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Starch-rich plant foods 780,000 y ago: Evidence from Acheulian percussive stone tools

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In contrast to animal foods, wild plants often require long, multistep processing techniques that involve significant cognitive skills and advanced toolkits to perform. These costs are thought to have hindered how hominins used these foods and delayed their adoption into our diets. Through the analysis of starch grains preserved on basalt anvils and percussors, we demonstrate that a wide variety of plants were processed by Middle Pleistocene hominins at the site of Gesher Benot Ya'aqov in Israel, at least 780,000 y ago. These results further indicate the advanced cognitive abilities of our early ancestors, including their ability to collect plants from varying distances and from a wide range of habitats and to mechanically process them using percussive tools.

starch | plant foods | hominins diet | Archaeobotany | Middle Pleistocene

Significance

Despite their potential implications for hominin diet, cognition, and behavior, only rarely have plants been considered as drivers of human evolution, in part because they are less archaeologically visible. We report the discovery of diverse taxa of starch grains, extracted from basalt percussive tools found at the early Middle Pleistocene site of Gesher Benot Ya'aqov. These include acorns, grass grains, water chestnuts, yellow water lily rhizomes, and legume seeds. The diverse plant foods vary in ecological niches, seasonality, and gathering and processing modes. Our results further confirm the importance of plant foods in our evolutionary history and highlight the development of complex food-related behaviors.

Excavations at Gesher Benot Ya'aqov (henceforth GBY; *SI Appendix*, *Supporting Information A*) unearthed a series of over 20 hominin occupations (Archaeological Horizons; henceforth AH) assigned to MIS (Marine Isotope Stages) 18 to 20 and embedded within a generally fine-grained sedimentary sequence, typical of a low-energy fluctuating lake margin environment (1, 2). This setting preserved the original spatial location of different archaeological finds (3, 4) and enabled spatial analyses of cultural remains, including hearths (5). The remains of various aquatic and terrestrial species demonstrate the exploitation of diverse taxa, including small and large game and fish (5–9). The waterlogged environment enabled the preservation of abundant macrobotanical remains including wood, bark, fruits, nuts, underground storage organs (USOs), and grains, whose composition is in accordance with identified pollen taxa (*SI Appendix*, Tables S1 and S2) (10–12). Most of the plant taxa grow in wet habitats (e.g., lakes, lake margins, swamps, and near streams), yet the abundant fruit remains of woodland species (e.g., *Vitis sylvestris, Ziziphus spina-christi*, *Amygdalus* sp., *Pistacia atlantica, Pyrus* sp., *Olea europaea, Quercus* spp.) imply human involvement, as their habitat is located some distance from the lakeshore (12–14). The GBY hominins repeatedly occupied the lakeshore, had a comprehensive knowledge of their environment, and consumed various plant and animal resources.

Basalt percussive tools and sediments from two AH (Layer II-6 Levels 2 and 6) were sampled for analyses to examine the possible preservation of plant microremains. Only one sediment sample was available for Layer II-6 Level 6, while for Level 2, 7 samples were studied (*Materials and Methods*). The sampled basalt artifacts (N = 8) include two thin anvils and two percussors from each of the AH (*SI Appendix*, Figs. S1 and S2). The typological classification of thin anvils and percussors is based on their morphological attributes (2, 15). Percussors (i.e., hammerstones) are semirounded cobbles with battering damage marks visible on their surfaces, while thin anvils are small, flat, slabs, characterized by two parallel unflaked surfaces. The sampled percussive tools vary in typology, size, and shape, but all exhibit small depressions (pits) characteristic of pitted stones. Leakey (16, 17) suggested that pitted stones are components of a pair, consisting of an immobile element (an anvil) and a mobile one (a hammer). Previous analyses of basalt and limestone pitted stones from GBY suggested that the pits resulted from repetitive percussive activities (2, 13, 15). Given their close proximity to nutshells and bone fragments, we assume that these percussive tools were used, among other tasks, for processing food (2). The general surface alteration of basalt artifacts at GBY prevents the use of microwear analyses of these tools (*SI Appendix*, *Supporting Information A*). Detailed analyses of these artifacts are provided elsewhere (2, 13, 15, 18), while the current study focuses primarily on the variety of microremains preserved on them.

Plant microremains were extracted from the surfaces of the basalt percussive tools using a sequential sampling method (*Materials and Methods*). This process, as well as the analysis of sediment samples from the same AH, allowed us to assess the potential of

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The authors declare no competing interest.

