Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium)

Amanda G. Henry[a,b,1], Alison S. Brooks[a], and Dolores R. Piperno[b,c,1]

[a]Department of Anthropology, Center for Advanced Study of Hominid Paleobiology, Washington, DC 20052; [b]Archaeobiology Laboratory, Department of Anthropology, Smithsonian National Museum of Natural History, Washington, DC 20013-7012; and [c]Smithsonian Tropical Research Institute, Box 2072 Balboa, Panama

The nature and causes of the disappearance of Neanderthals and their apparent replacement by modern humans are subjects of considerable debate. Many researchers have proposed biologically or technologically mediated dietary differences between the two groups as one of the fundamental causes of Neanderthal disappearance. Some scenarios have focused on the apparent lack of plant foods in Neanderthal diets. Here we report direct evidence for Neanderthal consumption of a variety of plant foods, in the form of phytoliths and starch grains recovered from dental calculus of Neanderthal skeletons from Shanidar Cave, Iraq, and Spy Cave, Belgium. Some of the plants are typical of recent modern human diets, including date palms (*Phoenix* spp.), legumes, and grass seeds (Triticeae), whereas others are known to be edible but are not heavily used today. Many of the grass seed starches showed damage that is a distinctive marker of cooking. Our results indicate that in both warm eastern Mediterranean and cold northwestern European climates, and across their latitudinal range, Neanderthals made use of the diverse plant foods available in their local environment and transformed them into more easily digestible foodstuffs in part through cooking them, suggesting an overall sophistication in Neanderthal dietary regimes.

The temporal and geographic overlap between modern humans and Neanderthals has led many anthropologists to look for differences between the groups that might explain the disappearance of the latter. Recently, researchers applied the framework and methods of dietary ecology to further explore this question and used available dietary data to propose models for Neanderthal and modern human interaction. Several authors argue that Neanderthals were unable to acquire as many calories from the same environments as were modern humans (1–4) and were thus easily outcompeted. These views are supported by data suggesting that Neanderthals focused primarily on large game and for the most part eschewed foods more common in modern human diets, such as marine resources, small, hard-to-catch animals, and protein-rich plant foods like nuts (5–7).

Other evidence suggests that Neanderthal foraging patterns were much like those of modern humans (8, 9), including small game (10), marine resources (11), plant foods (12–17), similar use of fire (18), some cooking, and other food processing (10, 13), and that these behaviors may have extended back in time to the Middle Pleistocene (19). These dietary behaviors are not only important in terms of energy they provide, but also can suggest sophistication in other areas of Neanderthal behavior. For example, the inclusion of plant foods can significantly structure the mobility patterns and gendered division of labor in recent (20–22) and presumably past hunters and gatherers (7, 9). Cooking also represents a significant shift in human behavior, by improving the nutritional quality of plant foods and potentially altering the social organization of human groups (23, 24). Assessing the characteristics of Neanderthal plant food preparation and consumption can help us to address whether dietary breadth may have played a role in Neanderthal replacement and could also substantially inform our understanding of behavioral and cognitive comparisons between Neanderthals and modern humans. However, due to vagaries of preservation and insufficient attention to plant remains, data on plant consumption are rare or completely lacking from most Neanderthal occupations.

The existing evidence for Neanderthal plant consumption is richest for Near Eastern sites. Micro- and macrobotanical studies suggest that Levantine Neanderthals made use of several kinds of plants, including date palms, grasses, legumes, acorns, and pistachios (12–16). However, these remains, derived from sediments, are sometimes fragmentary and not always unequivocally linked to diet. Furthermore, grass seed bract phytoliths, which commonly occurred in the phytolith records, could not be identified at taxonomic levels below the family. Although hearths and burned materials have implied the controlled use of fire in many Neanderthal occupations (12, 13), direct evidence for preparing plant foods via cooking is lacking.

In contrast to the Near Eastern record, there are very few data on the potential importance of plants in the diets of northwestern, "classic" European Neanderthals. Spanish Neanderthals made use of several kinds of plants, including grasses, as bedding (25). Pollen records have suggested that the plant communities of Northern Europe varied significantly depending on the glacial cycle (26). Even during cold cycles, however, certain calorie-dense plant foods like grass seeds (*Poaceae*) and cattails (*Typha*) would have been available (26, 27). Analysis of residues on stone tools has suggested some use of plants and wood by European Neanderthals (28), although it is not clear what species were used and if they were eaten. This overall sparse and inconclusive record of Neanderthal use of plants limits our interpretations of their diet and related behavior.

