

We propose that these algal populations were physically concentrated during frazil ice formation. Frazil ice develops as suspended crystals in turbulent waters, and because of its surface properties, particles in the water column adhere to the crystals; the harvesting of sediments and other material by frazil ice is well known¹⁵. Ackley¹⁶ suggests that algal cells could also be concentrated if crystallization occurred preferentially around algal cells. He calculated that such preferential nucleation could account for concentrations up to 10^6 cells per litre, and he even reports observing some cells within ice crystals. But as we found algal densities greater than 10^7 cells per litre in young ice, we believe that the most important concentrating mechanism is the harvesting of algal cells by frazil ice crystals rising to the surface to form new sea ice.

Physical accumulation may help explain some regional differences among ice algal populations. For example, ice algal populations are restricted to bottom or surface layers in many polar areas¹⁻³ but are found throughout the ice floes of the Weddell Sea³. Frazil ice generally characterizes the initial stages of sea ice growth; most floes then thicken because congelation ice forms under an established ice sheet at the ice-water interface¹⁷. The landfast ice floes at McMurdo Sound are composed primarily of congelation ice¹⁸ and algae are largely restricted to the bottom few centimetres¹⁴, or they develop in an aggregation of under-ice platelets⁷. In contrast, studies of Weddell Sea floes suggest that frazil ice production is continuous there: even older floes comprise mostly frazil ice¹⁸. Continuous frazil ice production and concurrent harvesting of algal cells may well account for the algae within floes from this region.

Populations accumulated by frazil ice are likely to be heterogeneous because frazil ice forms in patchy environments such as leads, polynyas, and along the ice edge where conditions are turbulent¹⁵. Certainly the young sea ice we saw was not discoloured uniformly. The variability of algal populations throughout older ice floes may reflect both ice-forming events and temporal changes in the species composition of water-column assemblages while the floes are growing.

Unlike ice populations in other polar regions, internal populations may not be available to metazoan grazers. But because they are trapped, they remain in floes throughout the year. Some of the algal cells may subsequently grow *in situ*; others may be consumed by similarly trapped heterotrophic protozoans, or bacteria may use the extracellular products of active cells and decompose dead ones. These populations and associated detritus are apparently released into the water column throughout the spring and summer and may thus provide a predictable and important food source for pelagic consumers³. Moreover, resting stages of pelagic forms are incorporated yearly into sea ice (J. G. Mitchell & M. W. Silver, personal communication); when released, these stages and surviving vegetative populations may constitute an important inoculum for pelagic populations.

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Lainyamok, a new middle Pleistocene hominid site

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It is generally believed that, during the middle Pleistocene in Africa, archaic *Homo sapiens* arose from *Homo erectus* and Acheulian tool industries were replaced by Middle Stone Age industries. The details of these transitions are poorly known because of the paucity of associated hominid, faunal and archaeological remains in datable contexts^{1,2}. We describe here Lainyamok, a new middle Pleistocene site. Fossil material includes three hominid teeth attributed to *Homo* sp. and a diverse fauna represented by unusually complete skeletal material. Acheulian artefacts are found both within bone clusters and thinly scattered throughout the site. The clustering of associated or articulated partial skeletons and artefacts suggests that Lainyamok may preserve evidence of the killing or butchering of individual, small- to medium-sized animals. Such sites have not previously been identified in the Pleistocene.

Lainyamok lies ~8 km north-west of Lake Magadi in Kenya (Fig. 1a, b). Fossils and artefacts were collected by Phillip Leakey and a team led by Kamoya Kimeu; a team led by the late W. W. Bishop undertook preliminary dating and geological mapping³. We report our preliminary analysis of the fossils and artefacts in the context of the geological data.

The Lainyamok fossil locality lies in a deep (23 m) graben that narrows and shallows southwards, deepening to the north. It is one of a series of grabens formed during grid-faulting of the southern Kenya rift valley, which probably predated sediment accumulation^{3,4}; faulting episodes also occurred during and after sedimentation^{5,6}. Thinning of fossiliferous sediments at Lainyamok towards the south and east suggests that the graben floor dipped to the north-west at the time of deposition.

The Lainyamok graben opens into a broad plain bounded on the west by a major fault scarp and to the east by a gently westerly-tilting block of the Kordjya Basalt, a thick, widespread basalt that forms the floor of the southern Kenya rift⁵. Overlying the basalt are the Magadi (or Plateau) trachytes, dated elsewhere from 1.4 Myr to 0.7-0.9 Myr⁶⁻⁹. Trachyte samples yield both normal and reversed polarities and may span the Jaramillo event (dated to about 0.89 Myr) in the late Matuyama epoch^{3,6,9}.

