Pleistocene Milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel

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The Acheulean site of Gesher Benot Ya'aqov in the Dead Sea Rift of Israel documents hominin movements and technological development on a corridor between Africa and Eurasia. New age data place the site at 780,000 years ago (oxygen isotope stage 19), considerably older than previous estimates. The archaeological data from the site portray strong affinities with African stone tool traditions. The findings also reflect adroit technical skills and in-depth planning abilities, more advanced and complex than those of earlier archaeological occurrences in the Levant.

During the Early Pleistocene, hominins began to expand their range out of Africa, bringing with them their lithic technologies. Several routes may have been involved in this dispersal, including a corridor from northeastern Africa through southwestern Asia. Direct evidence for Early Pleistocene movement through the Levant, however, is limited to a few sites in Israel: 'Ubeidiya at 1.4 million years ago (Ma) (*1*), Evron Quarry at about 1 Ma (*2*), and Gesher Benot Ya'aqov (henceforth GBY) (*3*), now dated to 0.78 Ma. We describe here new data regarding the age of the rich archaeological accumulations at GBY, along with details of their technological importance and biotic context. Spanning some 100,000 years at the Early Pleistocene–Middle Pleistocene boundary (oxygen isotope stage 19), the GBY occupation fills a temporal and spatial gap in the Old World archaeological record. Technological innovations recorded for the first time outside Africa at GBY are seen later in early European sites [i.e., the use of soft percussors in Boxgrove (*4*)].

Acheulean bifaces and hominin remains were discovered in excavations at GBY (Fig. 1) in the 1930s (*5, 6*). The draining of Hula Lake in the 1950s and the associated entrenchment of the Jordan River resulted in new exposures and prompted renewed investigations (*7–9*). The sedimentary rocks at GBY dip 25° to 45° southwest (*10*). Early geological work on these exposures assigned them to the Benot Ya'akov Formation on the basis of characteristic marker fossils (*11*).

Recent work on the site has established a reference section for this formation from seven geological trenches, the archaeological excavations (120 m^2 total), and the limited outcrop along the banks of the Jordan River (Fig. 1). The composite sequence of 34 m of strata (Fig. 2) consists primarily of cycles of organic-rich calcareous muds, coquinas, and conglomerates deposited along the margin of the paleo–Hula Lake. Fluvial conglomerates occur at the top and bottom of the sequence, whereas the intervening strata are wholly lacustrine or lake margin in character. Five short cycles are nested within a single longer period oscillation, and these may reflect the 20,000- and 100,000-year Milankovitch cycles. Within these cyclical trends, shorter term climatic events are documented in brief exposure of lake beds with incipient soil formation and evidence of hominin activities.

A previous paleomagnetic study of Benot Ya'akov Formation sediments in the vicinity of the site yielded only normal polarities, which led us to conclude that the entire formation was probably less than 780,000 years old and that the site itself was probably about 500,000 years old (*8*). To refine the age estimate for the GBY archaeological site, we conducted a magnetostratigraphic study of sediments exposed in trenches II, III, V, and VI. We collected 155 samples in oriented plastic boxes spanning 26 of the 34 m of section exposed, including all of the key archaeological layers. After correction for the tilt of the bedding, almost all of the samples in the upper 17 m of the sampled section had northward declinations and moderately steep, positive inclinations, whereas samples from the lower 9 m generally had southward declinations and moderately steep, negative inclinations (Fig. 2). The simplest interpretation of these data is that the site consists of a reversed-polarity zone overlain by a normal-polarity zone. The presence in each zone of a few samples of intermediate or opposite polarity is readily explained by variable paleomagnetic reliability associated with the changes in lithology. Mineral magnetic studies indicated that the primary magnetic carrier was magnetite and that there were no noticeable changes in magnetic mineralogy or grain size throughout the section. Measurements of anhysteretic remanent magnetization and of magnetic susceptibility showed that the concentration of magnetic material was considerably higher in the normal-polarity zone than in the reversed-polarity zone, but the increase was gradual across the polarity boundary and did not appear to coincide with it. Thus, there was no magnetic evidence for an unconformity at the polarity boundary.