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Table 1. Counts of starch grains from basalt pitted percussive tools and sediment samples (S) from Layer II-6 Level 2 and Level 6 at GBY

Layer and Level		II-6 L2						II-6 L6					
				Anvils		Percussors			Anvils		Percussors		Total
Identified Taxa	Common name*	S17	S38	7030	8628†	12004	8627	S13	9265	7527	12097	5699	
Quercus spp.	Oak [acorn]	1	1	16		7	1	1	65	30	44	38	204
cf. *Quercus*				1									1
TASH	Wheat, barley, rye, goat-grass [grains]			20		9			41	19	8	19	116
cf. TASH				1					4	15		1	21
Liliaceae sp. 1	Lily family [bulb]								69			3	72
Liliaceae sp. 2	Lily family [bulb]											3	3
Nuphar lutea	Yellow water lily [rhizome]				1	1	1		4		1	1	9
cf. *Nuphar lutea*	Yellow water lily [rhizome]					2			6	3	2	4	17
AP grasses	low-growing turf-grass [grains]					1			3	6	3	1	14
Trapa sp.	Water chestnut [nut]			1					6	2	6		15
Fabeae	Legumes [seed]			1						1			2
cf. Fabeae	Legumes [seed]			1					1	1			3
Avena sp.	Oat [grain]								1			1	2
Unidentified													
Unclassified				57		5	1		21	13	4	9	110
Ambiguous				7		6	1		13	11	9	8	55
Compound 1												6	6
Compound 2												1	1
Total		1	1	105	1	31	4	1	234	101	77	95	651

*The starch-containing anatomical plant part is specified in brackets; sediment samples from which no starch was recovered (5 samples from Layer II-6 Level 2) are not listed.
†This anvil yielded only 1 starch grain extracted with dry brush, while none were recovered with the wet brush and picking; it was not sonicated due to its large dimensions (*SI Appendix*, Table S4).

contamination. Table 1 lists the identified starch remains from all samples. Very few starches were found in the sediment samples (only 3 of 8 contained starch), especially when compared to the several hundred starches preserved on the tools (Table 1), indicating that contamination is unlikely. Most starches originate from the sonicated samples of the stone tools and therefore represent the material most deeply embedded into the tool surface (*Materials and Methods* and *SI Appendix*, Table S4).

Results

Over 650 starch grains were recorded and classified into 23 morphological groups (MG) (*SI Appendix*, Table S5). Classification followed several characteristics, including grain shape (in plan view and side view), grain size, location and form of the hilum, varieties of the extinction cross, distinctiveness of lamellae, and surface texture (19, 20). The MG were then identified to plant