To better explore Neanderthal use of plant foods, we analyzed the plant microfossils (starch grains and phytoliths) trapped in dental calculus of Neanderthal individuals. Dental calculus has been repeatedly shown to be a reliable source of plant microfossils for dietary reconstruction (29–35). The precipitation of minerals onto the surface of the teeth traps and preserves many components of the oral environment, including bacteria and food particles. The resulting dental calculus is heavily mineralized, survives well in archaeological contexts (36), and is easily recognizable on fossil teeth. Our recent study showed that calculus deposits on teeth are minerologically similar to enamel, although with clear organic deposits, and are easily distinguishable from adherent sediments (37). Microfossils recovered from calculus

ANTHROPOLOGY

Table 1. Counts and descriptions of plant microfossils recovered from the dental calculus from Shanidar III

Tooth no.	Type 1 Triticeae (cf. *Hordeum*)	Type 1 cooked	Type 2	Type 3	Type 4	Other	Other cooked	Dmg/Enc	*Phoenix* spp. (date palm) phytolith	Other phytolith	Total
Shanidar III tooth 3 LuC	4	0	2	4	1	2	0	4	7	3	27
Shanidar III tooth 4 RM^3	4	3	0	2	0	7	2	5	7	1	31
Shanidar III tooth 5 LI$_2$	2	12	0	1	1	0	14	3	2	0	35
Totals per type	10	15	2	7	2	9	16	12	16	4	93

Type 1: Medium, circular to oval to D shaped, lenticular when turned, center usually dimpled/marked hilum, usually with clear lamellae visible under normal light but always visible at least under polarized light, cross arms are occasionally faded, line down center of grain when turned, sometimes dimpled. Type 2: Small, decorated oval with distinct projections, center hilum, clean cross. Type 3: Small, oval to circular, mostly central dimpled hilum occasionally with a fissure that crosses the grain entirely, too small for other features. Type 4: Small, subangular/rectangular, center dimpled hilum, clean cross. Other: A variety of unique/unusual forms that do not fit into the other types. Dmg/Enc: A variety of starches that may belong to one of the named types but are too damaged (cracked, broken) or encrusted (covered in calculus material) to be confidently identified.

are therefore a direct record of the plants an individual put in his mouth, which may include some nondietary plants, but should overwhelmingly consist of plant foods. Here we present results from dental calculus of two northern European Neanderthals, Spy I and Spy II from Spy Cave in Belgium, and one Near Eastern Neanderthal, Shanidar III, from Shanidar Cave in Iraq (for more information on each site and the fossil remains studied, see *Materials and Methods*).

Results

We collected and studied small calculus samples from seven teeth: three from Shanidar III (∼46 ka) and two each from Spy I and II (∼36 ka). Plant microfossils were recovered from all calculus samples, although the amount varied significantly between teeth even within individuals (Tables 1 and 2). The analysis below combines data from all teeth for each individual.

Shanidar III, Shanidar Cave, Iraq. We examined the calculus from three teeth from this individual: a left upper canine (tooth 3), a right third upper molar (tooth 4), and a left lower second incisor (tooth 5) (Fig. S1). A total of 73 starch grains were recovered from the three teeth. Ten of these starch grains exhibited features that allowed us to identify them as grass seed starches from the Triticeae tribe, including circular to subcircular shape in plane view, lenticular cross-section, central hilum usually marked with a thin line, and distinctive dimples and lamellae. Starch grains from this tribe, which includes the wild relatives of wheat, barley, and rye, share identifiable features and size ranges when raw as well as when cooked (38, 39) (Fig. 1, Table S1, Figs. S2–S4). Several features align these starch grains with those from *Hordeum* (barley). None had the characteristic crater-like dimples that are diagnostic of modern bread wheat (*Triticum aestivum*) and most other wild wheat species (e.g., *Triticum monococcum*, *Triticum urartu*, *Triticum vavilovii*, and *Triticum turgidum*). Only a few had lamellae, and these were thinner and finer than those found in *Aegilops* (goat-grass) species. None of the starches had the central pleating that is a marker of the *Aegilops* species. None had the invasive craters common in *Secale* (rye) species, and the starches were significantly larger and with different morphologies than other members of the Triticeae such as *Elymus* and *Leymus*. The shape and size of the dimples and appearance of the rare lamellae match those from *Hordeum*, with some starches appearing more similar to *Hordeum spontaneum*, whereas others are more like *Hordeum hexastichon*. It is likely that the Neanderthals would have eaten a number of closely related species.

Also of considerable interest were the 15 grains that were identical in appearance to cooked starches from the Triticeae (Fig. 1C, Fig. S5). Cooked starches have been identified in a variety of archaeological settings (40, 41). Our cooking experiments performed on a variety of grains and legumes

showed that Triticeae starch grains undergo several changes when cooked before becoming completely gelatinized and unrecognizable (38). When only partially damaged, the starches can still be confidently assigned to the Triticeae. The overall pattern of damage to the starch grains matches most closely with that caused by heating in the presence of water, such as during baking or boiling, rather than "dryer" forms of cooking like parching or popping (38). The finding of cooked Triticeae starches on the Shanidar teeth reinforces evidence from other studies (13) that suggest that Near Eastern Neanderthals cooked plant foods.