On the basis of biostratigraphy and the lithic assemblages at the site, we correlate the boundary between the polarity zones with the Matuyama-Brunhes chron boundary, dated at 0.78 Ma (*12*). This boundary is 4 m below the base of layer II-6 and a little more than 13 m below the base of layer V-5, the two primary archaeological complexes. The increase in concentration of magnetic material from the

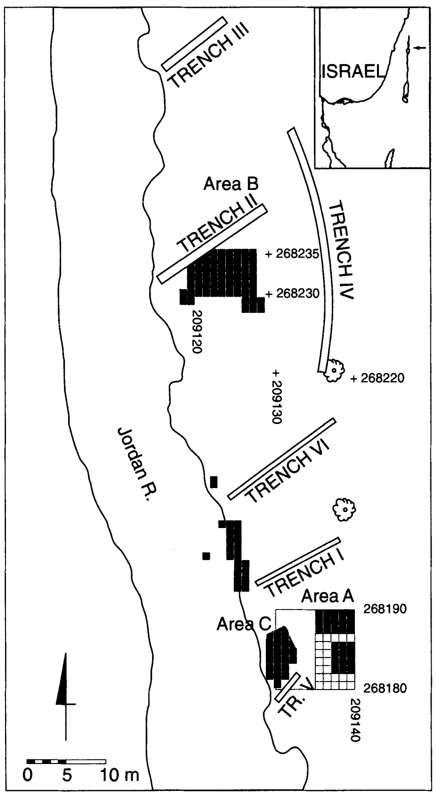

Fig. 1. Map of GBY showing the archaeological excavations and geological trenches in the recent (1989–1997) study area. Coordinate numbers refer to the Israel Grid. Arrow in inset shows the study area location (33°00'28"N, 35°37'40"E) within the Dead Sea Rift.

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bottom to the top of the section was not sufficient to explain the increase in the intensity of the natural remanent magnetization; this would imply that the intensity of the geomagnetic field had increased by a factor of 5 to 10. Such an increase in geomagnetic field intensity, which has been reported in detailed records of the Matuyama-Brunhes transition at other sites, suggests that the 26-m sampled section represents somewhat less than 100,000 to 150,000 years. This, together with the sedimentary cyclicity, implies that the 34-m sequence at the Gesher Benot Ya'aqov site probably formed between 0.7 and 0.8 Ma and correlates to the interval around oxygen isotope stage 19 (*12*).

The fossil vertebrate record at GBY derives primarily from the upper half of the section, immediately above the magnetic polarity transition. It reveals a mix of Asian and African components (Table 1) and includes *Procavia syriaca*, the earliest record from the southern Levant; *Lepus capensis*, which until now was not known from this region before the late Middle Pleistocene (*13*); and *Microtus* (*Tibericola*) cf. *jordani*, which was known until now only from the Lower Pleistocene of the 'Ubeidiya Formation (~1.4 Ma) (*14*).

The *Mimomys occitanomys-savini* (Arvicolidae, Rodentia) lineage provides biostrati-

