

Our calculations give rise to some interesting implications for the origin and early development of life on Earth. Although there are minor differences among different surface environments, we conclude that, for an ejecta blanket of 3 m as the criterion for serious disruption, the first primitive organism might have evolved at the surface between 4,000 and 3,700 Myr. Estimates for different assumptions about T_c and critical ejecta thickness can be found to be in the same range. In the deep ocean hydrothermal vents, the origin of life could have taken place as early as 4,200 to 4,000 Myr—substantially earlier than at the surface. In addition, the surface would probably have been sterilized as late as 3,600 to 3,700 Myr by global trauma due to impact processes, and even the deepest ocean environments might have been made terminally uncomfortable for life (except perhaps thermophilic forms) as late as 4,000 to 3,900 Myr.

Another factor is that severe climatic events would remain frequent (every 10^5 to 10^6 yr) until 3,600 to 3,800 Myr. Of course, if the reader has a different preference for the timescale of abiogenesis, he can choose his own estimate for these events from Fig. 2.

Some conclusions can be drawn from these inferences. If life could have evolved in or near the mid-ocean ridge hydrothermal systems, then it probably began there. Because of the interconnected nature of the ridges versus the more patchy nature of the suitable surface sites, it might have been more likely to propagate as well. Wherever life did first appear, it would seem possible that it was eradicated from at least the surface of the planet (perhaps several times), re-evolving in some new location or radiating from a preserved, more heat-tolerant population each time, before it took possession of the Earth undisputed by impact events. These multiple extinctions (and possibly origins) are inferred from the extent of overlap between the period at which life first would have appeared and the last probable instance of impact sterilization for any of these environments. An additional conclusion is that photosynthesis would have been rather difficult before 3,700 to 3,800 Myr because of frequent climatic events, including a near-total lack of sunlight for extended periods. It is also intriguing that the biosphere contained a relatively complex and diverse set of organisms by 3,500 Myr in light of the potentially short time period involved since the last sterilization event, and/or inception of life. This could imply a type and rate of evolutionary process no longer in operation.

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Thermoluminescence dating of Mousterian 'Proto-Cro-Magnon' remains from Israel and the origin of modern man

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The Qafzeh¹ and Skhul^{2,3} caves in Israel have yielded the remains of over 30 hominids. Despite their association with Mousterian deposits, these have been recognized as forerunners of other *Homo sapiens sapiens* on morphological grounds and have been called 'Proto-Cro-Magnons'¹. Other west Asian caves (Amud, Tabun, Kebara and Shanidar) have yielded skeletal remains of Neanderthals associated with similar Middle Palaeolithic deposits. The lack of precise dates for these deposits has made it difficult to ascertain which of the two hominids was present first in the area^{1,4–9}. Recently we reported an age of ≈ 60 kyr for the Neanderthal burial at Kebara⁶ (Israel). Here we report thermoluminescence dates for 20 specimens of burnt flints recovered from the hominid-bearing layers of Qafzeh¹. The dates, which range from ~ 90 to 100 kyr BP, provide an independent measure for the great antiquity of southwest Asian modern humans which have previously been dated to ~ 40 kyr BP on the basis of European models^{7–9}. Our results also exclude a close phylogenetic relationship between the Cro-Magnons and Neanderthals^{1,4–6}.

The Qafzeh cave (lower Galilee) was excavated by Neuville and Stekelis (1932–1935) and more recently by Vandermeersch (1965–1979)^{1,10}. The 4.5 m thick Mousterian sequence is subdivided into two major accumulation units. The first (layers V–XV) is 2 m thick and is rich in broken mammalian bones and lithic artefacts, demonstrating intensive human occupation. The second (layers XVII–XXIV) is 2.5 m thick and is rich in bones of microvertebrates, indicating ephemeral human use of the cave. The rodent assemblages^{11–13} of the second accumulation unit, from which all the hominid remains have come, include two archaic species of African rats (*Mastomys batei* and *Arvicanthis ectos*) and a subspecies of the Eurasian dormouse (*Myomimus roachi qafzensis*), all of which became extinct during the early Mousterian. The presence of new arrivals, such as *Cricetulus migratorius* (a grey hamster), and the evolution of the modern dormouse subspecies (*Myomimus roachi roachi*) mark the late Mousterian deposits such as Tabun C, Hayonim cave upper E., Kebara, Geula¹³.