Eleven of the remaining unidentified starches could be assigned to three main types. These three types and nine other unique grains have diagnostic features and probably derive from several different taxa (Fig. 2). They should become identifiable as the reference collections are expanded. One of the starches in the "other" category is likely from a legume, on the basis of its characteristic ovoid shape, distinctive longitudinal cleft fissure, and lamellae (Fig. 2 *G* and *H*). Starch grains such as these appear in *Pisum* spp. and *Cicer* spp. but the large diagnostic grains that would conclusively identify these genera were not observed in our sample. *Lens* and several species of *Vicia* can be ruled out, but there are other Near Eastern edible legumes that we were unable to sample and the unknown starches may belong to one of these taxa. Three of the other starches have characteristics
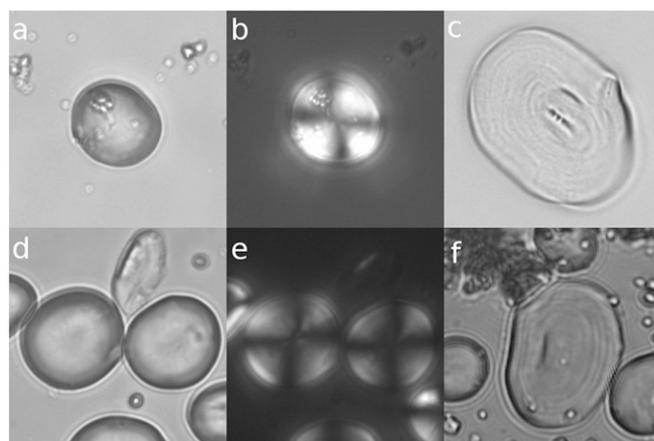

Fig. 1. Triticeae cf. *Hordeum* (barley and close relatives) starch grains recovered from the dental calculus from Shanidar III compared with modern *Hordeum* starch grains. Each box is 50 μm on a side. (*A* and *B*) *Hordeum* spp. starch grain from Shanidar tooth 4 under brightfield and cross-polarized light. (*C*) Cooked *Hordeum* spp. starch from Shanidar tooth 5. (*D* and *E*) Starch from modern *Hordeum hexastichon* under brightfield and cross-polarized light. (*F*) Starch from modern *Hordeum vulgare* (domesticated barley) boiled for 5 min.
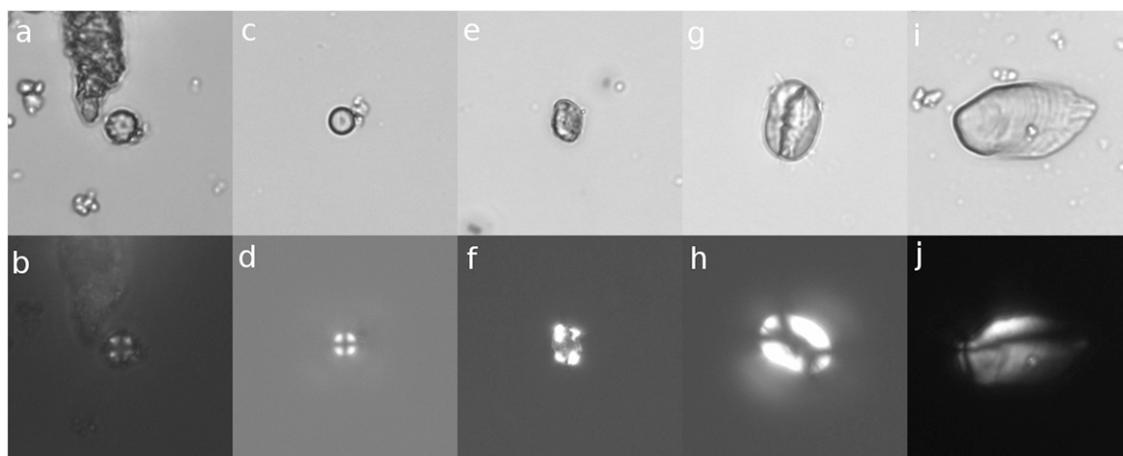
Fig. 2. Starch grains recovered from the dental calculus from Shanidar III. The *Upper* image of each pair shows the starch under brightfield light, and the *Lower* image shows it under cross-polarized light. Each box is 50 μm on a side. (*A* and *B*) Type 2. (*C* and *D*) Type 3. (*E* and *F*) Type 4. (*G* and *H*) Probable legume (Fabaceae) starch. (*I* and *J*) Possible underground storage organ starch. Each box is 50 μm on a side.

similar to known plant underground storage organ "USO" starches (Fig. 2 *I* and *J*), but no Middle Eastern USOs were included in our reference collection. The final 28 starches were severely damaged and retained few diagnostic characteristics. However, the damage to 16 of these is characteristic of cooking (38). In total, starches with damage that is consistent with cooking represent 42% of the starch assemblage (Table 1), but we expect that the actual proportion of cooked foods within the diet of this individual was probably much higher. Our cooking experiments have shown that within those samples cooked for long periods (≥30 min), only a very small proportion of the starch grains remain undamaged or only partially undamaged, which would reduce the number of identifiable starches preserved in calculus (38).

