



# The Exploitation of Plant Resources by Neanderthals in Amud Cave (Israel): The Evidence from Phytolith Studies

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The depositional environments of Amud Cave indicate that phytolith assemblages retrieved from the cave's sediments are an integral part of the Middle Palaeolithic sequence. As such, they provide direct evidence for plant use. The Amud Neanderthals emphasized both wood and grass exploitation. Ligneous parts of trees and shrubs were used mainly for fuel. Herbaceous plants were used for bedding, possibly fuel, and for food. There is clear and repetitive evidence for the exploitation of mature grass panicles, inferred to have been collected for their seeds. These findings suggest that, as with the pattern recently discerned for faunal resources, a broad spectrum of plants has been exploited from *at least* the end of the Middle Palaeolithic. Phytolith analysis now provides a tool for testing models explaining subsistence and mobility patterns during the Levantine Middle Palaeolithic and for better understanding the role of vegetal resources in shaping these patterns.

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## Introduction

**H**uman populations of the late Pliocene and Pleistocene subsisted as hunters and gatherers, relying on various combinations of plant and animal foods. Most researchers accept that carnivory, as a frequent and significant component of human diets, occurred in a relatively late stage of human evolution, and that the earliest humans relied heavily, although possibly not exclusively, on plant resources

(e.g., Aiello & Wheeler, 1995). However, where numerous hypotheses have been put forward to explain the changing modes of meat acquisition during the last 2.5 million years, only a few and general models relate to plant utilization until the very late Pleistocene. Such models suggested, on the basis of ecological and ethnographic observations, that plants have been important in shaping social organizations, diets and mobility patterns of human populations, especially in low and medium latitudes (e.g., Hatley & Kappelman, 1980; Hayden, 1981; Isaac & Crader, 1981; Kelly, 1983, 1995; Lieberman & Shea, 1994; O'Connell, Hawkes & Blurton-Jones, 1999; Wrangham *et al.*, 1999).

While ample physical remains attest to the use of faunal resources as food, raw materials for tools and

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for artistic manifestations (Klein, 1989, 1999), and possibly as fuel for hearths (Costamagno, Griggo & Mourne, 1999), evidence for the use of plants is scanty at best. Before the Late Glacial Maximum, only a few sites contain direct evidence for the existence of plant tissue (namely carbonized, mineralized or waterlogged seeds, fruits, bark and wood), let alone clues to its particular use as raw material for tools or as a source of food (e.g., Clark, 1969; Isaac, 1971; Akazawa, 1997; Belitzky, Goren-Inbar & Werker, 1991; Baruch, Werker & Bar-Yosef, 1992; Kislev, Nadel & Carmi, 1992; Lev, 1993; Mason, Hather & Hillman, 1994; Thieme, 1997; Goren-Inbar *et al.*, 2000). In the majority of other cases, evidence such as ash deposits suggests the past use of plant material as fuel (e.g., Schiegl *et al.*, 1994, 1996; Rigaud, Simek & Thierry, 1995; Albert *et al.*, 1999). However, in the absence of macrobotanical remains, it is impossible to formulate concrete hypotheses about the exact manner by which early humans might have exploited plants. This archaeological reality has probably led to the “meat fixation” common in many analyses of prehistoric economies and cultural ecology (Clark, 1987; Bar-Yosef, 1994; Hovers, 1998a).

The lack of plant evidence from the majority of prehistoric sites is frequently explained as the consequence of poor preservation of organic materials (Isaac, 1971: 280; Freeman, 1981: 106–112). In addition, the view that plants are only preserved under exceptional conditions may have deterred attempts at recovery (Mason, Hather & Hillman, 1994: 54). Still, plants can leave some extremely resilient microfossils, of which phytoliths are of particular note. These are biogenic opal silica bodies that originate in the lumen and between the cells of several plant tissues. Owing to their mineral composition, phytoliths are very resistant to decay and may survive in sediments far longer than other plant debris (Piperno, 1988). The deposition of phytoliths in prehistoric caves is related to animal frequentation, water percolation and wind, but also to anthropic action (Madella & Powers-Jones, 1996). They can thus provide valuable information about the past use of plant materials in such contexts, where other plant data are normally scarce or non-existent. Amud Cave is one such instance.

#### The site

The Middle Palaeolithic site of Amud Cave is located on the margin of the Dead Sea Rift Valley, 5 km to the northwest of the Sea of Galilee (Figure 1). At an elevation of 110 m below sea level, the cave is situated in a steep cliff overlooking the Wadi Amud, some 30 metres above the present channel bed. The cave is in the Irano-Turanian phytogeographical zone, with a mean annual precipitation of *c.* 450 mm. Presently the cave consists of a small chamber (some 7 × 5 m), a large open “middle” terrace (25 × 12 m), and a lower terrace that is actually a steep slope toward the channel

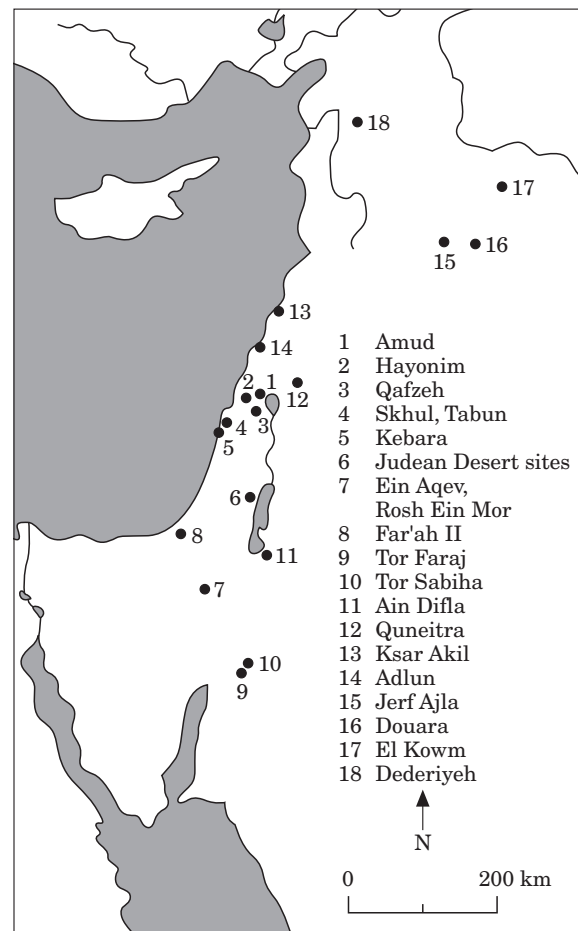


Figure 1. Location map of the Middle Palaeolithic sites in the Levant.

bed. Excavations at the site took place between 1961 and 1964, and again between 1991 and 1994 (Suzuki & Takai, 1970; Hovers *et al.*, 1991, 1995), and have established that Palaeolithic occupation of the cave took place in all these three areas. The current physical configuration of the cave is relatively recent and dates to the late Upper Pleistocene (Hovers, 1994; Inbar & Hovers, 1999; Valladas *et al.*, 1999 and see below).

The 4.5 metre column of sediments consists of Middle Palaeolithic deposits (unit B), unconformably overlain by unit A, dated to the Holocene (5th millennium BC and onwards). Unit B was originally divided into four stratigraphic units (B<sub>1</sub> to B<sub>4</sub>, top to bottom: Chinzei, 1970), with the lowest unit deposited directly on top of the bedrock. With the exception of some refinement of the internal stratigraphic division of these units (Hovers *et al.*, 1995), this broad framework was confirmed during the course of recent excavations of the site. TL age estimates (Valladas *et al.*, 1999) indicate human occupation of the cave between *c.* 70 kyr ago (unit B<sub>4</sub>) and *c.* 55 kyr ago (units B<sub>2</sub> and B<sub>1</sub>).

Units B<sub>1</sub>, B<sub>2</sub> and B<sub>4</sub> yielded numerous stone artefacts, typically flakes, blades and triangular flakes

rarely modified by additional retouch (Hovers, 1998b) and animal bones which are often fragmented and burnt. The remains of 15 Middle Palaeolithic hominids were recovered from units B<sub>1</sub> and B<sub>2</sub>. Their spatial arrangement was shown to be unrelated to post-depositional processes, and thus related to intentional disposal (Hovers *et al.*, 1995). While the majority of hominid remains consist of isolated and/or fragmentary bones, two relatively well preserved skeletons, an adult male, Amud I, and a 10-month-old infant, Amud 7, were recognizable as Neanderthals (Rak, Kimbel & Hovers, 1994; Hovers *et al.*, 1995).