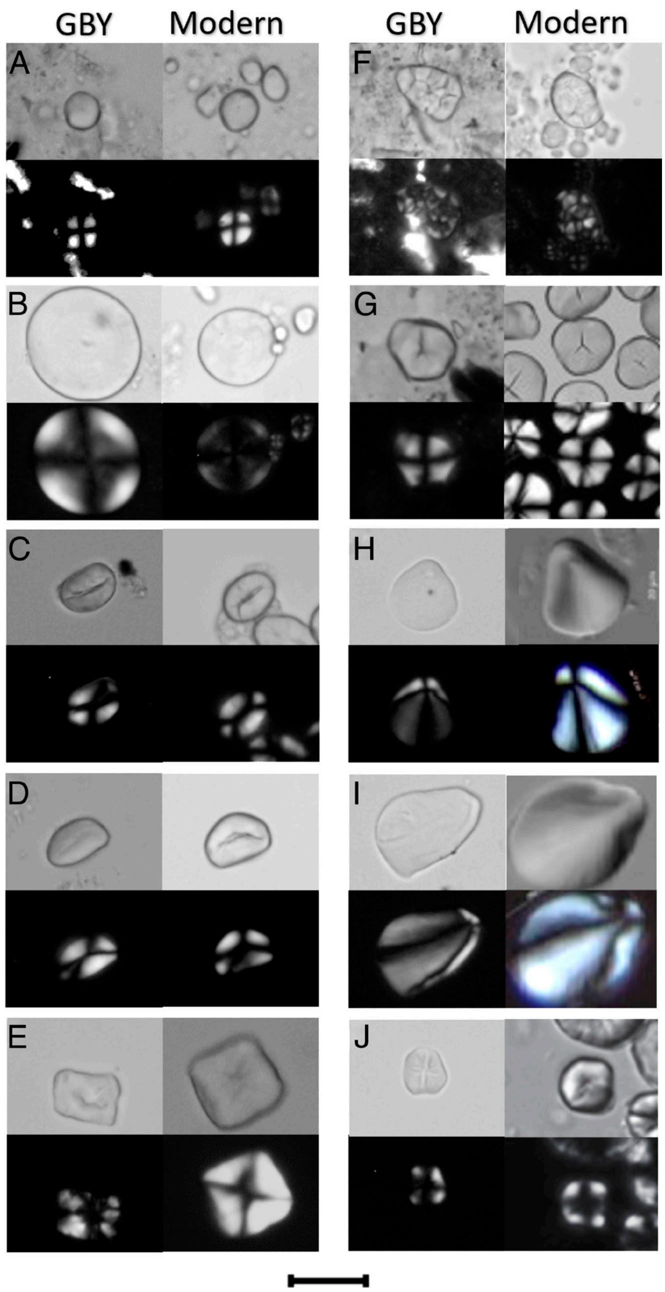

Fig. 1. Archaeological starches from GBY (*Left* columns) and their modern counterparts (*Right* columns). (*A*) *Quercus* spp. vs. modern *Q. calliprinos*; (*B*) TASH vs. modern *Aegilops geniculata*; (*C*) Fabeae vs. modern *Lens orientalis*; (*D*) *Quercus* spp. vs. modern *Q. ithaburensis*; (*E*) *N. lutea* vs. modern *N. lutea*; (*F*) *Avena* sp., vs. modern *Avena barbata*; (*G*) *Trapa* sp. vs. modern *T. pseudoinisa* (21); (*H*) Liliaceae sp. 1 vs. modern *Erythronium grandiflorum* (22); (*I*) Liliaceae sp. 2 vs. modern *Fritillaria pudica* (22); (*J*) AP grasses vs. modern *Setaria italica* ssp. *viridis* (ground) (23). Brightfield illumination above, cross-polarized illumination below; scale is 20 μm and applies to all subfigures.

type or taxon (*SI Appendix*, Table S5 and *Supporting Information B*) based on comparison to our previously published work (20), analyses of modern day taxa from the nearby Hula Valley (*SI Appendix*, Table S3), and other publications (21–23). Some of the plant species from this region likely evolved over the past 780,000 y (24), but as starches are generally very consistent among closely related species, we are confident in the identifications at broader taxonomic levels (e.g., genus, tribe or family).

The most common MG (N = 205, Fig. 1 *A* and *D* and Table 1) had a spherical to elongated "banana-like" shape typical of local oak species, possibly *Quercus ithaburensis* and/or *Quercus calliprinos*. Fragments of cupules and nutshells of these species were found at GBY (12). The second-most common type consisted of lenticular starches (N = 137) typical of the Triticeae tribe. Several important grass species from this tribe, including wild relatives of wheat (*Triticum*), goat grass (*Aegilops*), rye (*Secale*), and barley (*Hordeum*) overlap considerably in their size and morphology (25). Therefore, these starches were referred to as the "TASH" group (Fig. 1*B* and Table 1). Other grasses were less represented, but 14 starches shared the polyhedral, subangular shape commonly found in grasses in the Andropogonaeae and Paniceae tribes (AP grasses: Fig. 1*J* and Table 1), which include sorghum (*Sorghum*) and millets (*Panicum*, *Setaria*, and *Pennisetum*). Two starches had the compound structure indicating that they came from the grains of oats (*Avena* sp., Fig. 1*F* and Table 1). Several starches were consistent with those found in the roots of members of the Liliaceae family. Based on significant morphological differences, two different taxa were identified, Liliaceae (*s.l.*) sp. 1 (N = 72, Fig. 1*H* and Table 1) and sp. 2 (N = 3) (Fig. 1*I* and Table 1). Water plants are represented by the starches of yellow water lily (*Nuphar lutea*, N = 26, Fig. 1*E* and Table 1) and water chestnut (*Trapa* sp., N = 16 Fig. 1*G* and Table 1). Five starches were consistent with the morphology of those found in the Fabeae (=Vicieae) tribe (Fig. 1*C* and Table 1), which contains the edible Near Eastern vetchlings (*Lathyrus* spp.), lentils (*Lens* spp.), peas (*Pisum* spp.), and vetches (*Vicia* spp.). Unidentified starches include 110 grains that are either too damaged or their characteristics are indistinctive (i.e., unclassified, Table 1, MG 8 to 9, MG 21 to 22, Fig. 2 *F*–*I*), as well as 55 starch grains whose characteristics are consistent with more than one taxon (i.e., ambiguous taxa, Table 1); the majority of these (N = 50) belong to MG 14 (*SI Appendix*, Table S5 and Fig. 3*B*). In addition, two different types of compound starches (compound 1 to 2, Table 1) were found, exhibiting distinctive traits that are not comparable with any of the known taxa (Fig. 3 *A* and *C* and Table 1).

With the exception of *Liliaceae*, the identified starch remains all belong to taxa that were previously identified among the micro- and macrobotanical assemblages of GBY (*SI Appendix*, Tables S1 and S2 and *Supporting Information C*), including the locally extinct water chestnut (*Trapa*), currently not growing in the Levant (12). The closest modern habitats of water chestnut are those of the species *Trapa natans* in Northern Türkiye and Northern Iran (26), yet the GBY starches share more similarities with modern East Asian species (*Trapa incisa*, *Trapa quadrispinosa*, *Trapa pseudoinisa*, and *Trapa japonica*) (21, 27).