Phytoliths were less numerous than the starch grains, but they document the consumption of another plant that would continue to have significant importance in later, modern human plant economies. Sixteen of the 20 phytoliths are small, decorated spheres or subspherical shapes from the fruits of the date palm (*Phoenix spp.*) (Fig. 3). It does not appear possible to differentiate among the species of *Phoenix*; thus the identification must remain at the genus level. Nevertheless, the fruits of almost every species of date palm are edible (42) and would have been a nutrient-rich addition to the diet. Only two species of palms are native to the region, with date palm being the single edible one. This evidence, plus the morphological characteristics of the palm phytoliths from the teeth, matching in all respects the fruit of the date palm, strongly suggests that dates were consumed. The other four phytoliths are similar to those from tree fruit phytoliths but could not be confidently identified.
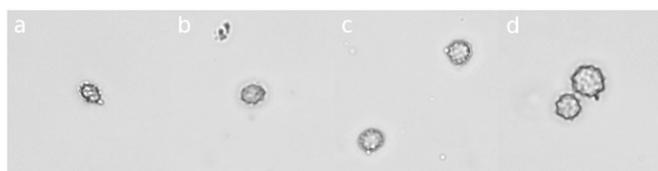

Fig. 3. *Phoenix* (date palm) phytoliths from the dental calculus from Shanidar III compared with modern *Phoenix* phytoliths. Each box is 50 μm on a side. (*A*) Phytolith from Shanidar tooth 3. (*B*) Phytolith from the fruit of *Phoenix reclinata*. (*C*) Stalk phytolith from *P. reclinata*. (*D*) Leaf phytolith from *P. reclinata.* Note that the recovered phytolith most closely matches the fruit phytoliths.

Spy I and Spy II, Spy Cave, Belgium. We sampled two teeth from both individuals (Fig. S6): From Spy I, we sampled the lower left fourth premolar from fragment 12A (11H) and the lower right first molar from fragment 12B (580c). From Spy II, we sampled the lower right fourth premolar from fragment 3 (577i) and the upper right third molar from fragment 2 (578f). The numbering reflects the most recent categorization by the Institute Royal des Sciences Naturelles de Belgique, which houses the fossils.

Both individuals from Spy had one tooth that contained many microfossils and one tooth that did not have as many (Table 2). Over 60 of the 136 starches had a unique, characteristic morphology, with a large ovoid shape, an eccentric hilum with a distinctive crack, distinct lamellae, and a polarization cross with smoothly curving "arms" (Spy I RM[1] 580c had a large clump of calculus with up to 30 starches embedded, most of which were probably from this type but were too encrusted to identify with confidence). These attributes suggest that the starches are from a USO (Fig. 4 *A* and *B*). These starches share many similarities with the starches from the USOs of water lilies, but do not match those from either of the common local water lily species (*Nymphaea alba* and *Nuphar lutea*) (Fig. 5). There are several other species of water lily that are native to the study area, but we have not acquired USO samples from them.
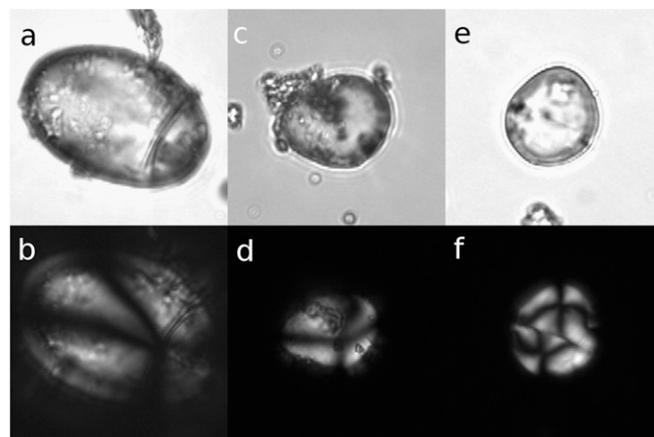

Fig. 4. Starch grains recovered from the calculus of Spy I and Spy II. The *Upper* image of each pair shows the starch under brightfield, and the *Lower* image shows it under cross-polarized light. Each box is 50 μm on a side. (*A* and *B*) Type 1, probable water lily starch. (*C* and *D*) Type 2. (*E* and *F*) Type 3.