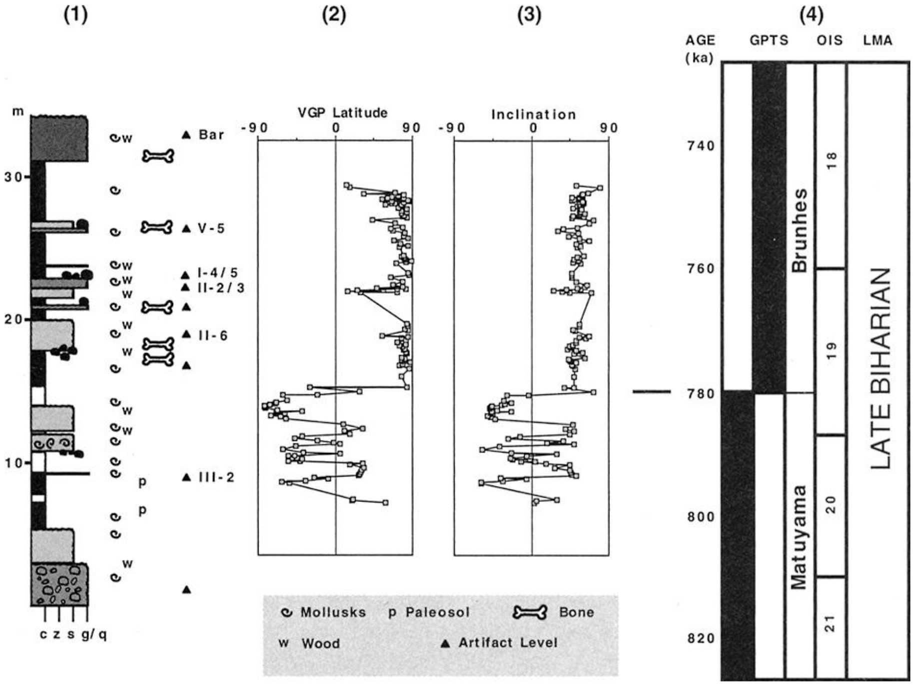

Fig. 2. Stratigraphic and paleomagnetic data from the study area. Column 1 shows lithology (c, clay; z, silt; s, sand; g/q, gravel or coquina). Fossils and occurrences of Acheulean artifacts are indicated beside column 1, along with levels discussed in the text. Columns 2 and 3 document results of magnetic polarity studies. Column 4 shows a 100,000-year segment of the geomagnetic polarity time scale (GPTS), oxygen isotope stage (OIS), and land mammal age (LMA) records correlated to the site.

Table 1. Micromammalian species from GBY, with their biogeographical position and their representation in the Pleistocene of the southern Levant (all Early Pleistocene first appearances are from the 'Ubeidiya Formation). I, incisor; M, molar; and NISP, number of identified specimens. Southern Levant is the area south of the Taurus-Zagros Mountains to the Arabian peninsula; Levant also includes Asia Minor.

Species	Level	NISP	Dental elements	Biogeographical origin (of genus or subgenus)	Biogeographical origin of species	First appearance	Last appearance
Lagomorpha							
Lepus capensis	II-6	1	I_2	Afro-Eurasian	Afro-Eurasian	GBY	Extant
Hyracoidea							
Procavia syriaca		1	I_1	Africa (Ethiopian)	African + Levant	GBY	Extant
Rodentia: Arvicolidae							
Mimomys cf. *ostramosensis*	II-6	15	$1I_1$; $1I^1$; $2M_1$; $1M_2$; $2M_3$; $2M^3$; $4M^2$; 4 broken molars	Palearctic	Palearctic	GBY	Eburonian–early Waalian
Microtus guntheri	V-4, V-5, I-4, II-2, II-3, II-5, II-6, II-7	221	$63I_1$; $84I^1$; $31M_1$; $21M^1$; $6M_2$; $17M^2$; $5M_3$; $6M^3$; $4M^3$; $4M^2$; 5 frag. mand., 12 broken molars	Holoarctic	Southern Levant	Early Pleistocene	Extant
Microtus (*Tibericola*) cf. *jordani*	II-6, II-7	4	$2M_1$; $4M_3$	Southern Levant	Levant	Early Pleistocene	GBY
Muridae							
Mus macedonicus	V-5, II-2, II-3, II-6	14	$9I_1$; $6I^1$; 1 frag. mand.	Asia	Levant	Early Pleistocene	Extant
Arvicanthis ectos	II-6	1	I^1	Africa (Ethiopian)		Early Pleistocene	Late Middle Pleistocene (*12*)
Gerbillidae							
Gerbillus dasyurus	II-5	1	I^1	Paleotropic	Southern Levant	Early Pleistocene	Extant
Spalacidae							
Spalax ehrenbergi	V-5, II-6	3	$2I_2$; $1I^1$; $1M_2$	Levant	Levant	Early Pleistocene	Extant
Hystricidae							
Hystrix cf. *indica*	V-5	1	I_1	Paleotropic	Levant	Early Pleistocene	Extant