Unit B<sub>3</sub> consists of coarse-grained stony debris with little matrix, and is of a non-anthropogenic nature (Hovers *et al.*, 1991, 1995). The sediment of this unit is derived from the dissolution of the brecciated bedrock from the cave's walls and roof. This hiatus in the human occupation of the cave is reflected by the distribution of the TL (Valladas *et al.*, 1999) and ESR estimates (Rink *et al.*, 2001).

Sediments of units B<sub>1</sub>, B<sub>2</sub> and B<sub>4</sub> are composed of alternating cemented, often laminated, ashy grey and black horizons, each several centimetres thick. The surrounding matrix is powdery and dry, of grey to white colour. Micromorphological analysis indicates that these sediments are highly homogenous across the stratigraphic column and over the excavated area. Materials exotic to the cave, such as basalt and quartz particles, and clay sediments, are rare in these units. Thus, the sediments of Amud Cave do not seem to have been derived from the surface above the cave, which is clayey silt or silty clay and darker brown (namely *terra rossa*), nor do they include a significant component of wind-blown material. Most likely the sediments of units B<sub>4</sub>, B<sub>2</sub>–B<sub>1</sub> are ash derived from anthropogenic activity and reworked to some extent by biological activity and possible human scattering and trampling. These ashes were originally associated with intact hearths, most of which have been modified by bioturbation. Intact material, little influenced by such processes, was found in units B<sub>1</sub> and B<sub>2</sub> in the stony deposits along the north wall of the cave and in cemented calcareous ash units (Figure 2). Presumably, these are hearths or burnt zones that were cemented shortly after their accumulation and thus escaped bioturbation. Within unit B<sub>4</sub>, the outlines of small, intact hearths could be discerned.

Clearly, at Amud Cave, as well as at the Levantine Middle Palaeolithic sites of Hayonim, Tabun and Kebara (Schiegl *et al.*, 1994, 1996; Albert *et al.*, 1999, 2000) plants were exploited in the context of the use of fire. While at Kebara Cave some charcoal was retrieved (Baruch, Werker & Bar-Yosef, 1992), none has been reported from the Middle Palaeolithic layers of Tabun and Hayonim, and to date, none has been at Amud Cave.

A pilot study of four sediment samples from units B<sub>4</sub> and B<sub>2</sub>, collected during the 1990s excavations at Amud Cave, was conducted by Arlene Miller-Rosen in

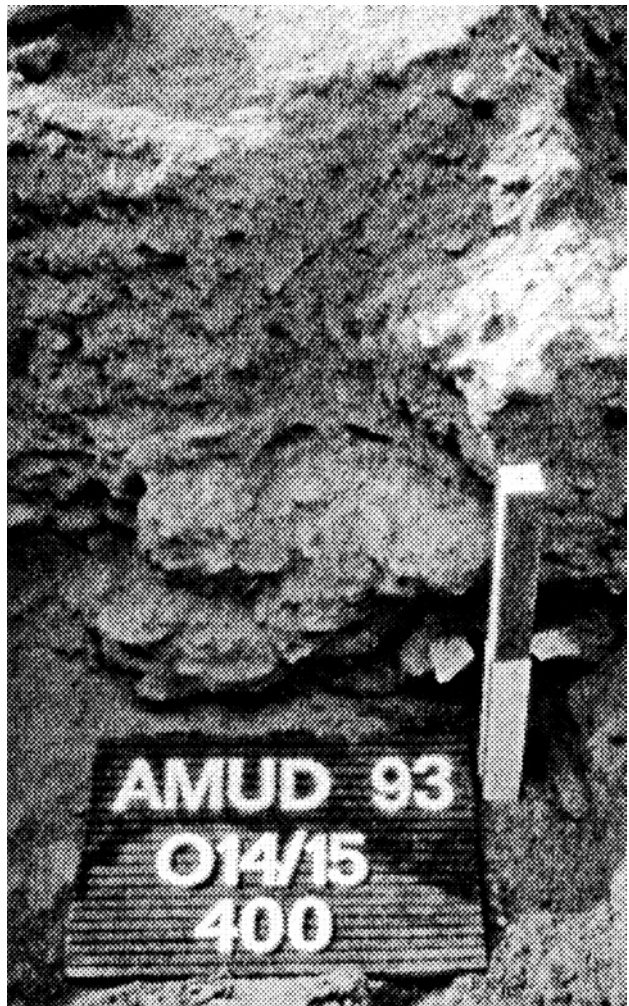


Figure 2. Cemented ash deposits as seen during excavation. Note the thickness of ash.

1993. Phytoliths were found in all the samples. These positive results led two of us (MM and EH) to initiate a systematic study of phytoliths from this site. The significance of this study is twofold. First, phytoliths constitute the only direct evidence for plant use on site, since no pollen was found, and such charred material as was found was too highly fragmented for conventional analysis, only observable in thin sections. Second, Amud Cave occupies a different ecological niche from the majority of well-studied Levantine Middle Palaeolithic sites (e.g., Kebara, Tabun, Hayonim and Qafzeh), all of which are found in the present day core Mediterranean region. Palaeoclimatic reconstructions suggest that an equivalent ecological distinction also prevailed, to varying degree, during the Middle Palaeolithic (Bar-Yosef, 1994, 1995; Hovers, 1997, in preparation). The study of the Amud Cave phytoliths thus provides data about the behaviour of Neanderthals in ecological conditions which are distinct from those postulated to characterize the



existence of this group in both Europe and the Levant (Bar-Yosef, 1994; Rak, 1993; Mellars, 1996).

## Methods

### *Sampling procedures*

Bulk sediment samples were collected during the 1991–1994 excavation in Amud Cave, in order to be used in subsequent specialized analyses, and stored in sealed plastic bags. For each sample the provenience in relation to the excavation grid and its elevation relative to the excavation datum was noted. We also recorded the characteristics of the features and sediments from which the samples were collected. In addition, smaller samples were systematically collected and recorded in three coordinates from each subsquare and each spit excavated from unit B<sub>4</sub> during the 1994 season. Twenty-nine sub-samples for phytolith analysis were then selected from this pool (see Table 1). Given the nature of the sediments in the cave, selection concentrated on features that were less disturbed—namely, cemented sediment patches in units B<sub>1</sub> and B<sub>2</sub>, and intact hearths of unit B<sub>4</sub>. For comparative purposes, we examined also samples derived from the bioturbated ashy component, as well as from the matrix of unit B<sub>3</sub>. The 29 sub-samples were combined into four groups according to the main stratigraphic framework of the Palaeolithic deposits (Table 1). Finally, two samples from present-day habitats were studied. One was taken from the wadi bed, a nature reserve rich in hydrophilus vegetation without any known significant human interference. A second modern sample was collected from the basaltic plateau on top of the cliff where the cave is located. This area is cultivated and wheat is grown there. In both cases the sediment was collected from a depth of about 10 cm below the present surface.

### *Phytolith extraction*

Phytoliths were extracted from the 29 archaeological and two modern sediment samples (Madella, Powers-Jones & Jones, 1998). A weighed aliquot of air-dried sediment, *c.* 3 gm or the maximum available in smaller sub-samples, was treated with 25 ml of a solution of 7% HCl and heated until the liquid was reduced to 5 ml. HCl was then added again and evaporated, until the reaction ceased. The residue left after dissolution of carbonates was rinsed in de-ionized water and de-flocculated with a 5% weight solution of sodium hexa-meta-phosphate (Calgon<sup>®</sup>), rinsed again with de-ionized water and 10 ml of a 33% volume solution H<sub>2</sub>O<sub>2</sub> was added. The sample was evaporated in a *bain marie* at 40°C, H<sub>2</sub>O<sub>2</sub> added until the reaction ceased, and then rinsed in de-ionized water. The silicate mineral component of the resulting residue was extracted by gravimetric separation using a sodium polytungstate (Na<sub>6</sub>[H<sub>2</sub>W<sub>12</sub>O<sub>40</sub>]·H<sub>2</sub>O) solution, of

2.35 g/ml density, to separate off any other mineral component left. Clay particles were removed by low speed centrifugation during the various steps of the extraction. The final residue was dried and stored in glass vials (For further details on the extraction technique see Madella, Powers-Jones & Jones 1998).

