ± 0.38	1.1120 ± 0.0036	$305.87^{+13.53}_{-11.97}$	$299.70^{+13.58}_{-12.03}$
569 Q3D2	0.18	0.9808 ± 0.0057	1.0299 ± 0.0092	78.00 ± 1.10	1.0888 ± 0.0097	$383.94^{+36.73}_{-26.65}$	$381.98^{+36.73}_{-26.65}$

TIMS ages were obtained with a Finnigan 262 RPQ mass spectrometer. Laboratory errors are reported with two standard deviations; $^{230}Th/^{232}Th$ ratios of more than 20 indicate that radiogenic ^{230}Th predominated and detrital contamination was not significant. Initial $^{234}U/^{238}U$ is stable over time, at 1.044 ± 0.038 (2σ), indicating that the calcite behaved as a closed system. Ages were corrected on the assumption that the initial $^{230}Th/^{232}Th$ ratio was 1.5.

of the cave therefore began well before about 382 kyr ago, probably during oxygen isotope stage 11. It ended before 152 kyr ago, possibly shortly after 207 kyr ago. Between about 382 and 207 kyr ago, human occupation could have taken place simultaneously with speleothem deposition, or during drier intermediate periods.

The Acheulo-Yabrudian complex contains three major lithic facies defined at Yabrud I in Syria[5,13] and at Tabun Cave in Israel[10,11] in the 1930s and 1950s. These were termed as follows: Yabrudian is dominated by thick scrapers shaped by steep Quina retouch; Acheuleo-Yabrudian contains Yabrudian scrapers and handaxes; and Pre-Aurignacian/Amudian is dominated by blades and blade-tools[5,13]. A renewed excavation at Tabun viewed these different facies as representing a gradual technological change within what was suggested as 'the Mugharan tradition'[12]. In 1925 the cave of Zuttiyeh in Wadi Amud (Israel) was excavated and part of a human skull ('Galilee Man') was found[17]. A renewed excavation at Zuttiyeh confirmed an Acheulo-Yabrudian occupation at the site[18]. This unique human fossil was seen as representative of the makers of Pre-Mousterian assemblages[19,20]. Recently it was suggested that the Zuttiyeh skull should be recognized as an anatomically modern human[21], thus suggesting a possible link between physical evolution and lithic technology. A few Acheulo-Yabrudian sites are known from Lebanon, Syria[5] and Israel (recently reported from Jamal cave[22] and Mysliya in Mount Carmel). The discovery of Qesem Cave, being the southernmost Acheulo-Yabrudian site yet found, extends the known geographic boundaries of this complex.

The Acheulo-Yabrudian was originally recognized by its characteristic lithic assemblages and its place in the Levantine prehistoric sequence. When in stratigraphic context, as at Tabun Cave, it is above late Lower Palaeolithic (Upper Acheulian) and below early Middle Palaeolithic (Mousterian) layers[10]. Absolute chronology for the Acheulo-Yabrudian has been difficult because almost all excavations predate the advent of modern radiometric techniques. However, in recent years archaeologists have provided series of radiometric dates of both Lower and Middle Palaeolithic sites in the Levant and made some attempts to date Acheulo-Yabrudian layers[22–28] by uranium isotopic series, thermoluminescence (TL) and electron spin resonance (ESR).

The oldest dates available for the Acheulo-Yabrudian complex are about 350 kyr and the most recent are up to 160 kyr. Early Middle Palaeolithic Mousterian deposits produced a few dates as early as about 200 kyr at Tabun and Hayonim caves and Rosh Ein Mor[23,29]. Although single dates for final Acheulo-Yabrudian seem to partly overlap the early Mousterian, we do not believe that this was so. A date of 400 kyr from Tabun layer E was recently obtained (W. J. Rink, H. P. Schwarcz, A. Ronen and A. Tsatskin, personal communication) and the Acheulo-Yabrudian might therefore have started before 350 kyr ago and ended about 200 kyr ago (Fig. 3).

Mainly on the basis of ESR dates from several sites, it was recently suggested that the Lower–Middle Palaeolithic transition was rapid, taking place at 215 ± 30 kyr ago[27]. Because these dates were

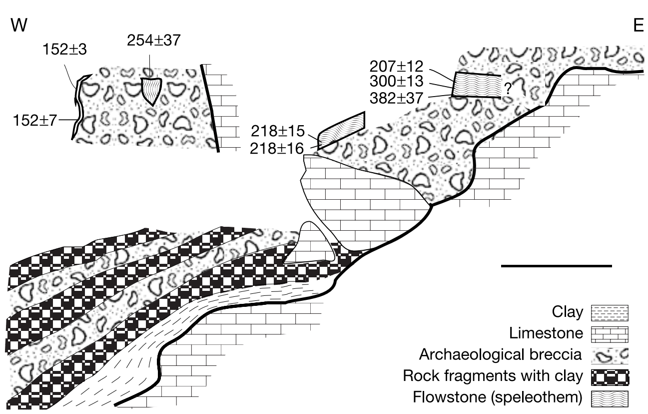

Figure 2 Schematic compiled section showing field relations and dates at the eastern side of Qesem Cave. The inset shows an additional section at the southeastern part of the cave, beyond the plane of the main section. Both parts are shown at the same relative elevation. Limestone blocks are associated with bedrock collapse and subsidence. Approximate uranium-series dates and errors (in kyr) of speleothems indicate the upper and lower limits of the age of the upper archaeological layers. For precise dates see Table 1. Scale bar, 1 m.