The methods for starch analysis also recovered a variety of other microremains (*SI Appendix*, Figs. S3–S8 and *Supporting Information D*). These include phytoliths (*SI Appendix*, Fig. S5), diatoms (*SI Appendix*, Fig. S6) and other algae, and a wealth of fungal spores preserved on the basalt artifacts (*SI Appendix*, Fig. S7). The latter includes lignicolous fungi, recovered only from the basalt anvils and not from percussors, suggesting the use of wooden pounding tools and/or the processing of wood on these tools. Of particular interest are the hair of the great mole rat and the plumulaceous barbule of a waterfowl (*SI Appendix*, Fig. S4 and *Supporting Information D*), both present in the faunal assemblages of GBY. Similarly, the identified pollen (*SI Appendix*, Table S6 and *Supporting Information D*) is comparable with previous studies of the GBY pollen (*SI Appendix*, Table S2) and, as recorded for the starch grains, is more frequently found within the basalt tools (N = 119) than in the sediments (N = 12).

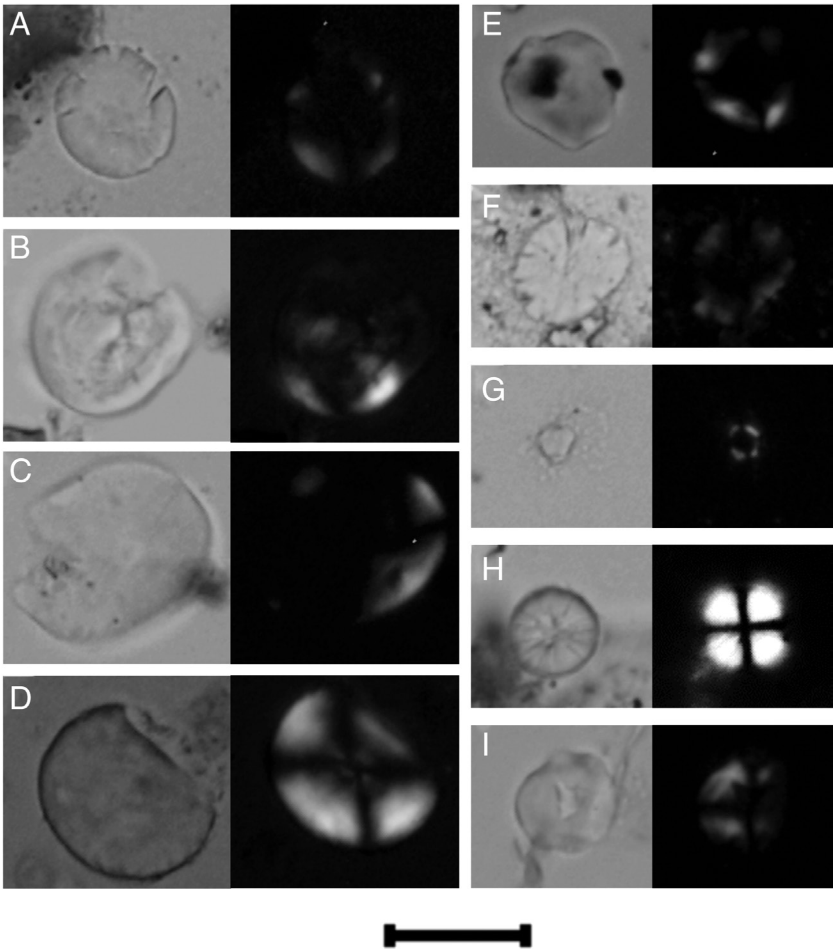

Fig. 2. Damaged starch grains from GBY. (*A*–*D*) TASH and cf. TASH, (*E*) cf. *N. lutea*, (*F*–*I*) Unidentified, unclassified, starches. Brightfield illumination on the *Left*, cross-polarized illumination on the *Right*; scale is 20 μm and applies to all subfigures.

Discussion

This study presented a rich inventory of starch grains from the Acheulian site of GBY. The outstanding preservation is likely aided by the complex surface of the stone tools that provides many pockets where plant material could be isolated and the subsequent waterlogging of the site that led to remarkable organic preservation (as also evidenced by the plant macroremains and bones). The characteristics of the starch grains assemblage suggest that it is not a natural representation of the ancient flora but rather that it represents the residues of plant food processing:

1) The identified starches originate in plants of diverse habitats, including not only the nearby lake (e.g., water lily, water chestnut) but also upland areas at some distance from the site (e.g., acorns).
2) Analysis of sediment samples provided minimal evidence for starch while that of the percussive tools yielded over 650 starch grains.