Phytolith assemblages were mounted with Entellan New (Merck) and scanned by optical microscopy at 400× and 600× magnification (Nikon Labophot 2-POL). Micrographs were taken with a Lumina Scanning CCD camera linked to a Macintosh computer. A minimum of 243 phytoliths per sample were counted. The number of phytoliths per gram of final residue was calculated, and the proportions of phytolith types estimated (Tables 1 and 3). Calculation of the amount of phytoliths per gram of final residue was done adjusting the formula used by Albert *et al.* (1999, 2000) to our extraction technique. Contrary to the situation in Tabun Cave, and in some of the Kebara samples (Albert *et al.*, 1999, 2000: 945), sediments in Amud Cave are usually in a chemically pristine state and have not undergone extensive dissolution (see below). Therefore it was not necessary to standardize the absolute number of phytoliths to the Acid Insoluble Fraction (AIF) as defined by Albert *et al.* (1999, 2000). Even if differences in the extractive process meant that direct numerical comparison is not straightforward, relative quantities of phytoliths are comparable.

### *Phytolith classification*

The phytolith study that is the object of this paper has been specifically targeted to grasp information on Middle Palaeolithic use of plant resources. Therefore primary phytolith morphologies were grouped according to plant anatomy and taxonomy.

For the purposes of this paper, we shall divide the Amud phytoliths into five categories (see Table 2). The first is a general category with insufficient diagnostic morphology to go beyond their identification as being from vascular plants of some kind. The second category comprises phytoliths with sufficient diagnostic morphology to place them in taxa other than grasses. They include phytoliths from dicotyledonous wood and leaves. The third category comprises phytoliths that form within the lumens of long and short epidermal cells of monocotyledonous leaves and stems. The only recognizable family of monocots contributing to the third category are the grasses (Poaceae) but strictly speaking, other families such as the Cyperaceae and Juncaceae (sedges) cannot be excluded. The fourth category include phytoliths that form in the lumens of non-epidermal monocotyledonous cells, such as parenchyma. The fifth category comprises distinctive phytoliths termed dendritics. These phytoliths are generated in the family Poaceae. Their characteristic elongated form with spiny, dendritic sides (Figure 3) develops in the lumen and interstices between the

Table 1. List of the phytolith sub-samples, according to their stratigraphic provenience. Extraction attributes, number of counted fields on the microscopy slide, and phytoliths counted are given for each sample. In addition the concentration per gram, v/c index and absolute number of articulated phytoliths are listed. IG=inflorescence from grasses; CLG=Culm and leaves from grasses; W=Dicotyledons (mainly wood); P=Palms; C=Cystoliths (from fig-tree family). (\*) See text, refs 10-11.

Sample	Stratum	Context	Weight of initial sediment (g)	Weight of final sediment (g)	Weight of sediment on slide (g)	Counted fields	Counted phytoliths	Absolute number of phytoliths per gram of final sediment (FS)	Components of phytolith assemblages	V/C index	Normalized V/C index (*)
A37	B1	Hearth	2.60	0.32732	0.00097	6	246	2.197.938	IG/GLG/W	0.82	1.17
A38		Hearth	2.60	0.23045	0.00071	9	258	2.099.530	CLG/W/C	0.26	0.37
A23		General sediment	3.00	0.29954	0.00029	8	243	5.446.551	CLG/W	0.38	0.29
A18	B2	Hearth	3.00	0.35037	0.00060	15	250	1.444.444	IG/CLG/W	0.20	0.69
A17		Hearth	3.00	0.47579	0.00036	11	250	3.195.673	IG/CLG/W	0.49	0.27
A16		General sediment	3.00	0.33400	0.00072	4	258	4.658.333	IG/CLG/W/P	0.19	0.45
A25		General sediment	3.00	0.55290	0.00066	4	251	4.943.934	IG/CLG/W/P	0.32	0.54
A21	B2/8	General sediment	3.00	0.29295	0.00084	5	252	3.120.000	CLG/W/P	0.21	0.30
A36	B2/8	Hearth	3.00	0.15140	0.00069	10	255	1.865.766	CLG/W	0.09	0.13
A22	B2/8	General sediment	2.70	0.60209	0.00029	11	255	4.156.739	IG/CLG/W	0.40	0.57
A19	B2/8	General sediment	3.00	0.61753	0.00035	8	261	4.847.142	IG/CLG/W	0.51	0.73
A20	B2/8	General sediment	3.01	4.21875	0.00064	4	254	5.159.375	IG/CLG/W	0.45	0.65
A39	B2/9	Hearth	3.00	0.29535	0.00069	14	249	1.294.152	CLG/W	0.93	1.32
A15	B3	General sediment	3.00	0.32209	0.00092	1	251	10.913.043	IG/CLG/W	0.30	0.43
A5	B4	General sediment	1.50	0.01295	0.00066	17	259	1.200.356	CLG/W/C	0.62	0.90
A8		General sediment	0.92	0.14686	0.00071	6	262	3.198.122	CLG/W	0.20	0.28
A4		General sediment	3.41	0.68421	0.00111	5	265	2.482.882	IG/CLG/W	0.26	0.37
A3		General sediment	3.43	0.77695	0.00070	7	262	2.780.408	IG/CLG/W	0.15	0.22
A6		Hearth	2.70	0.12216	0.00039	5	245	6.533.333	IG/CLG/W/C	0.83	1.18
A7		General sediment	3.00	0.37193	0.00090	4	255	3.683.333	CLG/W	0.13	0.19
A9+10		General sediment	3.00	0.24926	0.00053	4	248	6.083.018	CLG/W	0.16	0.22
A1		General sediment	3.00	0.24962	0.00053	3	264	8.633.962	IG/CLG/W/P	0.17	0.25
A24		Hearth	2.26	0.15212	0.00105	2	251	4.780.952	CLG/W/P	0.23	0.33
A32		Hearth	2.78	0.71609	0.00069	7	257	2.766.873	CLG/W	0.40	0.57
A28		General sediment	0.68	0.16001	0.00132	6	252	1.654.545	CLG/W	0.60	0.86
A27		General sediment	1.05	0.22281	0.00103	3	250	4.207.119	CLG/W	0.61	0.91
A33		General sediment	2.97	0.43885	0.00069	5	253	3.813.333	CLG/W	0.44	0.59
A26		General sediment	1.60	0.09713	0.00035	5	259	7.696.000	CLG/W	0.63	0.90
A34		Hearth	3.00	0.35420	0.00075	2	250	8.666.666	IG/CLG/W	0.49	0.69

Table 2. Description of categories used in the classification of Amud Cave phytoliths

Category	Phytolith types	Description
1	Angiosperms/Gymnosperms	Forms with insufficient diagnostic form to go beyond their identification as being from vascular plants of some kind
2	Angiosperms non-Poaceae	Phytoliths with sufficient diagnostic forms to place them in taxa other than grasses. In this category are included the phytoliths from dicotyledonous wood and leaves
3	Poaceae epidermal tissue from leaves and culm	These phytoliths form within the lumens of long and short, epidermal cells
4	Parenchymata probably from Poaceae	This category includes phytoliths that form in the lumens of non-epidermal monocotyledonous cells, very probably of Poaceae
5	Poaceae inflorescence	Phytoliths are characterised by an elongate form with spiny, often dendritic sides which develop in the lumen and interstices between the epidermal cells of the modified leaves (glumes, paleas, lemmas), that make up the grass seed-head

epidermal cells of the modified leaves (glumes, paleas, lemmas), which make up the grass spikelets (Soni & Parry, 1973; Hayward & Parry, 1980; Sangster, Hodson & Parry, 1983; Hodson, Sangster & Parry, 1984, 1985).

Within the phytolith assemblages it is also possible to distinguish two major morphological groups: morphotypes with consistent morphology and morphotypes with variable morphology. Silica bodies with consistent morphology can be positively identified by their three-dimensional characteristics, which are repetitive and recognizable even when showing allometric differences. Mostly these are the silica bodies produced in the cells of the epidermal and sub-epidermal tissues of the Poaceae, Juncaceae and Cyperaceae families (grasses, sedges and rushes; Piperno, 1988; Pearsall, 2000). Variable morphology silica bodies have inconsistent three-dimensional characteristics and they tend to form mostly in the cells of the ligneous tissues, but also in the leaves, of trees and bushes.