graphic resolution of the Eurasian Plio-Pleistocene (*15*). GBY deposits contain *M. ostramosensis*, which represents an advanced stage, with a high hypsodont crown, yet it still preserves the enamel islet of M1, which was lost in its successive species *M. savini*. *M. ostramosensis* has been attributed to the Eburonian–early Waalian period (*15*). The high hypsodonty of *M. ostramosensis* from GBY reached its maximum development and represents a stage that is typical of *M. savini*, and it may indicate a transitional stage in the *M. savini–M. ostramosensis* chronocline. This stage is missing from the European record (*16*), and hence may have taken place in the southern Levant about 1.0 to 0.7 Ma.

Wood, bark, seeds, fruit, and pollen are common at GBY (*17*). Fossil seeds and fruits have been recovered from 32 layers. A total of 100 taxa were found, and 44 of them have been identified to the species level. Forty-two of the taxa are characteristic of wet habitats, and they record fluctuating lake-level conditions through the sequence.

Among the plant taxa identified, seven of the species do not grow in Israel today. These species are immersed or floating freshwater plants. Two are tropical-subtropical forms (*Euryale ferox* and *Najas foveolata*), three are inhabitants of temperate regions (*Nymphoides* cf. *peltata*, *Potamogeton coloratus/polygonifolius*, and the extinct *Stratiotes intermedius*), and two show a boreal-tropical distribution (*Trapa natans* and apparently *Sagittaria sagittifolia*). There are also bank forest taxa such as wild grape (*Vitis sylvestris*) and ash (*Fraxinus syriaca*) (*8*).

Many edible species were found, including wild grape, water chestnut (*Trapa natans*), prickly water lily (*Euryale ferox*), cattail (*Typha* sp.), oak (*Quercus* sp.), wild pistachio (*Pistacia atlantica*), wild olive (*Olea europaea*), plum (*Prunus* sp.), and jujube (*Ziziphus spina-christi*). Some of these fruits may have been brought to the site by hominins. The variety of species indicates that plant food was available at this site throughout the year.

There are numerous archaeological levels throughout the 34-m sequence at GBY (Fig. 2). Most of the archaeological occurrences consist of lithic assemblages with thousands of in situ artifacts in association with archaeobotanical and paleontological remains. Less frequently, lithic artifacts appear as isolated items. Most of the lithic assemblages were preserved in their original depositional setting, and only rarely were artifacts found to be redeposited. The archaeological occurrences are typically located at the contacts between fine and coarse sediments (i.e., II-2/3, I-4/5). They range from single-item-thick horizons to successions of superimposed thin horizons, forming a largely anthropogenic unit more than 1.5 m thick (II-6). More than a dozen archaeological occurrences were identified in the sequence, demonstrating repetitive hominin occupation of the same area over a prolonged period of time.

All the lithic assemblages retrieved from the site are assigned to the Acheulean Industrial Complex (*18–20*). Those of sufficient sample size always include a bifacial component (both hand-axes and cleavers) as well as special flakes indicative of the production of bifaces (*éclat de taille de biface*). The latter indicate that some of the bifaces were modified in situ.

Three different rock types were selected by the hominins for the production of specific morphotypes (Fig. 3): limestone pebbles for the production of chopping tools; flint for the modification of cores, flakes, and flake tools; and basalt primarily for the production of bifaces (hand-axes and cleavers). Raw material procurement strategy, as revealed at the site, was dictated by the specific need and by the search for suitable materials in general (flint, limestone, basalt) and for certain properties of each (size of pebbles and/or suitability of the material in hardness, porosity, etc.). Basalt is the dominant raw material in the vicinity of the site (in the form of flows, boulders, cobbles, and pebbles); other sources are located farther away (~10 km), and thus rarer flint and limestone pebbles were likely collected from wadi beds and terraces in the vicinity of the site. They are thus more rare in comparison with the basalt that forms the landscape in the study area.