Table 2. Counts and descriptions of plant microfossils recovered from the calculus from the teeth of Spy I and Spy II

Tooth no.	Type 1 USO	Type 2	Type 3	Type 4 Andropogoneae?	Type 5	Type 6	Other	Dmg/Enc	Totals
Spy II RM3 578f	1					1	1	1	4
Spy II RP4 577i	27	2	1	6	9	3	13	21	82
Spy I LP4 11H				1	1			2	4
Spy I RM1 580c	32	1	1	2	4	1	3	1*	45*
Totals per type	60	3	2	9	15	5	17	25	136

Type 1: Large, oval to egg shaped to avocado shaped, ovoid in 3d, hilum very eccentric, usually at the thinner end of the oval. Hilum is marked with a fissure or dimple of varying forms: small dimple, single transverse fissure, one transverse and one longitudinal fissure, or X-shaped fissure. Lamellae are quite visible, most often at the end opposite the hilum. Occasional small surface dimples are shown. Cross arms are clear and smoothly bending across the surface of the grain. Type 2: Medium, clamshell shaped with eccentric, dimpled hilum near bulging long side. Cross is clean, with straight arms. Type 3: Two tightly compound grains, with the juncture between the two unclear. The overall shape is ovoid, whereas each grain is hemispherical. The hila are centric and unmarked. Type 4: Small to medium, subangular/faceted with slightly eccentric dimpled/open hilum, usually but not always marked with a deep single, Y-shaped or stellate fissure; cross arms are clean but usually bend over facets. Sometimes two grains are seen still in compounds. Type 5: Small, spherical to ovoid, center hilum that is sometimes marked with a dimple or a dimple and fissure. Cross arms are clean and straight across. Type 6: Large, very irregular, usually ovoid to subrounded, with deep lines and cracks radiating from the hilum, which is slightly off center and usually raised above the rest of the grain. Overall the starch appears to have a "volcano" shape. Other: A variety of unique/unusual forms that do not fit into the other types. Dmg/Enc: A variety of starches that may belong to one of the named types but are too damaged (cracked, broken) or encrusted (covered in calculus material) to be confidently identified.

*This sample includes a large clump of calculus with up to 30 starches embedded in it. Some of the starches appeared to be similar to type 1, but were too encrusted to be accurately identified, and have not been included in the overall counts for this sample.

Thirty-four of the remaining starches could be grouped into one of five types that represent potentially identifiable plant taxa (Figs. 4 and 6). One of them, type 4, is a medium, subrounded to subangular grain with a dimple or fissure at the hilum, which is similar to starches in some species of grass seeds, particularly those in the Andropogoneae tribe (which includes *Sorghum* and relatives) (Fig. 6 *A* and *B*). Type 5 is a small, circular grain with central hilum and distinct cross. This type of starch grain is found in a variety of plants and thus may represent one or many different plant components in the diet (Fig. 6 *C* and *D*). The remaining types, although appearing in small numbers, are distinctive and each likely represents a taxon-specific, although currently unidentified, plant type. Type 6 is particularly unusual, being very irregular and volcano shaped. It is of note that starches from all six types were found on both individuals, suggesting that a number of diverse plants were important dietary components. No phytoliths were found in these calculus samples.

Discussion

These sites record some of the extremes of the environments experienced by Neanderthals, from a Mediterranean, although inland and mountainous, environment at Shanidar to a northern, although oceanic, environment at Spy. Our data show that Neanderthals in both environments included a spectrum of plant foods in their diets, including grass seeds (Triticeae cf. *Hordeum*), dates (*Phoenix*), legumes (*Faboideae*), plant underground storage organs, and other yet-unidentified plants, and that several of the consumed plants had been cooked. The identified plant foods from Shanidar match well with the soil phytoliths and macrobotanical remains found at other Neanderthal sites in the Near East (12–16), whereas those from Spy show use of USOs as predicted for European Neanderthals (27). Neanderthals' consumption of these starchy plant foods does not contradict data from isotope analysis, because nitrogen isotopes record only the consumption of meat and protein-rich plant foods (6).

We note that, as at other Neanderthal sites, there is no evidence of intensification (e.g., stone artifacts specialized for use as grinding implements or storage features) in the use of certain foods as seen in later, Upper Paleolithic (43, 44), Epipaleolithic, and Natufian preagricultural modern human groups. However, there is clear evidence of cooking in the recovered starch grains, and furthermore, several of the identified plant foods would have required moderate to high levels of preparation, including husking the grass seeds and harvesting the submerged USOs of water lilies. These lines of evidence indicate Neanderthals were investing their time and labor in preparing plant foods in ways that increased their edibility and nutritional quality (24, 45). It should also be noted that date palms and possibly other unidentified plants have different harvest seasons than barley and legumes, a factor that may suggest that the Shanidar Neanderthals practiced seasonal rounds of collecting and scheduled returns to harvest areas. Overall, these data suggest that Neanderthals were capable of complex food-gathering behaviors that included both hunting of large game animals and the harvesting and processing of plant foods.