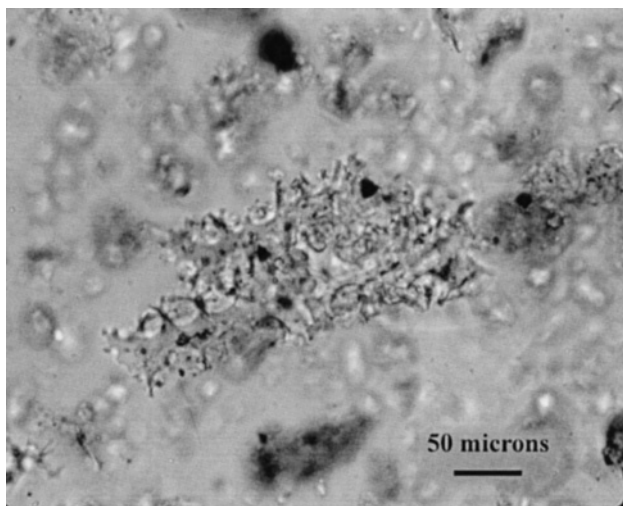


Figure 3. Articulated dendritic phytoliths from grass inflorescence heads (A37).

## Results

Mineralogical analyses conducted by FTIR (S. Weiner, pers. comm.; see Weiner, Goldberg & Bar-Yosef, 1993 for details about the method) and petrographic analyses reveal the almost exclusive presence of primary calcite, a typical product of wood fires (Schiegl *et al.*, 1994, 1996; Albert *et al.*, 1999: 1257), in both loose white ashes and in the cemented bands of ash. Similarly, typical ash rhombi are observed in the micromorphological thin sections. These data allow us to infer that the diagenesis of calcite originating from wood has not played a major role in determining the observed densities of wood phytoliths in the sediments (Schiegl *et al.*, 1994, 1996; Albert *et al.*, 1999, 2000). It is for this reason that the results of this analysis are not hampered by the absence of calculations of phytolith frequencies in AIF (Albert *et al.*, 1999, 2000).

Three general observations can be made about the Amud phytoliths. First, they occur in relative abundance for pre-agricultural deposits. Second, they are relatively intact and undamaged. Third, the characteristic morphotypes of both woody and grass plants are equally prominent.

Table 3 and Figure 4 present the absolute numbers and composition of phytolith assemblages in the various stratigraphic units of Amud Cave as well as in the two modern samples. All the samples from the four strata are rich in phytoliths. Absolute numbers per gram of final residue fall within a single order of magnitude, with frequencies varying between circa 1.2 million and 10.9 million phytoliths per gram of final residue (Tables 1 & 3). This suggests that there were little, if any, significant changes in phytolith input and preservation among the units. Surprisingly, the non-anthropogenic stratum B<sub>2</sub> has the highest frequencies of phytoliths. It is important to note here that, although all the fine-grained sediments in Amud Cave derive from similar origins, the phytolith assemblages are not homogeneous. In fact, there is a high degree of variability between and within the two major context groups, namely relatively intact hearths

Table 3. Summary of the absolute numbers of phytolith in Amud Cave sediments and the two modern analogues, and frequency of the main categories discussed in the text. Modern A sample is the terra rossa from the plateau on top of the cave. Modern B is from the wadi. A./G. = Angiosperm/Gymnosperm

Stratum	Total count per stratum	Number of samples	Absolute number of phytoliths per gram of final sediment (10 <sup>6</sup> )	Phytolith categories			Dendritics as a percentage of categories 3-4-5	Articulated phytoliths (silica skeletons) (not included in total count)
				1 A./G.	2 Ligneous	3-4-5 Grasses		
B <sub>1</sub>	747	3	2.1-5.5	1.90%	34.70%	63.40%	17.30%	9
B <sub>2</sub>	2535	10	1.3-5.2	5.30%	27.50%	67.20%	22.60%	32
B <sub>3</sub>	251	1	10.9	1.20%	23.10%	75.70%	50.00%	3
B <sub>4</sub>	3832	15	1.2-8.6	9.70%	24.10%	66.20%	10.70%	144
Modern A	300	1	0.08	12.50%	31.40%	56.10%	5.10%	Not counted
Modern B	300	1	0.037	15.50%	43.70%	40.80%	3.90%	Not counted

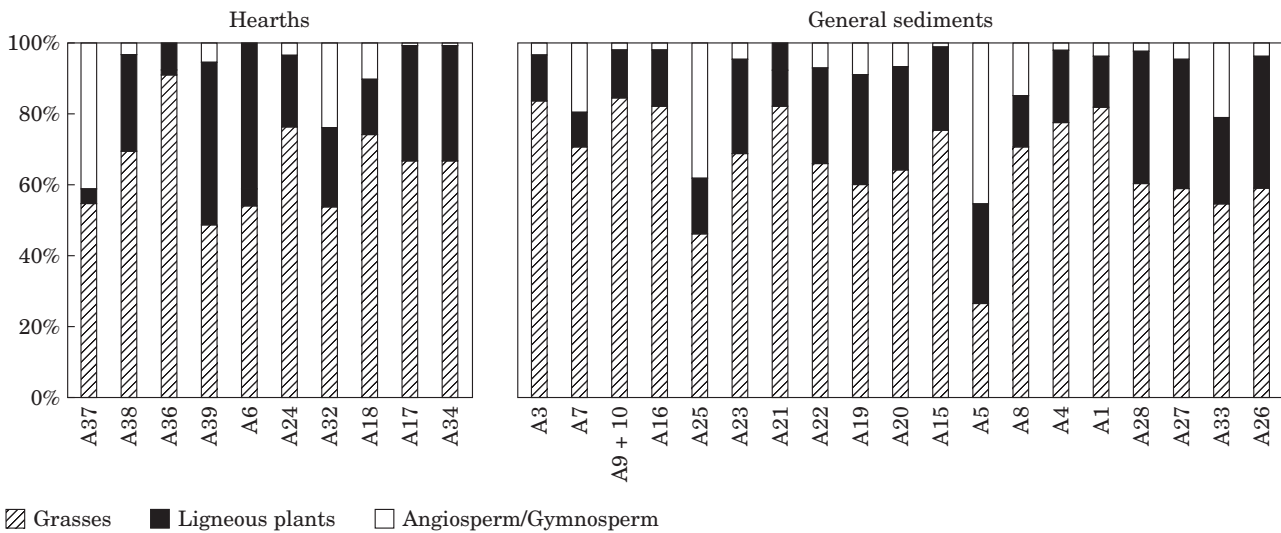


Figure 4. Frequencies of morphotype categories in Amud Cave assemblages. Category 1: Grasses; Category 2: Ligneous plants; Category 3: Angiosperm/Gymnosperm.

(represented by the cemented ash deposits) and the *general sediment*, consisting of scattered hearth ashes (see Figure 4). However, the samples originating from the relatively intact hearth sediments show considerably higher concentrations of wood phytoliths, suggesting a major wood input in this particular context.

Phytolith preservation in the cave’s sediments appears to be good; they are relatively intact and undamaged. The phytolith surfaces present a low to medium taphonomical sculpturing (rugose and pitted surfaces) and the fragile branches of the ornamented morphologies were relatively unbroken. No “secondary morphotypes” (forms created by erosion and dissolution of the original morphotypes; Madella, 2000) were in evidence. A proportion of the phytoliths, between 1.2% and 4.1% of the total number of phytoliths counted per unit, remain articulated, as in the original parent tissue.

The phytolith assemblages from Amud Cave show input both from dicotyledonous wood and leaves (Figures 5 & 6), and from monocotyledonous

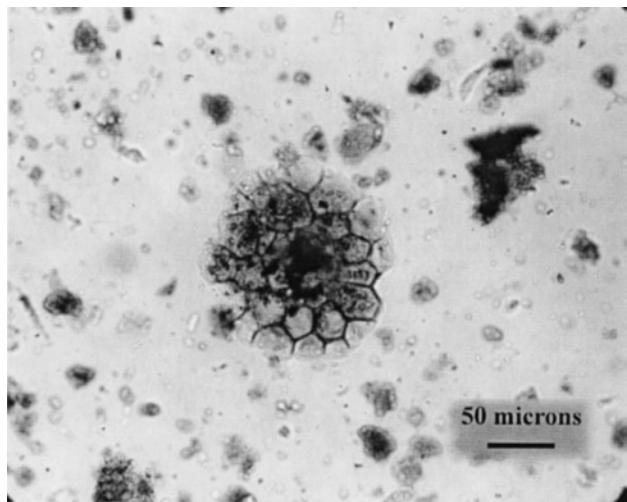


Figure 5. Epidermal hair of dicotyledonous plant, probably from a leaf or an herbaceous stem/twig (A1).