Basalt biface manufacture was mostly based on the production of large flakes by the application of the Kombewa, Levallois, and other opportunistic techniques. It is at GBY that these techniques make their first appearance outside Africa, and the same holds true for the systematic exploitation of large flakes for biface production. The large basalt flakes were transformed into bifaces with minimal modification, resulting in an end product that closely resembles those known from the Acheulean Industrial Complex of Africa (*3, 21–26*). The GBY cultural material is similar in various aspects to lithic assemblages of sites such as Olduvai Gorge Bed IV and Masek Beds (*21, 23–25*), Olorgesailie (*19, 27*), Isimila (*28*), Kalambo Falls (*29*), Terni-

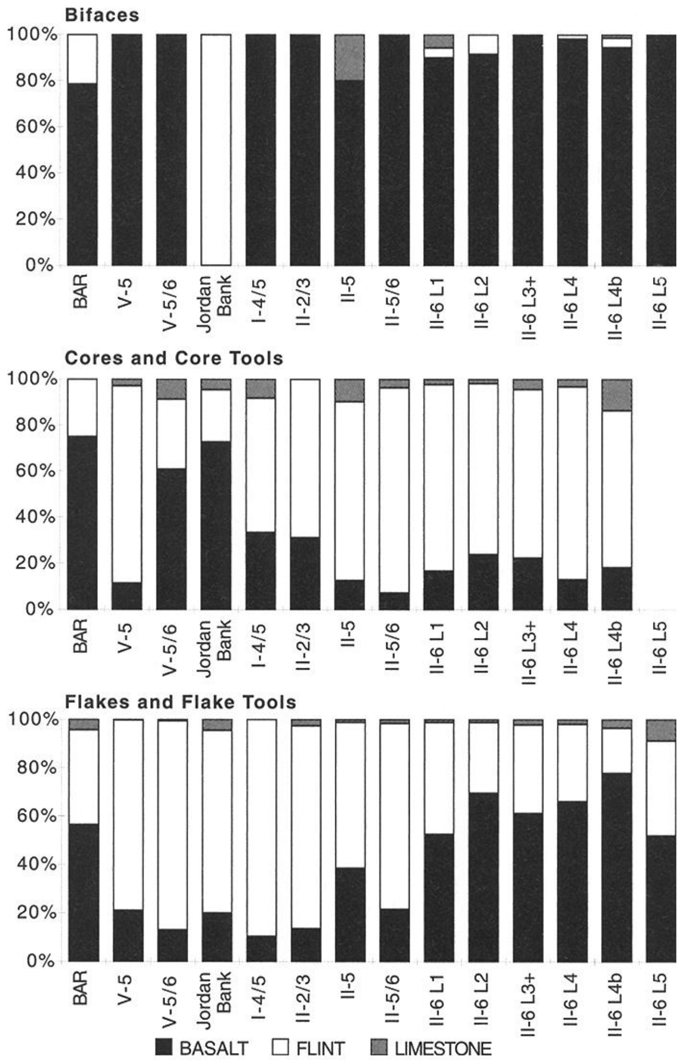

Fig. 3. Composition of the lithic artifact assemblages from GBY, displayed as raw material contributions to three major categories. Columns reflect the main archaeological layers from oldest (II-6 L5) to youngest [the Bar (*7*)]. Bifaces are predominantly formed on basalt, whereas cores and core tools use high proportions of flint.

fine (Tighnif) (*30*, *31*), and especially Isenia (*32–34*).

The archaeological horizons are characterized by a great diversity in the frequencies of the various components (i.e., bifaces) and of waste types. This diversity likely reflects different hominin activities along the shores of the paleo–Hula Lake over time. The GBY lithic assemblages bear evidence of the presence of complex cognitive abilities (*35*) because the production of the desired tools entails design, dexterity, and flexibility.