The timing of two major hominin dietary adaptations, cooking of plant foods and an expansion in dietary breadth or "broad spectrum revolution," which led to the incorporation of a diversity of plant foods such as grass and other seeds that are nutritionally rich but relatively costly to exploit, has been of
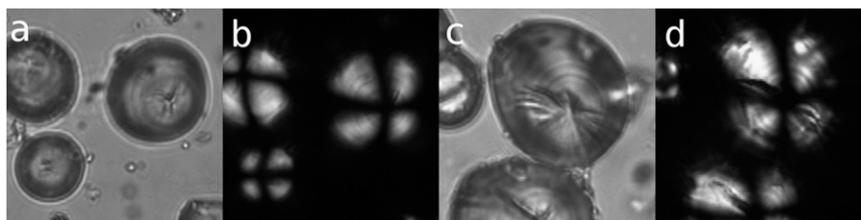

Fig. 5. Starch grains from modern water lilies under brightfield and cross-polarized light. Each box is 50 μm on a side. (*A* and *B*) *Nymphaea alba*. (*C* and *D*) *Nuphar lutea*.
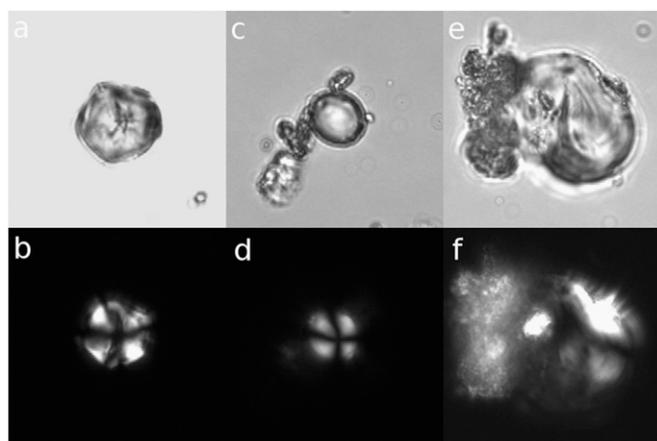
Henry et al.

Fig. 6. Additional starch grains recovered from the calculus of Spy I and Spy II. The *Upper* image of each pair shows the starch under brightfield light, and the *Lower* image shows it under cross-polarized light. Each box is 50 μm on a side. (*A* and *B*) Type 4, starch possibly from the Andropogoneae grass tribe. (*C* and *D*) Type 5. (*E* and *F*) Type 6, unusual starch grain.

central interest in anthropology (1, 2, 46, 47). Our evidence indicates that both adaptations had already taken place by the Late Middle Paleolithic, and thus the exploitation of this range of plant species was not a new strategy developed by early modern humans during the Upper Paleolithic or by later modern human groups that subsequently became the first farmers. Further plant microfossil research will continue to address the substantial data lacunae on dietary diversification during the Middle and Upper Paleolithic caused by inadequate floral records, and also better document trends that may have existed in Neanderthal diets through time and space. Our studies extend the known record of starch survival in dental calculus into the Middle Paleolithic and indicate that starch grain analysis will enable reconstructions of diet in a range of fossil specimens.

Materials and Methods

Site and Sample Descriptions. Shanidar Cave is located in the Zagros Mountains of northwestern Iraq (44° 13′ E, 36° 50′ N). It was excavated between 1952 and 1957 by Ralph Solecki and colleagues (48–55). Four main archaeological layers were described in the nearly 14 m of sediments removed (48), and Mousterian artifacts and Neanderthals' remains were found in the lowest layer (layer D) (48, 56). A date of 44,000 B.P. was acquired using a bulk sample radiocarbon analysis on sediments at the top of this 10-m-thick layer; the lower age is unknown. Palynological samples indicated a warm climate and the presence of a variety of edible plants in the site's vicinity, including date palms (*Phoenix dactylifera*), walnuts (*Juglans*), chestnuts (*Castanea*), oaks (*Quercus*), relatives of chicory and lettuce, and relatives of culinary herbs (49, 57–59). The Shanidar III fossil remains were found at 5.4 m below datum and 1–1.4 m below the sloping surface of level D, in the northeast corner of square B9 and near to, but slightly below the remains of Shanidar I (48). The teeth were not immediately recognized during excavation and were found later in bone bags from that same square and level. On the basis of a radiocarbon date of 44,000 B.P. near Shanidar I, Shanidar III was thought to be slightly older, possibly as old as 50,000 B.P. (48).

Spy Cave is located in the commune of Jemeppe-sur-Sambre, province of Namur, Belgium, along the left bank of the Orneau River (50° 28′ N, 4° 40′ E). De

Puydt and Lohest uncovered the Neanderthal remains in 1885. They recognized several layers in the site (the number varied between four and six depending on the publication) (60–62), including a surface layer and three "ossiferous layers." The lowest of these was sometimes broken into two or three sublevels and contained the fragmentary remains of several Neanderthal skeletons, as well as many Mousterian artifacts, most likely from a transitional technocomplex similar to the Châtelperronean, called the "Lincombian–Ranisian–Jerzmanowician" (63). Faunal profiles suggested an intensely cold climate (64). De Puydt and Lohest initially assigned the fossil remains to two individuals, but more recent studies revealed that the remains of a child and up to five adults were lumped together (65). The two fragmentary skulls and mandibles retained the names Spy I and Spy II. Previously unrecognized human teeth that refitted with Spy I and II were found in faunal bags, and these were directly dated using accelerator mass spectrometry radiocarbon to ~36 kya (63).