The sediments at Lainyamok were identified by Bishop³ as a thin, outlying development of the Oloronga Beds described by Baker³. The evidence for this view is: (1) Magadi trachytes underlie the Oloronga Beds and the sediments at Lainyamok; (2) both the Oloronga Beds and the Lainyamok sediments are lacustrine in origin, similar in colour and grain size, and accumulated in grabens associated with grid-faulting in the rift floor^{3,4,11,12}; (3) the type Oloronga Beds are capped by a thick, pisolithic caliche, as are the Lainyamok sediments¹⁰. An obsidian flow within the Oloronga Beds is dated to 0.78 ± 0.04 Myr⁸. The youngest part of the Oloronga Beds is believed by Eugster^{4,10} to be about 0.4 Myr, although they may be as young as 0.1 Myr.

Table 1 Lainyamok faunal list

Geological bed	Taxon		
Capping calcrete	Artiodactyla	Suidae	indet.
Rootcast silts	Pisces		cf. <i>Tilapia</i>
	Artiodactyla	Bovidae	<i>Gazella</i> sp. <i>Parmularius</i> sp.
Khaki tuff	Perissodactyla	Equidae	indet.
	Carnivora	Canidae	indet.
	Aves	Struthionidae	<i>Struthio</i> sp. (eggshell)
	Reptilia	Phidia	indet.
	Primates	Cercopithecidae	<i>Papio</i> sp.
	Lagomorpha	Leporidae	<i>Lepus</i> cf. <i>capensis</i>
	Rodentia	Thryonomyidae	<i>Thryonomys</i> cf. <i>swinderinus</i>
		Pedetidae	<i>Pedetes</i> cf. <i>caffer</i>
		indet.	
		Carnivora	Canidae
		Hyaenidae	<i>Crocuta</i> sp.
		Felidae	<i>Felis</i> cf. <i>libyacus</i> <i>Felis</i> sp. <i>Panthera</i> cf. <i>leo</i> <i>Orycteropus</i> <i> afer</i>
	Tubulidentata	Orycteropidae	indet.
	Proboscidea	Elephantidae	indet.
	Hyracoidea	Procaviidae	<i>Procavia</i> cf. <i>capensis</i>
	Perissodactyla	Equidae	indet.
	Artiodactyla	Suidae	<i>Phacochoerus</i> sp.
		Giraffidae	<i>Giraffa</i> sp.
		Bovidae	<i>Parmularius</i> sp. <i>Gazella</i> sp. <i>Hippotragini</i> sp. indet.
Cellular rock	Pisces		cf. <i>Tilapia</i>
Pink/brown silts	Mollusca		<i>Limicolaria</i> sp.

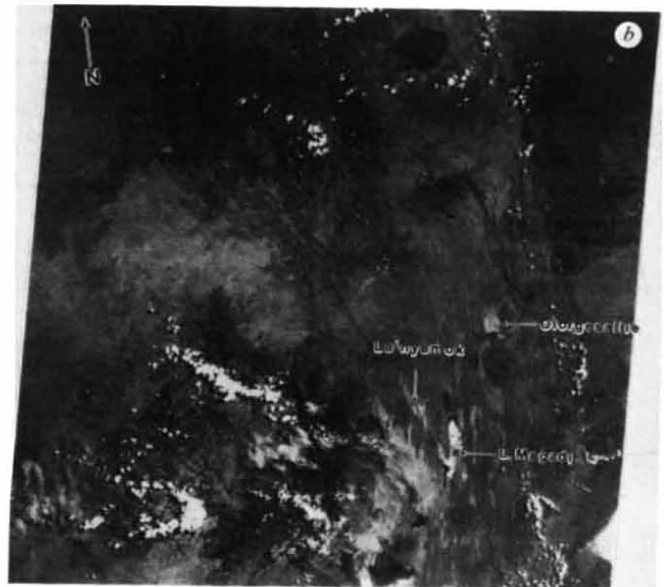
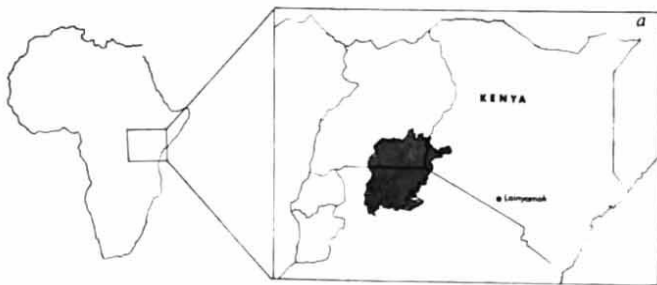


Fig. 1 *a*, Map of Kenya showing the location of the Lainyamok fossil locality. *b*, This Landsat photograph of southern Kenya shows the location of the Lainyamok fossiliferous sediments, Lake Magadi, and the nearby Acheulian site, Ologesailie. (Photo courtesy of NASA.)