Figure 6. Silica skeleton of an epidermal hair base from a dicotyledon. Note the concentric arrangement of the cells around the base of the hair (A7).

herbaceous plants (categories 3–5; Figures 7 & 8). A distinctive feature of these assemblages is the high proportion of the latter group. This indicates a significant input from monocotyledonous herbs, of which the grasses are the one positively identified family. Plants from the Poaceae (grass family) are heavy accumulators of silica and the production of opal silica can be up to 20 times than in arboreal plants (Albert & Weiner, 2001; Carnelli, Madella & Theurillat, 2001). This has to be taken into consideration when comparing phytolith frequencies of grasses versus woody plants.

Morphologies similar to the ones formed in the grass tissues may be also produced in the tissues of sedges (e.g., Cyperaceae family). However, this family produces characteristic morphotypes (Ollendorf, 1992) which have not been encountered in the Amud Cave sediments.

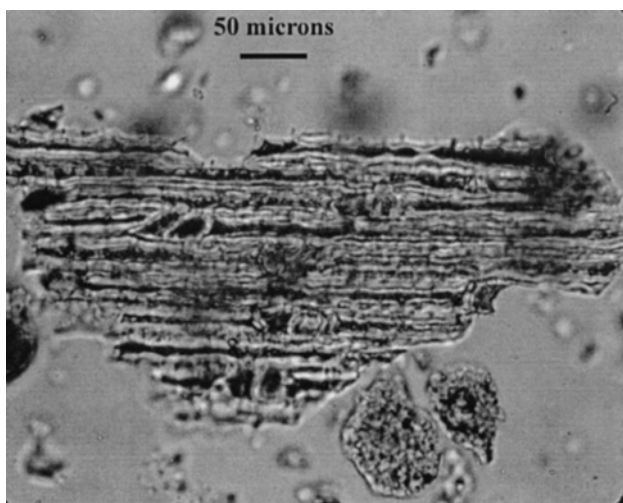


Figure 7. Silica skeleton from the culm of a grass (A15).

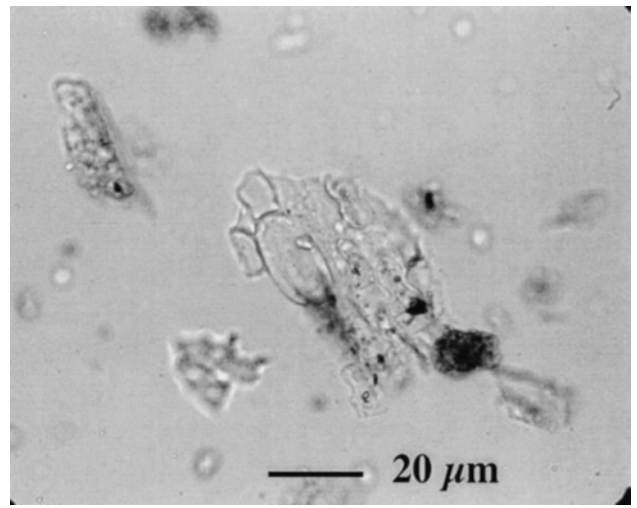


Figure 8. Silica skeleton from the epidermis of a Panicoideae-type grass. Note the Panicoideae short cells (dumbbells; A1).

Looking in more detail at grass morphotypes, the dendritic phytoliths are of particular note (Figures 3 & 9). Their proportions in the four sedimentary strata in respect to the total grass phytoliths range between 10.7% and 50%. Within the authropogenic units, the frequencies of dendritic phytoliths increase from the older to the younger deposits (see Table 3). The formation and development of dendritic morphologies is at its most active during the later stages of panicle development, and the presence of well developed dendritic forms is thus indicative of mature grass seed-heads.

The silica bodies of two important arboreal families have been identified in Amud Cave deposits: Palmae (palms) and Moraceae (fig-tree family), grouped in category 2 (Angiosperms non-Poaceae; see Table 3). Palm phytoliths (Figure 10) produced in the leaves

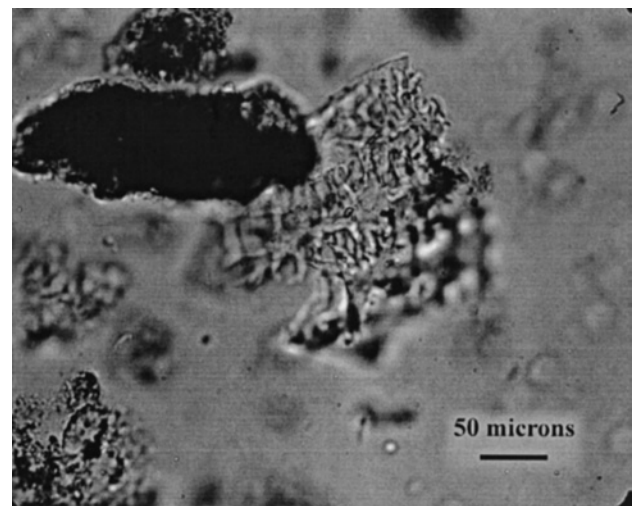


Figure 9. Articulated dendritic phytoliths from the inflorescence of a grass (A34).



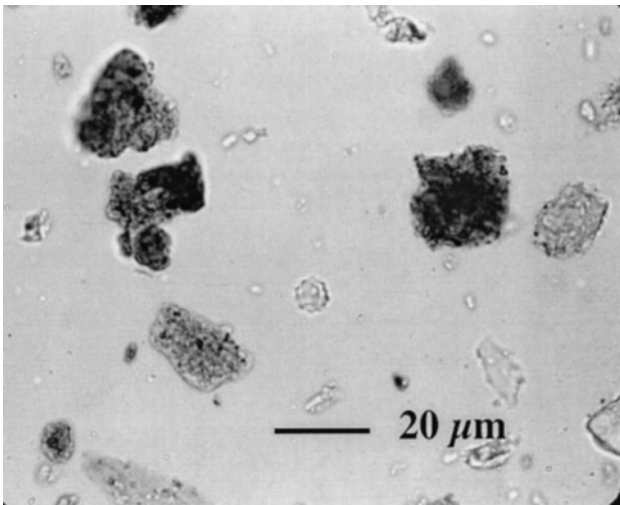


Figure 10. Spherical, spinulose phytolith from the palm leaf (A1).

(echinate spherical bodies) were recovered from strata B<sub>4</sub> and B<sub>2</sub>. Cystoliths similar to the type produced in the leaves of modern Moraceae were identified in samples from strata B<sub>4</sub> and B<sub>1</sub>. Cystoliths are mineralized bodies produced in the structure of epidermal hairs and are normally formed of calcium oxalate. Occasionally, when evapotranspiration is high, cystoliths may silicify so that the entire structure becomes resistant to treatment with HCl and is preserved as phytoliths.

The two modern samples (sample A from the plateau above the cave and sample B from the present flood plain of Wadi Amud) differ from the archaeological ones and the frequency of phytoliths is ten times less. They also differ from each other, probably reflecting the two types of vegetation cover from which they originated: the cultivated field and the natural vegetation of the wadi, respectively. The comparison of ancient and modern samples indicates that the modern soils have a significantly higher frequency of phytoliths of the first and second categories (general vascular plant forms and taxa other than grasses) or third category (grass epidermis), and a lower frequency of those from the fifth category (dendritics) (Table 3).

## Discussion

The phytolith assemblages from Amud Cave raise several intriguing issues. First among these is the use of plants by Neanderthals occupying the cave, as reflected in the phytolith record. Our findings are important also for elucidating other, broader issues. Below we touch briefly upon two such points: (1) patterns of plant use by Levantine Middle Palaeolithic populations, and (2) the implications of the finds of this study for understanding the antiquity of the use of grass seeds. In order to address these issues, it is necessary to first evaluate the integrity of the data at hand.

### *Are these really Middle Paleolithic phytoliths?*

The high frequencies of phytoliths in the cave sediment, and their relatively unaltered state (low breakage rate and taphonomic surface sculpturing) are remarkable in such old deposits, raising the issues of their authenticity in the Middle Palaeolithic sediments. Several lines of evidence suggest that the phytoliths are likely to be an integral part of these deposits.