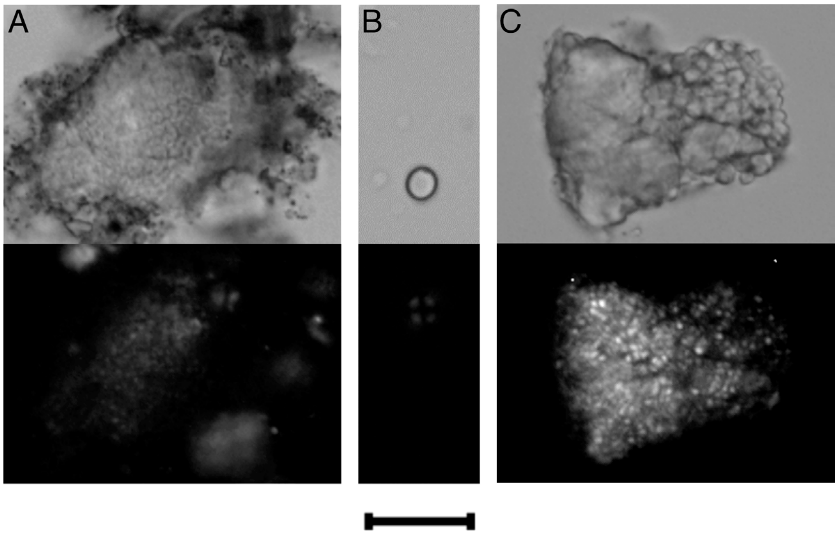

Fig. 3. Three morphological groups of unidentified archaeological starches from GBY. (*A*) MG 6 (Compound type 1); (*B*) MG 14 (Ambiguous taxa); (*C*) MG 7 (Compound type 2). (*SI Appendix*, Table S5 and *Supporting Information B*). Brightfield illumination above, cross-polarized illumination below; scale is 20 μm and applies to all subfigures.

3) Most starches originate from the sonicated samples of the stone tools (*Materials and Methods* and *SI Appendix*, Table S4), representing the material most deeply embedded into tool surface, indicative of minimal postdepositional contamination.
4) Both the identified and unidentified starches include damaged unclassified grains (Fig. 2).

These were observed in 7 of the 8 analyzed percussive tools, alongside undamaged ones. This may be the outcome of processing of plant foods using percussive tools, activity known to induce damage to starch (28).

We suggest that the characteristics of the starches and their association with the percussive tools provide direct evidence for plant food processing. The variety of targeted plants shed light on other issues related to hominin evolution and behavior, including seasonal round, diet, and the development of technologies related to the gathering and processing of plant foods.

Each of the plant taxa differ considerably in their hardness, toxicity, and nutritional values (*SI Appendix, Supporting Information B*), thus requiring different processing methods. Acorns and water chestnuts both need to be shelled prior to consumption. Acorns from contemporary Near Eastern oaks usually require leaching or roasting after shelling to reduce their tannin content (29, 30). Water lily rhizomes and some lily bulbs can be eaten raw but contain some toxins which are removed by roasting (31–33). Depending on which species of Fabeae is represented, some amount of leaching or roasting would be needed to make it edible (34). No gelatinized or otherwise cooked starches were recovered from the percussive tools, but this secondary processing likely occurred elsewhere in the site, such as the nearby hearths (e.g., refs. 9 and 14). Other edible plants, recovered from the macrobotanical analysis but not found in the starch assemblage, were likely shelled using the percussive tools. These include Prickly water lily (*Euryale ferox*), Atlantic pistachio (*P. atlantica*), and Almond (*Amygdalus* sp.) (*SI Appendix*, Tables S1 and S2) (12, 35). The latter two do not contain starch in their stones/nuts (20), and the starches of the former are small, loose compounds, which makes their identification in a mixed assemblage difficult. In addition, roasting, which is crucial for the shelling and popping of the *E. ferox* seeds (14), may obstruct the preservation of starchy components (28). Furthermore, the proximity of the tools to hearths (Fig. 4) suggests the involvement of fire in the processing of these plant foods. As the use of fire in food preparation is documented at GBY, in association with fish cooking (9), it is likely that fire was similarly used in the preparation of plant foods.

The technological complexity of plant food processing is also manifested in the collection of such a wide diversity of plants. Collecting acorns and grass grains at large distances from the site would be efficient only with the use of containers. The edible rhizomes of water lily grow in shallow lakes and swamps (31) requiring digging to reach these resources. Prickly water lily sink and they need to be carefully collected, again implying a container or perhaps a loose, sieve-like basket (e.g., ref. 36). The Acheulian foragers would have had to dive and dig underwater, potentially with the use of baskets and/or containers, as previously suggested for GBY (2, 14).

The pitted percussive tools preserved the remains of various edible plants, which are currently known to be available at different seasons throughout the year (Fig. 5). This suggests that plant foods were available year round (12) and were habitually collected and processed by hominins.