Fig. 2 Occlusal (left) and lingual (right) views of the Lainyamok hominid, a right P⁴M¹⁻² attributed to *Homo* sp. All three teeth are heavily worn; M² shows a facet, indicating that the third molar was present in life. The teeth are shown held in anatomical position by matrix; no alveolar bone persists. Note that both P⁴ and M² are splayed by matrix-filled cracks; the dimensions in Table 2 are corrected for this problem.

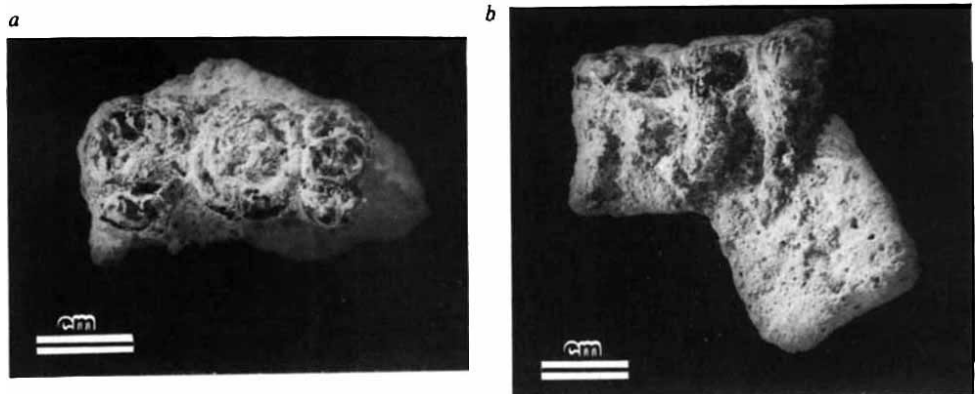
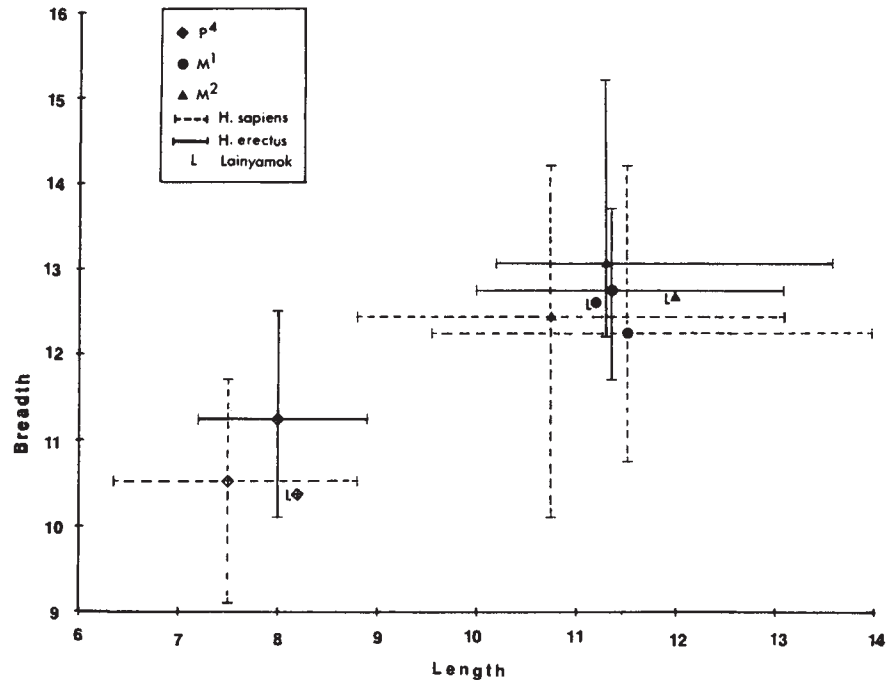