The cultural stratigraphy of the Tabun cave⁷ is often taken as a yardstick for Levantine Middle Palaeolithic sites. Artefact morphology and the thickness/width ratio of flakes indicate that the Qafzeh Mousterian resembles that of Tabun C¹⁴ or later assemblages and should therefore be dated to the end of the Middle Palaeolithic, that is ~ 40 kyr BP^{7,15}. The discrepancy between relative dates based on metrical lithic analysis (suggesting that the Neanderthals predated the Qafzeh hominids) and those derived from the seriation of microvertebrate assemblages

Table 1 Thermoluminescence results and radioactivity data for the flints from Qafzeh

| Sample | U* | Th* | K* | S α † | D α ‡ | D β § | Internal dose | External dose | Annual dose | Palaeodose (10 ⁻² Gy) | Age (kyr BP) |
|-------------|----------|-------|-------|--------------|--------------|-------------|---------------|---------------|-------------|----------------------------------|--------------|
| | (p.p.m.) | | | | | | | | | | |
| Layer XVII | | | | | | | | | | | |
| 13 | 0.762 | 0.038 | 290 | 1.88 | 26.6±1.8 | 13.6 | 40.8±3 | 24.3 | 65±5 | 6,149±325 | 94.3±8.8 |
| 14 | 0.859 | 0.043 | 550 | 1.51 | 24.2±2.7 | 17.1 | 41.9±3.7 | 24.5 | 66±5 | 7,044±272 | 106.0±9.6 |
| 29 | 1.922 | 0.051 | 450 | 1.21 | 43.1±3.4 | 31.9 | 76.2±5.7 | 24.4 | 101±7 | 10,79±463 | 107.2±8.8 |
| 33 | 2.239 | 0.088 | 600 | 2.27 | 94.7±7.8 | 37.9 | 135±11 | 24 | 159±12 | 14,16±797 | 89.2±8.4 |
| 34 | 1.058 | 0.04 | 430 | 1.63 | 32.0±2.6 | 19.1 | 51.9±4 | 24.2 | 76±6 | 6,692±227 | 87.8±7.2 |
| 36 | 1.238 | 0.032 | 260 | 1.29 | 29.6±1.9 | 20.3 | 50.4±3.6 | 24.5 | 75±5 | 7,556±282 | 100.7±8.2 |
| Layer XVIII | | | | | | | | | | | |
| 38 | 1.314 | 0.086 | 960 | 2.13 | 52.5±2.3 | 27.3 | 81.1±5.3 | 23.1 | 104±7 | 9,173±471 | 87.9±7.2 |
| 40 | 1.13 | 0.035 | 310 | 1.50 | 31.4±1.8 | 19.1 | 51.4±3.6 | 23.7 | 75±5 | 6,733±205 | 89.5±7.0 |
| 42 | 1.45 | 0.034 | 240 | 1.61 | 43.1±4.2 | 23.2 | 67.0±5.8 | 23.5 | 91±7 | 8,460±337 | 93.4±8.2 |
| Layer XIX | | | | | | | | | | | |
| 45 | 1.005 | 0.065 | 770 | 2.46 | 46.2±3.7 | 21.1 | 68.7±5.5 | 22.8 | 92±7 | 9,056±449 | 98.8±8.9 |
| 47 | 2.17 | 0.072 | 790 | 2.38 | 95.9±4.7 | 38.4 | 136±9 | 23.4 | 159±10 | 13,12±885 | 82.4±7.7 |
| 49 | 1.091 | 0.084 | 870 | 2.55 | 52.3±4.1 | 23.3 | 76.4±6.2 | 23.4 | 100±7 | 8,478±368 | 84.9±7.3 |
| 77 | 1.149 | 0.342 | 1,610 | 1.95 | 44.8±3.6 | 30.9 | 77.0±5.9 | 23.1 | 100±7 | 9,615±443 | 95.9±8.1 |
| Layer XXI | | | | | | | | | | | |
| 1 | 1.675 | 0.045 | 440 | 1.69 | 52.6±5.7 | 28.2 | 81.8±7.5 | 21.8 | 104±8 | 11,41±455 | 109.9±9.9 |
| 2 | 2.205 | 0.087 | 370 | 1.52 | 62.5±7.9 | 35.5 | 99.9±9.9 | 21.6 | 122±11 | 10,84±516 | 89.2±8.9 |
| 61 | 1.451 | 0.049 | 840 | 1.58 | 42.6±4.6 | 28.2 | 71.8±6.3 | 21.8 | 94±7 | 8,518±436 | 90.9±8.7 |
| Layer XXII | | | | | | | | | | | |
| 65 | 2.234 | 0.05 | 450 | 1.97 | 81.5±4.4 | 36.4 | 119±8 | 23.4 | 143±9 | 12,36±693 | 86.6±7.4 |
| 66 | 1.138 | 0.022 | 220 | 1.92 | 40.4±4.4 | 18.5 | 59.4±5.7 | 23.5 | 83±7 | 7,573±340 | 91.2±8.7 |
| 67 | 1.065 | 0.054 | 190 | 1.97 | 39.1±2.1 | 17.2 | 56.9±4 | 23.5 | 80±6 | 6,879±262 | 85.4±6.9 |
| Layer XXIII | | | | | | | | | | | |
| 76 | 1.486 | 0.069 | 900 | 1.78 | 49.1±4.2 | 29.3 | 79.4±6.3 | 23.4 | 103±7 | 9,774±344 | 95.0±7.7 |