Earlier evidence for hominin migration out of Africa is seen at 'Ubeidiya, with an Acheulean assemblage comparable to that from upper Bed II at Olduvai Gorge (~1.4 Ma). GBY provides evidence of a separate, chronologically younger, and culturally different entity, reflecting yet another human movement out of Africa. Lithic assemblages similar to those at GBY are unknown from contemporaneous sites in Eurasia. However, many technological patterns that make their first appearance outside Africa at GBY are characteristic of the later Eurasian record (*36–41*). Multidisciplinary investigations at GBY provide a unique opportunity to reconstruct the ecological background of hominin behavior during the early stages of human globalization.

References and Notes

1. O. Bar-Yosef and N. Goren-Inbar, *The Lithic Assemblages of 'Ubeidiya* (Qedem 34, Institute of Archaeology, Hebrew University, Jerusalem, 1993).
2. E. Tchernov, L. K. Horwitz, A. Ronen, A. Lister, *Quat. Res.* **42**, 328 (1994).
3. N. Goren-Inbar and I. Saragusti, *J. Field Arch.* **23**, 15 (1996).
4. W. Roebroeks and T. van Kolfschoten, in *The Earliest Occupation of Europe*, W. Roebroeks and T. van Kolfschoten, Eds. (Leiden University, Leiden, Netherlands, 1995), pp. 297–315.
5. M. Stekelis, *Bull. Res. Council Isr.* **G9**, 61 (1960).
6. E. Tchernov and D. Geraads, *L'Anthropologie* **87**, 138 (1983).
7. N. Goren-Inbar, S. Belitzky, Y. Goren, R. Rabinovitch, I. Saragusti, *Geoarchaeol.* **7**, 27 (1992).
8. N. Goren-Inbar *et al.*, *Quat. Res.* **38**, 117 (1992).
9. N. Goren-Inbar, A. Lister, E. Werker, M. Chech, *Paleorient* **20**, 99 (1994).
10. N. Goren-Inbar and S. Belitzky, *Quat. Res.* **31**, 371 (1989).
11. A. Horowitz, *Isr. J. Earth Sci.* **22**, 107 (1973).
12. F. C. Bassinot *et al.*, *Earth Planet. Sci. Lett.* **126**, 91 (1994).
13. E. Tchernov, *Cour. Forschungsinst. Senckenb.* **153**, 103 (1992).
14. W. von Koenigswald, O. Fejfar, E. Tchernov, *Neues Jahrb. Geol. Palaeontol. Abh.* **184**, 1 (1992).
15. J. Chaline and G. Farjanel, *Boreas* **19**, 69 (1990).
16. W. von Koenigswald and W.-D. Heinrich, *Kaupia* **9**, 53 (1999).
17. Y. Melamed, thesis, Bar Ilan University (1998).
18. D. L. Clark, *Analytical Archaeology* (Methuen, London, 1968).
19. G. L. Isaac, *Olorgesailie, Archaeological Studies of a Middle Pleistocene Lake Basin, Kenya* (University of Chicago Press, Chicago, 1977).
20. ———, in *Stone Age Prehistory: Studies in Memory of Charles McBurney*, G. N. Bailey and P. Callow, Eds. (Cambridge University Press, Cambridge, 1986), pp. 221–241.
21. D. A. Roe, in (*25*), pp. 146–234.
22. ———, in (*25*), pp. 299–309.
23. P. Callow, in (*25*), pp. 235–253.
24. P. R. Jones, in (*25*), pp. 254–298.
25. M. D. Leakey and D. A. Roe, Eds., *Olduvai Gorge Excavations in Beds III, IV, and the Masek Beds 1968–1971* (Cambridge University Press, Cambridge, 1994).
26. J. D. Clark, in *After the Australopithecines: Stratigraphy, Ecology, and Culture Change in the Middle Pleistocene*, K. W. Butzer and G. L. Isaac, Eds. (Mouton, The Hague, 1975), pp. 605–659.
27. R. Potts, *J. Hum. Evol.* **18**, 477 (1989).
28. M. R. Kleindienst, *S. Afr. Arch. Bull.* **16**, 35 (1961).
29. J. D. Clark, *Am. Anthropol.* **8**, 202 (1966).
30. L. Balout, P. Biberson, J. Tixier, *L'Anthropologie* **71**, 217 (1967).
31. D. Geraads *et al.*, *Quat. Res.* **25**, 380 (1986).
32. H. Roche, J.-P. Brugal, D. Lefèvre, S. Ploux, P.-J. Texier, *Afr. Arch. Rev.* **6**, 27 (1988).
33. H. Roche and P.-J. Texier, in *Evolution and Ecology of* Homo erectus, J. R. F. Bower and S. Sartono, Eds. (Leiden University, Leiden, Netherlands, 1995), pp. 153–167.
34. P.-J. Texier, in *La vie préhistoriques* (Faton, Dijon, France, 1996), pp. 58–63.
35. A. Belfer-Cohen and N. Goren-Inbar, *World Arch.* **26**, 144 (1994).
36. M. Santojna and P. Villa, *J. World Prehist.* **4**, 45 (1990).
37. W. Roebroeks, J. Kolen, F. Resnik, *Hellinium* **38**, 17 (1988).
38. A. Tuffreau, in *The Definition and Interpretation of Levallois Technology*, H. L. Dibble and O. Bar-Yosef, Eds. (Prehistory Press, Madison, WI, 1995), pp. 413–427.
39. A. Selkirk and W. Selkirk, *Curr. Anthropol.* **13**, 324 (1997).
40. M. Pitts and M. Roberts, *Fairweather Eden: Life in Britain Half a Million Years Ago as Revealed by the Excavations at Boxgrove* (Century, London, 1997).
41. M. B. Roberts and S. A. Parfitt, *Boxgrove: A Middle Pleistocene Hominid Site at Eartham Quarry, Boxgrove, West Sussex* (Archaeological Report 17, English Heritage, London, 1999).