Both micromorphological and stratigraphic observations indicate that Amud Cave was a closed-in, roofed cave during the Middle Palaeolithic, and that the major event of roof collapse post-dates the Mousterian occupation in the cave (Hovers, 1994; Inbar & Hovers, 1999; Valladas *et al.*, 1999). These observations render unlikely a phytolith input from external sources through natural processes. Micromorphological analysis of thin sections obtained from cemented ash lenses show that most of the components were stratified, including phytoliths, calcitic rhombi of ash, clayey aggregates (*terra rossa*), and bone fragments (both burned and unburned) (Figure 11). The geometric relationships among these components (i.e. fabric) demonstrate that the sediments represent *in situ*, non-disturbed ashy hearth materials. These same components within other ashy lenses do not show any signs of bedding, and in fact there is a virtual lack of preferred orientation, particularly in the phytoliths. In this latter case, the implication is that these sediments were subjected to some reorganization or turbation during Middle Palaeolithic times, specifically between the time of burning and the event of cementation. Even in this latter case, the micromorphological analyses indicate that phytoliths should be considered an intrinsic constituent of the Middle Palaeolithic deposits. The same holds true for the phytoliths derived from the uncemented sediments of hearths from unit B<sub>4</sub>. Importantly, the good mechanical and chemical preservation of the phytoliths suggests that depositional and post-depositional processes did not significantly modify the original phytolith assemblages. Unit B<sub>3</sub> is an exception to this pattern. This unit is archaeologically sterile and composed of large clasts with many voids and relatively little matrix between them. We therefore infer that the high frequency of phytoliths in this unit results from infiltration of ashy sediments from the overlying Middle Palaeolithic layers. Repetitive episodes of sediment entrapment in the voids would act to elevate the frequencies of phytoliths in the fine grained fraction sampled from this unit. This is seen also through micromorphological examination of the sediment, which revealed that the detrital accumulation of the *éboulis* rock fragments is embedded in silty, calcareous powdery matrix. The matrix contains angular chert chips (presumably artefacts), burned and unburned bone fragments and coprolites, all fairly coated in clay. These translocated remnants also include charred organic matter, rhombus and pseudomorphs of calcite originating from wood tissues and phytoliths.

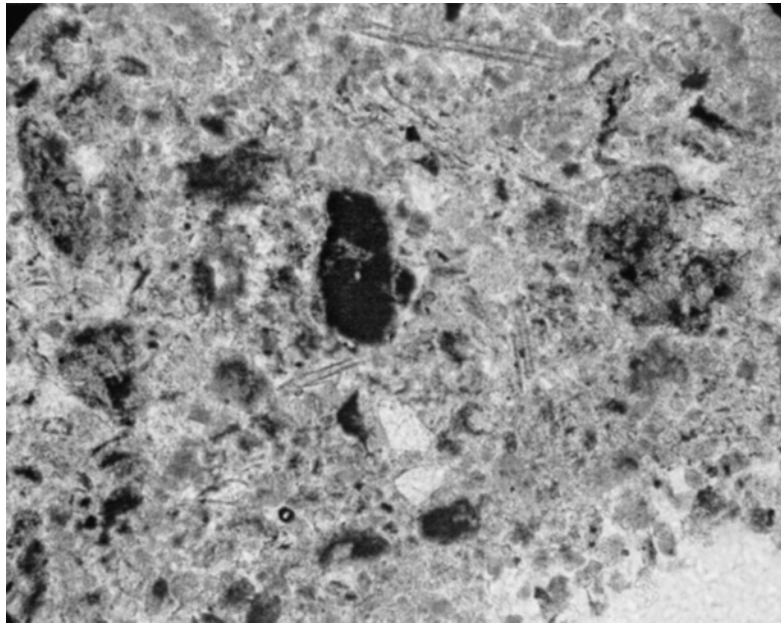


Figure 11. Ash deposit from Amud Cave showing undisturbed, horizontally bedded phytoliths in the centre of the photograph set into a matrix of calcite rhombi produced by the burning of wood. Plane polarized light: width of field of view ca. 3.2 mm.

However, the phytolith composition of unit B<sub>3</sub>, as seen in Table 3, is rather different from that of unit B<sub>2</sub>. This is probably due to the fact that for the purpose of this paper the assemblages of each archaeological unit, as expressed in Table 3, average the compositions of several sediment samples combined together (in this case, 10 for unit B<sub>2</sub>).

The comparative sample from the wadi bank has an important presence of woody plant phytoliths, as would be expected in blank vegetation. In contrast, the terra rossa sample from the plateau is rich in grass phytoliths, probably because of the addition of these morphotypes to the soil phytolith pool following cereal cultivation in modern times. While different from one another, both modern phytolith assemblages are also strikingly different from the cave assemblages and therefore are unlikely sources of recent contamination.

On the basis of all these data, we interpret the phytolith assemblages recovered from the anthropogenic units of Amud Cave as an authentic component of the Middle Palaeolithic sediments, reflecting in large part plant-related human activities.

#### *How were plants used in Amud Cave?*

*The uses of woody plants.* The distribution of the various phytolith categories suggests two main modes of plant exploitation by the Amud Cave's occupants. Irregular morphotypes typically produced in ligneous tissues (Albert *et al.*, 1999; Barboni *et al.*, 1999; Bozarth, 1993; Madella, 2000) constitute a significant part of the assemblage in each unit (Figure 4). This

observation, coupled with on-site evidence for the use of fire (e.g., hearths, burnt lithics and bones), suggests the probable use of wood as fuel. In fact, such a hypothesis is consistent with the mineralogical studies and with the micromorphological analyses of Amud Cave sediments, where the primary calcite and ash rhombi indicate that wood was burned in the cave as fuel (see Watzel, 1988; Schiegl *et al.*, 1994, 1996; Albert *et al.*, 1999, 2000, on wood ashes).

Spinulate, spherical phytoliths produced in the leaf mesophyll of palms attest to the use of at least the green parts of these plants. Similar finds were reported from the Late Middle Palaeolithic site of Tor Faraj (Miller-Rosen, 1995a), comparable in age to Amud Cave. Today, palm leaves are still used for a wide variety of purposes, including container production, shelter and fuel (Madella, 2002). The palm family also includes a large number of taxa producing edible fruits (Sturtevant, 1919).

Silicified cystoliths testify to the presence of another important group of woody plants. The Moraceae is a large family of several hundred genera with a wide geographical distribution. A species of this family that has been present in the Levant since the early Middle Pleistocene is *Ficus carica* L. (Werker & Goren-Inbar, 2001), a plant that can be an important source of edible fruits. Fig trees do not occur in the present day vegetation of wadi Amud.

*The use of herbaceous plants.* The ratio of variable to consistent morphologies (v/c index; Albert *et al.*, 1999) is a useful tool to summarize the generally phytolith input in an assemblage. Opal silica bodies with

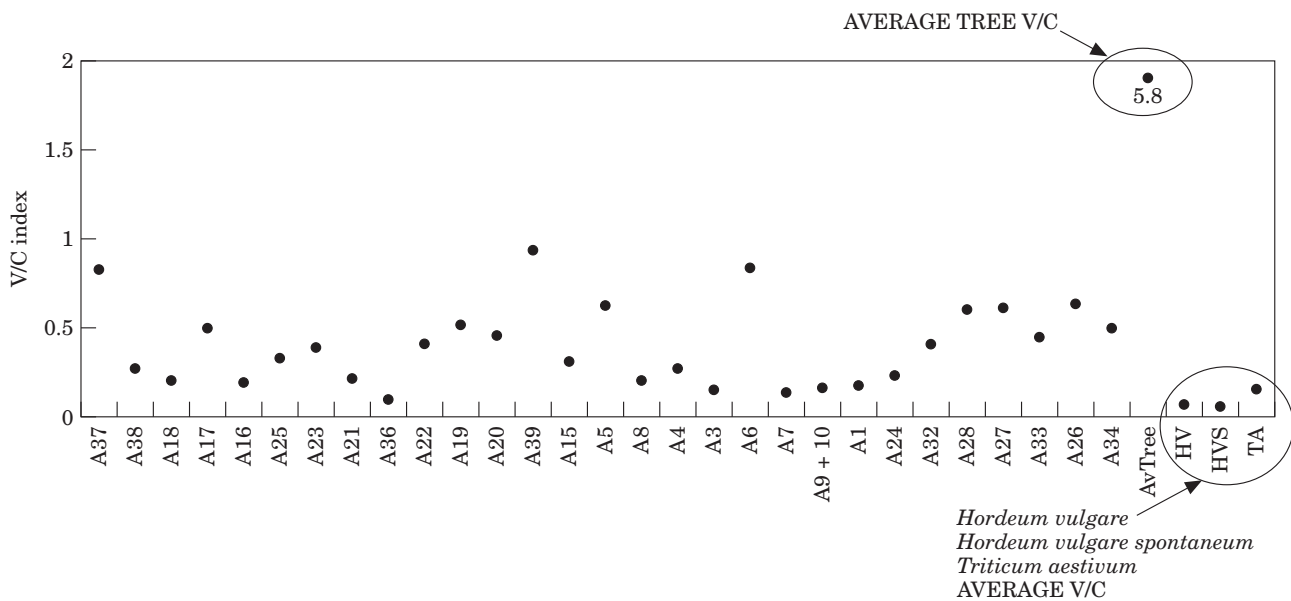


Figure 12. Scatterplot of the v/c index values (see text) for Amud Cave assemblages compared to the average for modern trees from the Levant and three cereals (data for modern assemblages from Albert *et al.*, 1999). Note the low index values, similar to grass assemblages, for all the Amud Cave samples.