Calculus Sampling. The sampled teeth were heavily encrusted with visible deposits of calculus (Figs. S1 and S7). A dental curette was used to loosen and remove small areas of calculus (~2 mm in area), which were scraped into microcentrifuge tubes. These samples were mounted in water on a slide and examined under brightfield and cross-polarized light on a Zeiss Axioscope at 400× magnification. Each microfossil was photographed, described, and documented, and the entire slide was examined. Two calculus samples were removed from each of the Shanidar teeth, and the results of the two samples were combined.

Starch grains and phytoliths were grouped into types on the basis of shared morphology or counted as unique forms. The types were consistent only within each site. The types and unique forms were compared with our modern reference collections of economic and other plants, including >2,000 species for phytoliths and >400 for starches, and were identified on the basis of matched morphological and size traits. Plants sampled from the National Herbarium housed at the Smithsonian National Museum of Natural History were included in the reference collection, as were several plants collected in the wild; published literature was also consulted (66, 67).

Cooking damage was identified on the basis of a series of experiments we performed (38), as well as on the basis of literature documenting the patterns and types of damage these procedures leave on the microfossils (68–71). The damage to starch grains caused by heating in the presence of water, such as would occur with methods like baking and boiling, is particularly distinctive and has been observed in other archaeological records (35, 38, 40, 41). Mastication of raw and cooked starch grains does not appreciably alter their morphological characteristics (*SI Materials and Methods*, Fig. S7).

1. O'Connell JF (2006) *When Neanderthals and Modern Humans Met*, ed Conard NJ (Kerns, Tübigen, Germany), pp 43–65.
2. Kuhn SL, Stiner MC (2006) What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. *Curr Anthropol* 47:953–980.
3. Binford LR (1989) *The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene*, ed Trinkaus E (Cambridge Univ Press, New York), pp 18–41.
4. Soffer O (1994) *Origins of Anatomically Modern Humans*, eds Nitecki MH, Nitecki DV (Plenum, New York), pp 101–119.
5. Bocherens H, Drucker DG, Billiou D, Patou-Mathis M, Vandermeersch B (2005) Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: Review and use of a multi-source mixing model. *J Hum Evol* 49:71–87.
6. Richards MP, Trinkaus E (2009) Out of Africa: Modern human origins special feature: Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc Natl Acad Sci USA* 106:16034–16039.
7. Stiner MC (2006) *Transitions Before the Transition: Evolution and Stability in the Middle Paleolithic and Middle Stone Age*, eds Hovers E, Kuhn SL (Springer, New York), pp 213–231.
8. Adler DS, Bar-Oz G, Belfer-Cohen A, Bar-Yosef O (2006) Ahead of the game: Middle and Upper Palaeolithic hunting behaviors in the southern Caucasus. *Curr Anthropol* 47:89–118.
9. Bar-Yosef O (2004) Eat what is there: Hunting and gathering in the world of Neanderthals and their neighbors. *Int J Osteoarchaeol* 14:333–342.