*The values of U, Th and K each have an error of $\pm 6\%$. Fission-track analysis of five flints containing in excess of 1.5 p.p.m. uranium showed practically uniform distribution of the element.

† β dose equivalent to the flux of one α cm⁻², as deduced from fine grains measurements^{17,25}. The error on S α ranges from $\pm 5\%$ to $\pm 12\%$.

‡ β dose equivalent to the α dose in flint calculated using the specific annual flux deduced from ref. 26.

§ The β dose in flints was calculated using the specific values given in ref. 27. The γ internal dose is less than 0.02 mGy yr⁻¹.

|| The external dose (estimated error: ± 0.04 mGy) includes a cosmic contribution of 0.12 mGy yr⁻¹. It has been calculated using the data given in refs. 28 and 29. The thickness of overburden is about 3 m.

The uranium series radionuclides are essentially at equilibrium in the sediment: the activities of ²³⁸U, ²³⁴U, ²³⁰Th and ²¹⁰Po measured by α spectrometry are respectively 0.84 ± 0.07 , 0.78 ± 0.06 , 0.86 ± 0.04 and 0.67 ± 0.04 d.p.m. g⁻¹; the activities of ²²⁶Ra and ²¹⁴Pb measured by γ spectrometry, on another sample of sediment are respectively 0.70 ± 0.08 and 0.71 ± 0.02 d.p.m. g⁻¹.

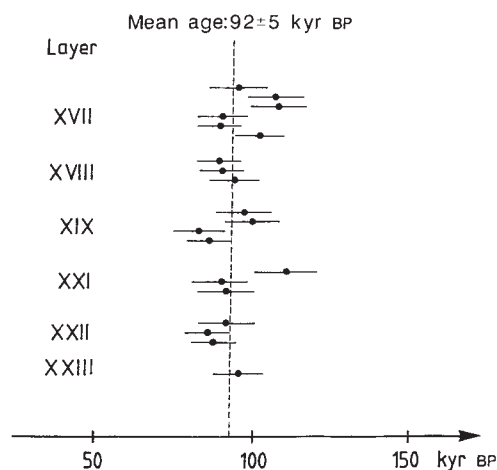


Fig. 1 Horizontal bars representing the thermoluminescence ages of burnt flints from Qafzeh cave as a function of depth of the unit in which the flints were found. The weighted average age deduced is given at the top. The errors (statistical plus systematic) at 68% confidence level are calculated as in ref. 30. A systematic error of $\pm 7.5\%$ has been assumed for the external dose to take into account possible variations in water content of the archaeological sediments (M. J. Aitken, personal communication).

(suggesting the opposite) can only be resolved by an independent dating technique, such as thermoluminescence (TL)^{6,16-18}.

Twenty burnt flints recovered from the Mousterian layers, which yielded Proto-Cro-Magnon remains 15 years ago, have been dated by TL. The experimental details of our dating method have been discussed elsewhere^{5,19,20}. Six specimens came from layer XVII, three from layer XVIII, four from layer XIX, three each from layers XXI and XXII and one from layer XXIII.

The external dose was measured using 13 dosimeters (CaSO₄/Dy), which were buried for a year within the sections surrounding the excavated deposits. As the majority of flints came from metre squares C11 and C12, the dosimeters were buried in adjacent squares B11, D11 and D12, within a distance of 1 m from the point of recovery of the flints.

The recorded external dose (γ plus cosmic) ranged from 0.22 to 0.27 mGy yr⁻¹, of which approximately 0.12 mGy yr⁻¹ was

due to cosmic rays. The concentrations of radioactive elements (^{238}U , ^{232}Th and ^{40}K) within the flints was determined by neutron activation analysis²¹. Due to the relatively low level of the external dose, the internal dose represents from ~63 to over 80% of the total annual dose received by the specimens. Therefore errors in the measured environmental dose have relatively little impact on the calculated ages (see Table 1).