consistent morphologies, typical of grass tissues, are the main component in the Amud assemblages. The v/c indexes for the Amud assemblages are consistently well below the average value of this index derived from a reference collection of trees from the Levant (Table 1 and Figure 12). Given that grasses are silica accumulators, the absolute biomass that created the inputs of consistent morphology phytoliths was lower than that of wood, from which originated the variable morphology phytoliths (Carnelli, Madella & Theurillat, 2001, and references therein). The plant reference collection from Mt Carmel studied by R. M. Albert (pers. com.) highlighted that part (about 30%) of the phytoliths extracted from wood and bark can be positively identified as grass morphologies. This is possibly due to the action of the wind, carrying the phytoliths onto the bark where they are probably trapped in the growing tissue. Table 1 shows both absolute values of the v/c index and *normalized* values considering an average of 30% of the grass phytoliths as originating from wood inclusions. Nonetheless, the high proportion of grass versus wood phytoliths in the Amud assemblages highlights an important contribution from herbaceous plants. This inference is substantiated when the subject assemblages are compared with the assemblages from Tabun and Kebara Caves, where grass phytoliths are characteristically under-represented (Albert *et al.*, 1999, 2000). In conclusion, while in Tabun most of the phytolith input is attributable to wood (Albert *et al.*, 1999), in Amud two clearly distinct principal sources are recognizable: namely wood *and* grasses.

Within the group of grass morphotypes there are those produced in the culm and leaves but also the dendritic type, a morphology positively identifying

mature grass spikelets (glumes, paleas and lemmas; Kaplan, Smith & Sneddon, 1992; Miller-Rosen, 1992; Ball *et al.*, 1996, 1999), is well represented (Table 3). Phytoliths from grass vegetative organs (culm and leaves) attest to the possible use of grasses for non-dietary purposes. Dry plants could have been used as fuel, while both fresh and dry plants might have served as bedding materials, as indeed is documented ethnographically (e.g., Galanidou, 2000: 251).

The dendritic morphotype occurs in relatively high proportions, which would usually be more familiar in agricultural sites where cereal grains were extensively exploited (Madella, 1997, 2000). It also contrasts with the general pattern of phytoliths recovered so far from many Palaeolithic sites in which leaves and stems of dicotyledons are more in evidence, such as Tabun and Hayonim (Miller-Rosen, 1995b; Albert *et al.*, 1999; Madella, 2000). Experimental data have shown that the production of dendritic morphologies from the glumes and paleas of cereals, for instance, increases several times in the last few hours of the life of the plant (Jones, Milne & Wadham, 1963; Handreck & Jones, 1968; Hutton & Norrish, 1974; Power-Jones, pers. comm.). Similar patterns of silicification have been noted also in Canary grass (*Phalaris canariensis* L.) (Hodson, Sangster & Parry, 1985). This suggests that higher levels of floral cell silicification in connection with seed ripening may be a common pattern in grasses. Assuming that the grasses of the Late Pleistocene exhibited a similar silicon physiology, it follows that dendritic forms in the Amud phytolith assemblages attest to the presence of mature panicles. The presence of components of the mature panicles also suggests a frequentation of the cave at least during



spring and early summer, when the mature grains from grasses are available.

Additional considerations lead us to suggest that the deposition of the phytoliths in the ashy units of Amud Cave results from intentional collection of the mature seed-bearing grasses. Survival of plants in the wild depends on dispersal success and various grasses have evolved complex dissemination mechanisms. The vast majority of the wild grasses (including cereals) have shattering spikelets when they reach maturity. In wild wheats and barley, for instance, the dispersal unit consists of a single ear's internode, with two kernels (wheat) or one kernel (barley) (Zohary & Hopf, 1993). "Disarticulation of the spike's rachis at each segment is thus an essential element of the wild-type dispersal" (Zohary & Hopf, 1993: 17). Thus, unless special attention is paid to preserve the mature seeds in wild grasses, this very adaptation would cause the loss of the majority of the seeds during the collection of the plants (Hillman & Davies, 1990). This would be the case when grasses were collected for using the vegetative parts (e.g., stem and leaves). Conversely, the relative importance of spikelet phytoliths (dendritics, category 5) in comparison with leaf and stem phytoliths (category 3 and 4, see Table 3), implies that ripened grass panicles were being brought intentionally into Amud Cave by its hominid inhabitants, and deposited in the anthropogenic ashy units within. Deposition of mature panicle phytoliths originating from animal droppings is less likely, as many grass ears are tough at maturity and armed with brittle awns. When eaten, these can break into sharp, flesh-penetrating pieces, and therefore are carefully avoided by most of the grazing animals (e.g., gazelles) (Hillman, Legge & Rowley-Conwy, 1997).

Many of the articulated phytoliths from spikelets, despite the small dimensions, show morphological characteristics of the cereal articulated phytoliths—namely wheat and barley—of our reference collection and as illustrated in the literature (Miller-Rosen, 1992). However, there is no clear indication as to which taxa of grass are involved, and indeed the wild cereals are only a few among many edible grasses found in the region today (Zohary, 1973).

We do not argue that the Amud Neanderthals practised intensive grain collection, similar to the Natufians at the close of the Pleistocene (Bar-Yosef & Belfer-Cohen, 1991, 1992). However, the evidence does suggest they were *seed gatherers*. The absence from Amud Cave of typical artefacts (e.g., sickle blades, grinding and pounding implements), traditionally associated with *intensive* seed exploitation and/or fully agricultural practices does not necessarily undermine this hypothesis. As Hillman & Davies (1990) discuss at length, the use of sickles is only one of several optional ways of collecting grass seeds, others being basket-beating (for which, again, there is no archaeological evidence at Amud Cave) or hand-reaping (for which there can be no archaeological evidence in any site).

While much literature deals with the processing of grain among present-day agricultural societies (e.g., Hillman, 1984), little has been written about the ways in which modern *non-agrarian* communities, who gather wild grasses, process their harvests (Thompson, 1996; although see Harris, 1984 for an exception). Among the Ojibwa of Wisconsin, wild rice (*Zizania aquatica* L.) was dehulled by "men who placed the seed in a skin bag and treaded it in a pit dug in the soil. Dehulled seed was stored in bark boxes or large skin bags" (Harlan, 1992: 12). In Arnhem Land (northern Australia), wild rice was soaked in water before the husks were being rubbed off by hand. There are also records of bundles of ripe grasses being dried in the sun, then burnt to separate the grain from the straw (Thompson, 1996: 120).

By the same token, collection and use of seeds by the inhabitants in Palaeolithic sites in the Near East is attested, albeit rarely, by macrofossil plant remains. The retrieval of several thousand carbonized seeds from the Mousterian layers of Kebara Cave, the majority of which are legumes (Lev, 1993), demonstrates that hard seeds, requiring some form of "external digestion", such as germination, milling, cooking etc., were a part of the diet of the Kebara Neanderthals. Another archaeological example comes from the 19,000-year old site of Ohalo, where the seeds of wild cereals, as well as many other taxa, were used in the diet (Kislev, Nadel & Carmi, 1992). None of these sites, however, contains any sickle blades, whereas groundstone artefacts are absent from Kebara and rare in Ohalo II (Nadel, 1998: 187–188, Table V. 17).

On the whole, the transformation of hard grass seeds into digestible food need not involve the grinding and pounding artefacts that subsequently became important in relation to some domesticated cereals, such as wheat and rye. The range of processes employed in the preparation of contemporary cereals includes boiling, roasting, soaking, germinating (malting), cracking and rolling. Such techniques may have been employed on prehistoric wild grasses, and need not have left characteristic durable artefacts. The absence of such durable remains from the Amud Cave assemblages is not inconsistent with the use of grass seeds as a dietary source.