Fig. 3 The dimensions of the Lainyamok teeth are compared with the means and ranges for P^4 M^{1-2} of a sample of *H. erectus* and of a pooled sample of archaic *H. sapiens* including Neanderthals. Neanderthals and other archaic *H. sapiens* are treated as a single sample because Student's *t*-tests reveal no significant differences in the sizes of their cheek teeth. *Erectus* P^4 specimens are significantly broader and longer than those of *sapiens* (Student's *t*-tests: length, $t = 2.067$, $P = 0.022$, d.f. = 37; breadth, $t = 3.2781$, $P = 0.001$, d.f. = 36). *Erectus* molars tend to be broader than those of *sapiens*, but the difference is not significant at the $P < 0.05$ level. *Erectus* second molars are significantly broader than those of the *sapiens* sample (Student's *t*-test: $t = 1.956$, $P = 0.29$, d.f. = 34). Note that the Lainyamok teeth are generally large but consistently fall within the ranges for both samples. (All measurements are in millimetres.) (The *H. erectus* sample included measurements on KNM-ER 3733, Sangiran 4 and 17, Rabat and the original Choukoutien materials from refs 19, 20 and A. Walker (personal communication). The archaic *H. sapiens* and *Homo neanderthalensis* data for specimens from Skhul, Qafzeh, Krapina, Arcy-sur-cure, La Ferrassie, Montsempron, La Quina, Tabun, Kulnal, Amud, Le Moustier and Chatelpéron were taken from ref. 19 and E. Trinkaus (personal communication).)



The Lainyamok sediments are certainly younger than the underlying trachytes (about 0.9–0.7 Myr); if Eugster and Bishop are correct, they are older than about 0.4 Myr.

Beds in the Lainyamok succession suggest alternating lacustrine and subaerial/lake margin conditions. Some beds are well laminated, diatomaceous sediments containing fossil fish and prominent algal limestone horizons. Thus, the Lainyamok graben may have contained part of a fault-bounded lake, possibly Lake Oloronga^{4,10}. Repeated cycles of transgressions—represented by fine-grained, often laminated sediments bearing fossils of terrestrial animals—are interspersed with regressions—as shown by calcrete formation, mild erosion of underlying beds, or mud-cracking. The artefacts and vertebrate fossils described here occur within and on a thick (1.7 m) khaki tuff. This fine-grained, tuffaceous silt or silty-sand, with rootcasts at its top, was waterlain in lake margin or lake flat conditions.

Approximately 200 fossil specimens from the khaki tuff are identified in Table 1. A single hominid individual, adult at the time of death, is known from three teeth (RP^4M^{1-2}) held in anatomical position by matrix (Fig. 2, Table 2). The second molar bears a clear facet for the third molar. Figure 3 compares the Lainyamok dental dimensions with samples of *H. erectus* and archaic *H. sapiens* teeth. The Lainyamok teeth are large mesiodistally, making them more *erectus*-like, but they are within the range of variation of both samples in dimensions and morphology.

Other mammalian species range from small (cane rat, hyrax, hare, murid, spring hare) through an intermediate size (bovid, equid, hyena, suid) to large (giraffid, rhino). Fish, a terrestrial gastropod, ostrich eggshell and a snake are also represented. *Papio* sp. is the only non-hominid primate from Lainyamok to date. Overall, the fauna is consistent with a middle Pleistocene age, but the only extinct genus (identified from horn cores and teeth) is *Parmularius*. Jaws and teeth are numerous (38% of the elements), as are limb (45%) elements. No evidence of hydraulic winnowing^{12,13} is present.

The collected fauna includes 15 partial skeletons; additional articulated or associated partial skeletons remain *in situ*. We know of no other site of comparable age with a similar proportion of articulated or associated material. Bones often occur in clusters 1–2 m in diameter that appear to be single animal scatters¹⁴. Five such clusters also contain cores or flakes;

Table 2 Dimensions of the Lainyamok teeth

Tooth	Length (M-D)	Breadth (B-L)
RP ⁴	8.2	12.8
RM ²	11.2	12.6
RM ²	12.0*	14.4

All measurements in millimetres.

* Estimated value.

M-D, mesiodistal; B-L, buccolingual.



Fig. 4 The stone artefacts from Lainyamok. Top row (left to right): fragment of a lava flake; discoidal hand-axe of green lava; discoidal core of dark-grey lava. Bottom row (left to right): small hand-axe of green lava; quartzite chopper; quartzite spheroid. Some but not all of the artefacts were collected *in situ* from the khaki tuff; others were in the surface lag.

artefacts lie within a few metres of other clusters. Although more rigorous evidence is needed, these data suggest that Lainyamok preserves animal death sites at which hominids may have exploited carcasses.