In Fig. 1 the ages, with their statistical errors, are plotted against depth of flint recovery. These ages fall between 85 and 105 kyr and exhibit no systematic change with recovery depth, within the experimental errors. The age (weighted mean) deduced for layers XVII–XXIII is 92 ± 5 kyr (statistical + systematic error). Consequently, the TL data support the geological observation¹⁰ of a rather rapid accumulation of lower levels when the cave was occupied.

The TL dates lead to two main conclusions. First, archaic forms of modern humans classified as 'Proto-Cro-Magnons' were already present in southwest Asia during isotopic stage 5, ~92 kyr BP (ref. 22), and may have coexisted at a later date with a population of Neanderthals, one of whose remains has recently been dated at Kebara to ~60 kyr BP⁶. This makes the proposition of a close phylogenetic relationship between the two human types untenable and supports the contention that the Neanderthals were a stock of European origin and arrived relatively late in south west Asia. They may have migrated East when glacial conditions settled over large areas of the European continent^{1,23}. These west Asian dates should increase our knowledge of the place of origin and dispersal of modern man²⁴. Second, the stratigraphic sequence of Tabun is either of geographically limited value or of much greater antiquity than hitherto suspected²³. The Mousterian of Tabun D could still be older than the 'Tabun C' lithic industry which dominates the Qafzeh assemblages, if chronological reinterpretation of the Tabun cave place the 'Tabun D' type industry near the beginning of isotope stage 5 (ref. 22).

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Pattern of covariation between life-history traits of European birds

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A large amount of variation is found in most reproductive traits of birds^{1,2}. Clutch size for instance, can vary from 1 to 15 between species of similar body weight. The adaptive significance of this variation is only poorly understood^{3,4}. According to life-history theory^{5,6}, large clutch size and early onset of reproduction are expected when the chances of survival are low. There is some support for the existence of such a relationship from studies of single species^{7–9}. Here I present evidence that, in European birds, clutch size is increased, and onset of reproduction occurs earlier in life, when the probability of survival is low.

This study is based on published adult survival rates of 107 species from 14 orders (data listed in ref. 10), making use of estimates based on ringing recoveries in which the number of returns is greater than 100. In most previous studies, mean adult survival rate has been computed using the estimators given by Lack¹¹ or Haldane¹². When no data on ringing recoveries were available, I included estimates based on the recovery rates of individually known birds, given that at least 100 birds have been at risk of dying. The two methods of estimating adult survival rate are strongly correlated¹⁰. Although several sources of error are involved in using those two methods^{13–15}, the precision of the estimates does reveal cross-species patterns. All variables were logarithmically transformed before analysis to obtain gaussian distributions.

The choice of taxonomic level is important when using the comparative method^{16–18}. Although analysis at lower taxonomic levels increases the sample size, such comparisons include data points that may not be statistically independent. A considerable proportion of the variance in clutch size (81.6%), age at maturity (36.6%) and adult survival rate (47.0%) was found at the level of family or above, using a nested analysis of variance^{19,20}. Here I analysed first for differences between families, and then between species within orders.

A close correlation was found across families between adult survival rate, clutch size and age at maturity (data on clutch size and age at maturity are listed for each genera in ref. 2). Clutch size decreased both with increasing age at maturity ($r = -0.74$, $n = 38$, $P < 0.001$) and adult survival rate ($r = -0.75$, $n = 38$, $P < 0.001$), as previously reported by O'Connor²¹. Maturation occurred at older ages in families in which the survival rate was high ($r = 0.83$, $n = 38$, $P < 0.001$)¹.

Body weight in birds is known to be correlated with age at maturity^{2,22}, clutch size²² and adult survival rate^{10,23}. Thus, the correlations between the life-history traits may simply be caused by their common correlation with body weight. To control for the effects of body weight I calculated the correlation between the residuals from the regression line of each life history trait on body weight. In families with a high adult survival rate for their body weight, clutch size was still relatively small (Fig. 1a, $r = -0.77$, $n = 38$, $P < 0.001$) and onset of reproduction occurred at relatively old age (Fig. 1b, $r = 0.75$, $n = 38$, $P < 0.001$). A similar pattern of covariation has previously been documented in mammals^{24–27}.

I also examined the patterns of covariation within orders. The relationships between clutch size, age at maturity and adult survival rates with body weight were established for the species within the orders Anseriformes, Charadriiformes and Passeriformes. These were the only orders in which estimates of adult survival rates of a sufficient number of species (>3) were available. I then computed the deviations of the species from the