Hardy et al. (44) suggested that plant foods containing high quantities of starch were essential for the evolution of Pleistocene hominins, as digestible carbohydrates were necessary to accommodate the increased metabolic demands of a growing brain. It is established that Middle Paleolithic Neanderthals exploited diverse plant foods and transformed them into more easily digestible foodstuffs, in part through cooking (34, 45, 46). The current study of starch remains

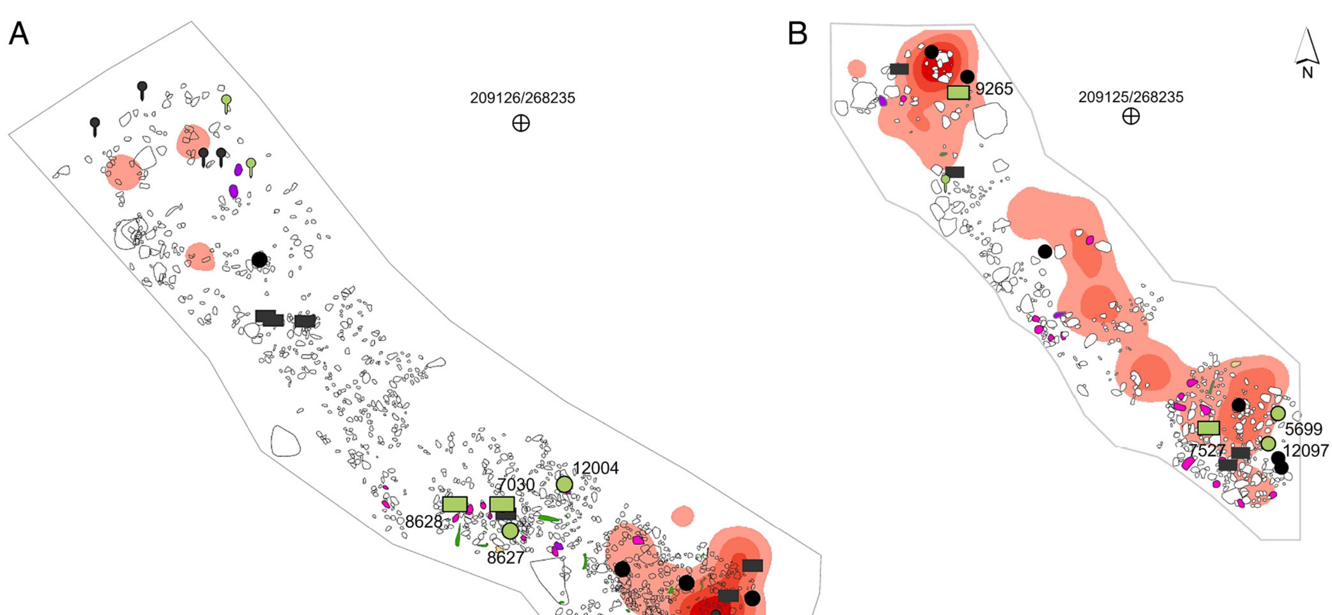

Fig. 4. Location of analyzed pitted basalt percussive tools and sediments from Layer II-6 Levels 2 (A) and 6 (B) at GBY. Kernel density maps of burned flint microartifacts mark the location of hearths (red) (3); Field maps show wood segments (green), bones (orange), and lithic artifacts (handaxes [pink], cleavers [purple], and other artifacts [white]). All pitted basalt percussors (circles) and anvils (rectangles) of these levels are marked black. Those sampled for starch analysis are marked green. Studied sediment samples (pushpins) are marked black, those containing starch are marked green.

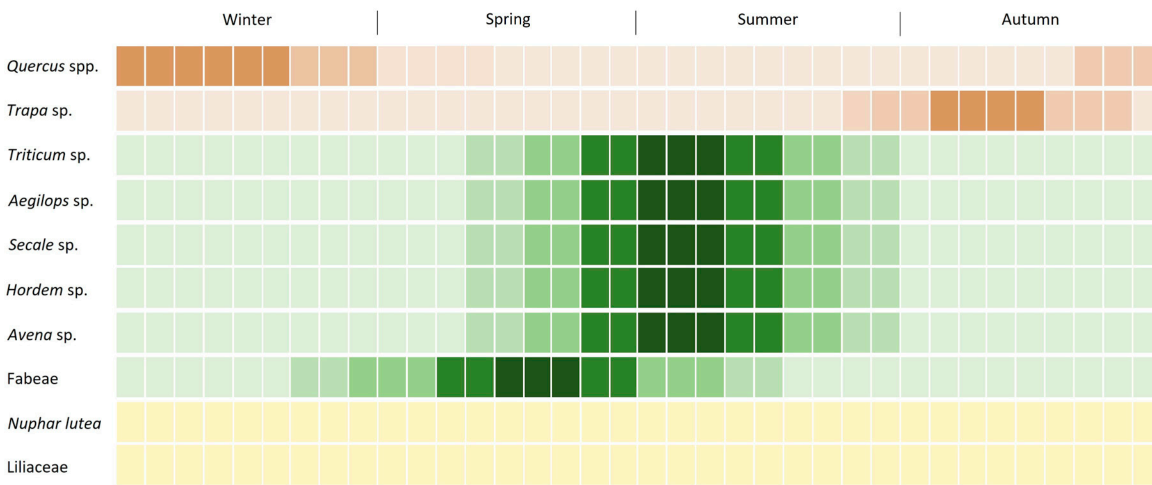

Fig. 5. Seasonal availability* of the plants identified on the percussive stone tools at GBY: Starch-rich nuts (brown), grains and seeds (green), and underground storage organs (rhizomes and bulbs, yellow). The darker the color, the higher is the availability of the edible part. *Based on present day seasonality in Israel, with a resolution of 10 d (18, 37). Faunal and floral analyses suggest environmental and ecological similarity of the past and present-day Hulla valley (2, 38–43). As the vicinity of the Hulla valley is characterized by 800 m. difference in elevation, it is likely that the temporal availability of the different species was mildly larger.