A thin scatter of isolated artefacts occurs in and on the surface of the khaki tuff; a single cluster of lava flakes may be a manufacturing site. Small, unretouched flakes predominate. Only six artefacts have been collected from Lainyamok to date (Fig. 4); several dozen are visible at the site. The small, well-made hand-axes, unretouched flakes and other core tools are

consistent with an Acheulian industry. Artefacts were made from two local varieties of lava and apparently exotic quartz, quartzite and chert.

Lainyamok can be compared with Olorgesailie, the middle Pleistocene site north-east of Lake Magadi, as both sites sample broadly similar lake margin or lake flat habitats¹⁵. However, Olorgesailie and Lainyamok differ in that: (1) Olorgesailie is rich in giant geladas (*Theropithecus oswaldi*) but lacks *Papio*, the only monkey at Lainyamok; (2) only four carnivore specimens are known from Olorgesailie (C. Koch, personal communication), whereas 21 specimens of at least four carnivore genera are known from the much smaller Lainyamok collection; (3) large hand-axes and cutting or heavy-duty tools typify the Olorgesailie assemblage¹⁵ whereas the known Lainyamok artefacts are small or light-duty implements.

It is not clear if the faunal contrasts are linked to the archaeological differences. Olorgesailie was apparently repeatedly occupied by many hominids engaged in specific, highly organized activities (for example, extensive tool manufacture¹⁵ or systematic butchery of large animals¹⁶). Lainyamok's paucity of

artefacts, single animal scatters and sole artefact cluster suggest it was transiently occupied by only a few hominids. A working hypothesis is that Lainyamok preserves small, short-term occupations where more opportunistic killing and butchering of carcasses of smaller species occurred. Such small-scale sites are common in the ethnographic record^{17,18}, but are not known from the Pleistocene.

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Relative fitness can decrease in evolving asexual populations of *S. cerevisiae*

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It is generally accepted from the darwinian theory of evolution that a progressive increase in population adaptation will occur in populations containing genetic variation in fitness, until a stable equilibrium is reached and/or the additive genetic variation is exhausted. However, the theoretical literature of population genetics documents exceptions where mean population fitness may decrease in response to evolutionary changes in gene frequency, due to varying selective coefficients¹⁻⁴, sexual selection^{5,6} or to epistatic interactions between loci⁷. Until now, no examples of such exceptions have been documented from fitness estimates in either natural or experimental populations. We present here direct evidence that, as a result of epistatic interactions between adaptive mutations, mean population fitness can decrease in asexual evolving populations of the yeast *Saccharomyces cerevisiae*.

Populations of haploid and diploid *S. cerevisiae* were grown in glucose-limited continuous cultures (chemostats) for up to 300 generations. Population sizes were large—approximately 4.9×10^9 for the haploid population and 4.5×10^9 for the diploid population. In these conditions reproduction is exclusively asexual by budding, and evolutionary changes occur by the replacement of one adaptive clone by another. As recombination is virtually absent in these populations, two or more adaptive

mutations must be incorporated into the population in a strict sequential fashion.

Adaptive changes were identified by monitoring the frequencies of independent neutral or weakly selected mutations in the populations. Being asexual, these evolving populations may be regarded as consisting of a series of clones over time, each new clone having a selective advantage over the immediately preceding clone. In each clone the initial frequencies of the independent neutral or weakly selected mutations will be zero, and their frequencies will increase over time at the mutation rate or slightly less, depending on the intensity of selection against the independent marker. The frequencies of the independent mutations will necessarily be lower in the newly emergent adaptive clone than in the preexisting clone, as the former has had less time to accumulate mutations. Therefore, during an adaptive change the population frequencies of the independent mutations will exhibit transient decreases. Repeated replacements of adaptive clones will result in repeated fluctuations in the frequency of the independent markers. These fluctuations, known as periodic selection in the microbiological literature, allow the unambiguous detection of all adaptive changes without prior knowledge of the phenotype of the adaptive mutation itself⁸.

The frequencies of mutants resistant to canavine, cycloheximide and 5-fluorouracil were monitored in the haploid population, and mutants resistant to cycloheximide and 5-fluorouracil were monitored in the diploid population. (Canavanine resistance is recessive and so could not be monitored in the diploid population.) Samples were taken every three to six generations (12-24 h) and aliquots of the cell suspension were stored at -70°C in 15% glycerol for future analysis. All markers monitored showed the same pattern of fluctuations in each population. From these data, 4 adaptive changes were identified in 245 generations in the haploid population and 6 adaptive changes were identified in 305 generations in the diploid population. The dynamics of the fluctuations of canavanine resistance for the haploid population and cycloheximide resistance for the diploid population are shown in Figs 2 and 3 of ref. 8.

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