#### *Implications of the environmental gradient*

Absolute production of phytoliths in plants is environmentally determined (warmer climates stimulate higher deposition of opal silica in the plants). However, relative productions (e.g., monocots versus dicots) should remain comparable as silicon physiology is genetically determined. This is especially the case of different ecotones pertaining to the same ecosystem or "*paysage végétale*" (as defined by Gordon, 1984: 141) as in the case of the southern Levant. It is this characteristic of the phytoliths which enables intra-regional comparisons.

The presence of seed husk phytoliths is known also from Tor Faraj and from the Mousterian layers of Hayonim Cave (Miller-Rosen, 1995a: Table 19.2, 1995b: Figure 3). Their relative frequencies in these two sites are lower than any of those seen in Amud Cave (see Table 3). The higher frequencies found in Amud strongly suggest that from the Late Mousterian, at least, the exploitation of monocotyledonous herbs for a variety of purposes, including food, was already underway.

In some of the Middle Palaeolithic caves and rock shelters in the Levant, phytolith analyses, when available, point to a single major mode of exploiting plant resources (e.g., Tabun; Albert *et al.*, 1999). The very same type of data indicates more diverse modes of plant exploitation by the occupants of Kebara (Albert *et al.*, 2000), and especially at Amud, Caves. In Amud, wood exploitation is attested to by the presence of phytoliths from ligneous tissues. However, there is also direct phytolith evidence for the use of leaves and possibly fruits of certain trees (palm and Moraceae taxa). Additionally, we have indications for a more elaborate utilization of the herbaceous resources. Phytoliths from culm/leaves *and* husks have important frequencies in the assemblages, attesting to the gathering of both the vegetative parts of the grasses and of the mature panicles. Thus the available evidence is suggestive of the use of grasses as possible fuel and bedding material, as well as a dietary component.

The sites of Tabun, Hayonim and Kebara are within the present-day Mediterranean core region, characterized by oak-pistachio woodlands and maquis (*Quercetea calliprini*; Zohary, 1973). Amud Cave is located in the eastern fringes of this Mediterranean region, where there is a gradual impoverishment of the Mediterranean floristic elements and an increased presence of semi-steppic and steppic plants (Zohary, 1973). Finally, Tor Faraj, in Trans-Jordan, is situated in an even drier, steppic environment, where rainfall ranges from 50–200 mm (Henry, 1998). Hillman (1996: 162–163) cites several works that show that annual grass stands, typically present in the Mediterranean park-woodland vegetation, also extend into such a drier vegetation zone.

A number of environmental studies indicate that a vegetation gradient similar to the modern one might have been present in the area here discussed between 70–50 Kyr (Baruch, Werker & Bar-Yosef, 1992; Henry, 1998). Such environmental data imply that the type of regional differences observed in present-day Levantine vegetation distributions might apply at the time of occupation in Kebara, Amud and Tor Faraj. While site function and seasonality would have contributed to the differences seen among the phytolith assemblages of these three Late Middle Paleolithic sites, it is clear that these differences are consistent with the postulated palaeoenvironmental conditions and reflect, in part, the relative availability of plant resources. The greater diversity of the Amud Cave

phytolith assemblages suggests the ready access to, and exploitation of, a mosaic of vegetation types, in accordance with the site's geographical location. The intra-sequence variation in the frequencies of grass seed phytoliths may reflect the changes over time in vegetal cover of this broader zone between the Mediterranean and the more steppic vegetation. Such a hypothesis is consistent with changes in climatic conditions from the end of Oxygen Isotope Stage 4 (unit B<sub>4</sub>) to Oxygen Isotope Stage 3 (units B<sub>2</sub> and B<sub>1</sub>).

#### *A Middle Palaeolithic broad spectrum economy?*

In 1969, Flannery noted a trend in which prehistoric economies underwent a “considerable broadening of the subsistence base” by moving from exploitation of a narrow to a broader spectrum of edible wild products (Flannery, 1969: 77). According to this hypothesis, the difference between prehistoric groups relying on broad resource spectra and those not utilizing an extended resource base resided mainly in the former expanding their diets to encompass small mammalian and non-mammalian game species “. . . and possibly wild cereal grains in some areas”. The relatively sudden expansion of the dietary niche was argued to be a direct result of environmental deterioration (Flannery, 1969: 78; Hillman, 1996) that necessitated a diversification of the resource base. This Broad Spectrum Revolution was the first of several changes that ultimately led to the appearance of agriculture in the early Holocene.

In the time that has passed since the first appearance of the Broad Spectrum Revolution hypothesis it has become evident that exploitation of small mammalian and of non-mammalian faunal resources was part of the human diet prior to the end of the Pleistocene (e.g., Hovers *et al.*, 1988; Edwards, 1989; Neeley & Clark, 1993; Stiner & Tchernov, 1998; Flannery, 2000). The ultimate significance of a broad spectrum diet, however, “lay not in small game and molluscs. When such previously ignored species are considered worth harvesting, it increases the chance that even grass seeds be considered worth harvesting” (Flannery, 1998: XVII). Coupled with the presence of legumes in Kebara Cave, the Amud phytolith data constitute evidence that two families of plants, which would subsequently provide some of the earliest domesticates (Zohary & Hopf, 1993), were already exploited in the Levant in the Late Middle Palaeolithic. The faunal and botanical records thus concur that exploitation of a broad spectrum of food resources was part of the Palaeolithic lifeways long before it became the foundation of, and a pre-requisite for, an economic revolution.

The findings presented here are consistent with grass seed exploitation prior to the close of the Pleistocene, indicating that it was not revolutionary insights into the economic potential of Levantine vegetal resources which led to resource intensification in the region c. 12 kyr ago. As in the case of intentional burials and

symbolic manifestations in the Middle Palaeolithic, the question underlying these results pertains to the nature and context of the processes by which long-practised behaviours and long-existing abilities attained new adaptive advantages and transform from inventions to innovations (Hovers, 1997; Hovers *et al.*, 1995, 1997; Stiner & Tchernov, 1998). Palaeolithic demography may well form part of such processes, where low population densities contribute to unchanging ways of behaviour (Binford, 1968; Flannery, 1969; Keeley, 1995). Indeed, the postulated pulse of population growth in the Late Middle Palaeolithic in the Levant (Stiner, Munro & Surovell, 2000) is as likely to reflect, short-term, localized fluctuations of population densities (Hovers, 2001) rather than an overall increase in population size. This hypothesis is consistent with the “broad spectrum *stasis*” implied by the current analysis.

## Conclusions

The depositional environments of the Amud Cave sediments indicate that the phytolith assemblages are an integral part of the Middle Palaeolithic sequence. As such, they provide direct evidence for plant use. The Amud Neanderthals emphasized both wood and grass exploitation for fuel and diverse other activities, possibly not unlike modern hunter-gatherers in medium and low geographical latitudes (Hayden, 1981; Kelly, 1983, 1995). The composition of the phytolith assemblages is consistent with the site’s geographical and ecological location. Finally, there is clear and repetitive evidence throughout the site’s sequence for the exploitation of mature grass panicles. We have here proposed that these were collected for their seeds. These findings suggest that, similar to the pattern recently discerned for faunal resources (Stiner, Munro & Surovell, 2000), a broad spectrum economy of plants has been in place from at least the end of the Middle Palaeolithic.

The grass family, as a food source, has had an unparalleled calorific impact on the human species, but all our evidence of grass-seed consumption and cereal-based diets has so far come from *Homo sapiens*. The Amud phytoliths suggest that Neanderthals, too, were experimenting with the family of plants that would ultimately come to dominate the human food chain.

Models that emphasize ecological factors as major forces in shaping Middle Palaeolithic technological variability, settlement behaviour and demographic patterns, have focused on the role of faunal resources (e.g., Lieberman & Shea, 1994; Shea, 1998; Speth & Tchernov, 1998). Recent studies suggest that the calorific contribution of meat is higher among recent hunter-gatherer societies than has been thought previously (Cordain *et al.*, 2000). However, in low and medium latitudes plants are highly significant in terms of caloric input (Cordain *et al.*, 2000), and may well be the critical resources in determining the patterns of

mobility and subsistence behaviour. For the Levant in particular it has long been argued, on the basis of ecological modelling and palaeoenvironmental reconstructions, that it was the spatio-temporal distributions of plant rather than animal resources which determined subsistence and mobility patterns among prehistoric populations (Hovers, 1998a, 1998b, 1997). Phytolith analyses now provide a tool for putting these models to the test of archaeological data.

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