expands our knowledge of the major food groups that formed the paleodiet of the hominins of GBY. Alongside the protein and fat components available from animal resources (7, 9), carbohydrates were regularly consumed through a rich diversity of acorns, grains, nuts, and USOs. Our results indicate that Lower Paleolithic, Acheulian, hominins invested time and labor in preparing a variety of plant foods in ways that increased their edibility and nutritional quality.

These results emphasize the advanced cognitive abilities of the GBY hominins (47, 48), adding unmatched evidence for the role of plant processing and consumption, a domain scarcely known but clearly a major component of the diet of our early ancestors. The profound knowledge of the lifecycles and nutritive benefits of various edible plants enabled the GBY hominins to construct organized, scheduled, exploitation sequences. These involved different gathering strategies, the carrying of food stuffs to the lakeshore from various distances, and the elaborated processing of the plants (shelling, roasting, pounding, and grinding). These sequences required that the GBY hominins used a variety of routines that involved different materials, different time intervals, and different settings, all integrated into an overarching plan of action executed through their expert cognition.

Materials and Methods

Analyses focused on two archaeological horizons, Layer II-6 Levels 2 and 6 (*SI Appendix, Supporting Information A*) from which sediment samples as well as basalt percussive tools were sampled and analyzed. Before each phase of analysis, the working environment was cleaned, and tests were carried out to ensure sterile conditions.

Ensuring a Noncontaminated Working Environment. The working space was tested for contamination following two steps. First, the main working surface (lab table) was wiped with distilled water (henceforth DW). The wipe was placed in a 50 mL tube and then actively rinsed with c. 30 mL of water for about 1 min. The wipe was then squeezed against the side of the tube using autoclaved forceps to remove water. The resulting water was then centrifuged (Eppendorf ® highspeed Centrifuge 5430 R) for 10 min at 4,000 rpm. The bulk of the supernatant was removed by aspiration, and the volume of the remaining liquid was measured by pipetting. Of the remaining sample, 10 μL was mounted (see a detailed description of slide preparation below) and examined.

The second phase included cleaning the entire working environment—all horizontal surfaces (i.e., shelves, closets, chairs, oven, hood, sink) were wiped using a starch-free soap followed by a second wipe with NaOH (5%) solution. Finally, the working surface was wiped with DW. This wipe was rinsed into a tube, centrifuged, and sampled, following the same process as in the first step described above.

Analysis of Sediments. Eight sediment samples were analyzed, originating from Layer II-6 Level 2 (7 samples) and Level 6 (1 sample). These sediments were sampled during excavation, dried at the site, and then bagged in plastic bags. Some were taken in close proximity to the percussive tools, while others were further away (Fig. 4). They were collected in order to provide contamination controls for the percussive tools.

For the current study, ca. 200 mL of sediment was taken. The samples included different size soil particles (e.g., silt, clay) as well as shells and small stones. From these, 0.5 mL of unsieved fine-grained sediments were manually scooped for analysis. Each sediment sample was inserted into a 50 mL tube (tube A) with 10 mL solution of 10% sodium bicarbonate ($NaHCO_3$) (i.e., 1 g:10 mL DW), vortexed for 1 min and left closed at room temperature for a duration of 8 d. After this incubation period, each tube was centrifuged for 15 min at 4,000 rpm, and the supernatant was discarded. Five milliliters of DW was then added, and the pellets resuspended. The tubes were then centrifuged for 10 min at 4,000 rpm. After this step, all the supernatant was aspirated using a 5 mL pipette and the liquid was discarded.

To remove the clays from the sample, 10 mL of 1.5 g/mL sodium polytungstate (SPT) was added and the sediment pellet was resuspended by vortexing for 1 min. The tubes were then immediately centrifuged for 15 min at 4,000 rpm. The upper 5 mL of liquid was aspirated using a pipette and discarded. Then to float the starches, the sediment pellet with the remaining liquid was resuspended in 10 mL of 1.9 g/mL SPT, vortexed for 1 min, and centrifuged for 15 min at 4,000 rpm. Finally, using a pipette, the upper 5 mL (potentially with starches) was collected and transferred to a new tube (Tube B). Ten milliliters of DW was then added into the remaining pellet in tubes A and these were vortexed and kept to enable future analyses. Ca. 40 mL of DW was added into each of the B tubes to reduce the specific gravity of the solution so that the starches could sink, and the tubes were then centrifuged for 15 min at 4,000 rpm. The upper 35 mL was aspirated and discarded. The tubes were filled again with 35 mL of DW and vortexed and then centrifuged for 15 min at 4,000 rpm. The upper 48 mL was discarded. The remaining material (1 to 2 mL) was mounted on the slides (see a detailed description of slides preparation below).