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A Single Adenosine with a Neutral pK_a in the Ribosomal Peptidyl Transferase Center

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Biochemical and crystallographic evidence suggests that 23*S* ribosomal RNA (rRNA) is the catalyst of peptide bond formation. To explore the mechanism of this reaction, we screened for nucleotides in *Escherichia coli* 23*S* rRNA that may have a perturbed pK_a (where K_a is the acid constant) based on the pH dependence of dimethylsulfate modification. A single universally conserved A (number 2451) within the central loop of domain V has a near neutral pK_a of 7.6 ± 0.2, which is about the same as that reported for the peptidyl transferase reaction. In vivo mutational analysis of this nucleotide indicates that it has an essential role in ribosomal function. These results are consistent with a mechanism wherein the nucleotide base of A2451 serves as a general acid base during peptide bond formation.

During the early stages of model building on the 50*S* ribosome crystal structure, Moore, Steitz, and co-workers came to the anticipated, but hitherto unproven, conclusion that the peptidyl transferase center of the ribosome is composed exclusively of RNA (*1*, *2*). Addition of peptidyl transferase inhibitors to the crystals led to the surprising observation that the nucleotide bases, rather than the phosphodiester backbone, are the components of the ribosome closest to the site of peptide bond formation (*2*). This suggested that the ribosome might catalyze protein synthesis using a nucleotide base as a general acid base, although the identity of the nucleotide was unknown to us at the outset of these experiments.

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Because none of the ribonucleotide functional groups in RNA have a pK_a near the neutral pH that would be required for acid-base catalysis, we hypothesized that the pK_a of an active site residue might be substantially perturbed in a manner analogous to that observed within protein enzymes and as proposed for the Hepatitis delta virus ribozyme (*3–6*). On the basis of the unperturbed pK_a values of the nucleotide bases, the two most likely candidates for such an effect are the N1 of adenosine (A) and the N3 of cytidine (C), which have pK_a's of 3.5 and 4.2, respectively (*7*). Both of these functional groups can be methylated by dimethylsulfate (DMS) to produce a nucleotide adduct that terminates reverse transcriptase one nucleotide before the methylated base (*8*). A solvent-accessible residue with a neutral pK_a should be unreactive to DMS modification at acidic pHs be-