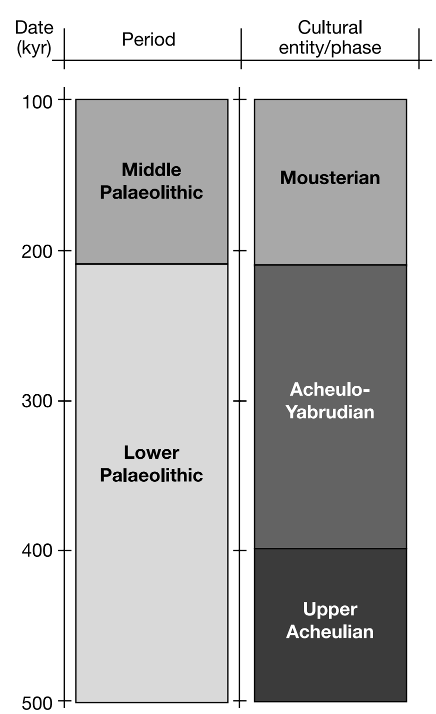

Figure 3 Palaeolithic chronological phases and cultural units in the Levant.

measured long after the excavations, however, appropriate on-site dosimetry was not available and it was suggested that these ESR dates underestimate the age of the teeth[24]. Although a date of about 200 kyr is acceptable for the end of the Acheulo-Yabrudian, the dates from Tabun and Qesem caves indicate a very long and dynamic cultural complex covering about 200 kyr between the two major Palaeolithic complexes, the Lower Palaeolithic Acheulian and the Middle Palaeolithic Mousterian.

Our study is the first to date Acheulo-Yabrudian deposits by the method of ^{230}Th/^{234}U TIMS. On the basis of samples extracted during the archaeological excavation, an exact stratigraphic association of the dates can be made. Three main points emerge from the findings. First, the Acheulo-Yabrudian complex probably started well before 382 kyr ago, presumably during oxygen isotope stage 11. Because we have not yet dated the lower parts of the sediments in Qesem Cave, it would be fair to assume dates that accord well with the early Tabun E dates up to 400 kyr. Second, Acheulo-Yabrudian sediments at Qesem Cave are covered by a speleothem dated to 152 kyr. The Acheulo-Yabrudian occupation in Qesem Cave therefore ceased long before that date. Third, the dates of Qesem Cave represent the last cultural phase of the Lower Palaeolithic, the Acheulo-Yabrudian complex, supporting a maximum age limit of about 207 kyr ago for the earliest stages of the Middle Palaeolithic Mousterian complex. No traces of Mousterian occupation were found at Qesem.

The rich Acheulo-Yabrudian deposits at Qesem Cave offer a rare opportunity to study human adaptation and evolution in the Middle Pleistocene. Because the dates indicate that human activity occurred mostly before 382 kyr, and because the site is located within the 'out-of-Africa' corridor, the information obtained by a study of Qesem Cave is likely to contribute substantially to our understanding of the origins and dispersal of modern humans[2]. The Levantine Acheulian assemblages predating the Acheulo-Yabrudian were probably made by *Homo erectus* (*sensu lato*), whereas Mousterian industries postdating the Acheulo-Yabrudian were made by both anatomically modern humans and *Homo neanderthalensis.* It would be interesting to learn who was the maker of the unique Acheulo-Yabrudian assemblages[3]. If human remains are recovered, Qesem might hold a key to the understanding of evolution and dispersal of modern humans. The stratigraphically distinct archaeological horizons at Qesem have already provided, and will continue to provide, information on the late Lower Palaeolithic Acheulo-Yabrudian lithic variability. Such knowledge will improve our understanding of technological innovations, such as the beginning of the systematic production of blades in the Levant[4,6] and the early stages of the Levallois technique, a technological breakthrough that became globally prominent in the Middle Palaeolithic. In contrast, this period also saw the final stages of hand-axe manufacture, a tradition that had accompanied humans for about one and a half million years. □

Received 25 March; accepted 23 April 2003; doi:10.1038/nature01718.

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Acknowledgements We thank N. Goren-Inbar, S. Rosen and S. Weiner for their comments on the original manuscript, and H. C. Linge and F. Saez for U–Th TIMS analysis. The Qesem Cave research project is supported by the Israel Science Foundation, the L.S.B. Leakey Foundation and the CARE Archaeological Foundation.

Competing interests statement The authors declare that they have no competing financial interests.

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The evolution of reproductive isolation through sexual conflict

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Classical population-genetics theory suggests that reproductive isolation will evolve fastest in small isolated populations[1]. In contrast, recent theory suggests that divergence should occur fastest in larger allopatric populations[2]. The rationale behind this is that sexual conflict, potentially the strongest driver of speciation, is greater in larger, higher-density populations. This idea is highly controversial[3] and has little experimental support[4,5]. Here we show, using replicate fly populations with varying levels of sexual conflict, that larger, more dense populations with more sexual conflict diverged to a greater degree than small populations with relaxed conflict. This result strongly suggests that speciation can occur rapidly in large populations through increased sexual conflict.

Sexual conflict is a potent evolutionary force that may lead to