Analyses of Percussive Tools. Eight basalt tools were analyzed for microremains (*SI Appendix*, Fig. S1). The tools [following (2, 13, 15)] were selected because they bear pits (*SI Appendix*, Fig. S2), suggestive of their use as anvils or percussors. These tools were unearthed during excavation and washed on-site with water to remove the coating sediment. Though bagged and boxed, the tools were subject to previous lab analysis (i.e., typo-technological attribute analyses) that necessitated their exposure to several individuals, a situation that may explain the presence of recent pollen and the cotton fibers that were identified (e.g., plant fibers: *SI Appendix*, Table S6 and *Supporting Information D*) [No other analysis (i.e., use wear analysis, basalt sourcing) occurred in this research]. These conditions required a careful multistep analysis [following Pearsall (49)].

1. Using a dry toothbrush, the tool was brushed for 1 min to sample the outer dust and sediment. Attention was given to pitted areas, suspected to be the working surfaces of the tool. The residues accumulated on the brush were then collected using weighing paper and inserted into a 50 mL tube. Five milliliters of DW was added into the tube.
2. Using a wet toothbrush, the tool was brushed for 1 min to sample the outer dust and sediment. Attention was again given to pitted areas. During brushing, 10 mL of DW was pipetted on the tool. Using a pipette, wet residues were collected from the stone and inserted into a 50 mL tube. Five milliliters of DW was added into the tube.
3. Autoclaved sharp needle-nose pointed tweezers were used to gently excavate the basalt vesicles. Picking was carried out at least five times, focusing on wet pitted areas. The residues accumulated on the tweezers were collected using weighing paper and inserted into a 50 mL tube. Five milliliters of DW was added to the tube.
4. The tool was inserted into a 1,000 mL lab glass cup and submerged with DW to full coverage. The cup was then inserted into a sonicator for 15 min without heating. The tool was taken out, and the sonicated water was inserted into 50 mL tubes (3 to 5 tubes for each tool). Each tube was centrifuged for 15 min at 4,000 rpm. The supernatant was aspirated leaving a 5 mL pellet per tube.

Twenty milliliters of sodium bicarbonate solution (10%) was added into the tubes of all 4 subsamples (dry brush tube, wet brush tube, picking tube, and sonicator tubes) and was vortexed and then left closed at room temperature for 3 to 8 d. After this incubation period, the tubes were centrifuged for 15 min at 4,000 rpm, and the supernatant was discarded. Five milliliters of DW was then added to resuspend and rinse the residue pellet, and the tubes were then centrifuged for 15 min at 4,000 rpm. The supernatant was then aspirated using a pipette, leaving a small residue pellet. These tubes are labeled tubes A.

To remove clays, 10 mL of 1.5 g/mL SPT was added and then vortexed for 1 min and centrifuged for 15 min at 4,000 rpm. The upper 5 mL of liquid was aspirated using a pipette and discarded. To float the starches, we added an additional 10 mL of 1.9 g/mL SPT to the remaining 5 mL of 1.5 g/mL SPT still in the tube, for a final solution of 15 mL at ca. 1.77 g/mL of SPT in the tube. This was vortexed and centrifuged as in the previous step. The starches were then pipetted off the top in the uppermost 5 mL of solution, which was transferred to a new tube (Tube B). To preserve the remaining residues in Tube A, 10 mL of DW was added and these were vortexed and centrifuged for 15 min at 4,000 rpm. The upper layer was discarded and 10 mL of DW was added again followed by vortexing the sample and storing it.

DW was added into each of the B tubes filling the entire 50 mL tube to reduce the specific gravity, and the tubes were then centrifuged for 15 min at 4,000 rpm. After the first centrifugation, the upper 35 mL was aspirated and discarded. The tubes were filled again with 35 mL of DW, vortexed, and centrifuged for 15 min at 4,000 rpm. The upper 48 mL was aspirated and discarded. The remaining material (1 to 2 mL) was mounted on the slides (see a detailed description of slides preparation below).

Preparation of Slides. To prepare slides for examination, 10 μL of the extracted material was placed on a clean borosilicate glass slide. An additional 10 μL of 20% glycerin solution was added to retard evaporation. Each slide was covered with an 18 mm × 18 mm cover glass slide and labeled with its details.

Microscopy. Slides were scanned and analyzed using Nikon Eclipse E200 under brightfield and cross-polarized light. Photographs were taken with GXCAM-U3PRO-6.3 camera under brightfield and cross-polarized light using GXCapture-T software for Windows. Measurements were taken and 20 μm scale bars were added to each image using the same software.

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*.

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