10. Blasco R, Fernandéz Peris J (2009) Middle Pleistocene bird consumption at level XI of Bolomor cave (Valencia, Spain). *J Arch Sci* 36:2213–2223.
11. Barton RNE, et al. (1999) Gibraltar Neanderthals and results of recent excavations in Gorham's, Vanguard and Ibex caves. *Antiquity* 73:13–23.
12. Madella M, Jones MK, Goldberg P, Goren Y, Hovers E (2002) The exploitation of plant resources by Neanderthals in Amud cave (Israel): The evidence from phytolith studies. *J Arch Sci* 29:703–719.
13. Lev E, Kislev ME, Bar-Yosef O (2005) Mousterian vegetal food in Kebara cave, Mt. Carmel. *J Arch Sci* 32:475–484.
14. Albert RM, Bar-Yosef O, Meignen L, Weiner S (2003) Quantitative phytolith study of hearth from the Natufian and Middle Paleolithic levels of Hayonim cave (Galilee, Israel). *J Arch Sci* 30:461–480.
15. Albert RM, Weiner S, Bar-Yosef O, Meignen L (2000) Phytoliths in the Middle Palaeolithic deposits of Kebara cave, Mt. Carmel, Israel: Study of the plant materials used for fuel and other purposes. *J Arch Sci* 27:931–947.
16. Rosen AM (2003) *Neanderthals in the Levant: Behavioral Organization and the Beginnings of Human Modernity*, ed Henry DO (Continuum, London), pp 156–171.
17. Hardy BL, Bolus M, Conard NJ (2008) Hammer or crescent wrench? Stone-tool form and function in the Aurignacian of southwest Germany. *J Hum Evol* 54:648–662.
18. Daniau AL, d'Errico F, Sánchez Goñi MF (2010) Testing the hypothesis of fire use for ecosystem management by Neanderthal and Upper Palaeolithic modern human populations. *PLoS ONE* 5:e9157.
19. Alperson-Afil N, Goren-Inbar N (2010) *The Acheulean Site of Gesher Benot Ya'akov: Ancient Flames and Controlled Use of Fire* (Springer, Dordrecht, The Netherlands) Vol II .
20. Lee RB (1979) *The! Kung San: Men, Women, and Work in a Foraging Society* (Cambridge Univ Press, Cambridge, UK).
21. Yellen JE (1977) *Archaeological Approaches to the Present: Models for Reconstructing the Past* (Academic, New York).
22. Hawkes K, Hill K, O'Connell JF (1982) Why hunters gather: Optimal foraging and the Aché of eastern Paraguay. *Am Ethnol* 9:379–398.
23. Wrangham R (2007) *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*, ed Ungar PS (Oxford Univ Press, Oxford), pp 308–323.
24. Carmody RN, Wrangham RW (2009) The energetic significance of cooking. *J Hum Evol* 57:379–391.
25. Cabanes D, Mallol C, Expósito I, Baena J (2010) Phytolith evidence for hearths and beds in the late Mousterian occupations of Esquilleu cave (Cantabria, Spain). *J Arch Sci* 37:2947–2957.
26. Müller UC, Pross J, Bibus E (2003) Vegetation response to rapid climate change in central Europe during the past 140,000 yr based on evidence from the Füramoos pollen record. *Quat Res* 59:235–245.
27. Hardy BL (2010) Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. *Quat Sci Rev* 29:662–679.
28. Hardy BL (2004) Neanderthal behavior and stone tool function at the Middle Palaeolithic site of La Quina, France. *Antiquity* 78:547–565.
29. Boyadjian CHC, Eggers S, Reinhard K (2007) Dental wash: A problematic method for extracting microfossils from teeth. *J Arch Sci* 34:1622–1628.
30. Henry AG, Piperno D (2008) Using plant microfossils from dental calculus to recover human diet: A case study from Tell al-Raqa'i, Syria. *J Arch Sci* 35:1943–1950.
31. Juan-Tresserras J, Lalueza C, Albert RM, Calvo M (1997) *First European Meeting on the Study of Phytoliths*, eds Pinilla A, Juan-Tresserras J, Machado MJ (Gráficas Fersán, Madrid), pp 197–203 (in Spanish).
32. Lalueza Fox C, Pérez-Pérez A (1994) Dietary information through the examination of plant phytoliths on the enamel surface of human dentition. *J Arch Sci* 21:29–34.
33. Lalueza C, Pérez-Pérez A, Turbón D (1996) Dietary inferences through buccal microwear analysis of middle and upper Pleistocene human fossils. *Am J Phys Anthropol* 100:367–387.
34. Scott Cummings L, Magennis A (1997) *First European Meeting on the Study of Phytoliths*, eds Pinilla A, Juan-Tresserras J, Machado MJ (Gráficas Fersán, Madrid), pp 211–218.
35. Piperno DR, Dillehay TD (2008) Starch grains on human teeth reveal early broad crop diet in northern Peru. *Proc Natl Acad Sci USA* 105:19622–19627.
36. Lieverse AR (1999) Diet and the aetiology of dental calculus. *Int J Osteoarchaeol* 9:219–232.
37. Henry AG, Brooks AS, Piperno DR, Rose T (2010) Assessing dental calculus as a source of archaeological plant microfossils using ESEM/EDS. *Abstracts of the Society for American Archaeology 75th Anniversary Meeting* (Society for American Archaeology, Washington, DC), p 116.
38. Henry AG, Hudson HF, Piperno DP (2009) Changes in starch grain morphologies from cooking. *J Arch Sci* 36:915–922.
39. Piperno DR, Weiss E, Holst I, Nadel D (2004) Processing of wild cereal grains in the Upper Palaeolithic revealed by starch grain analysis. *Nature* 430:670–673.
40. Zarrillo S, Pearsall DM, Raymond JS, Tisdale MA, Quon DJ (2008) Directly dated starch residues document early formative maize (*Zea mays* L.) in tropical Ecuador. *Proc Natl Acad Sci USA* 105:5006–5011.
41. Chandler-Ezell K, Pearsall DM, Zeidler JA (2006) Root and tuber phytoliths and starch grains document manioc (*Manihot exculenta*), arrowroot (*Maranta arundinacea*) and llerén (*Calathea sp.*) at the Real Alto site, Ecuador. *Econ Bot* 60:103–120.
42. Barrow SC (1998) A monograph of *Phoenix L.* (palmae: Coryphoideae). *Kew Bull* 53:513–575.
43. Aranguren B, Becattini R, Lippi MM, Revedin A (2007) Grinding flour in Upper Palaeolithic Europe (25 000 years bp). *Antiquity* 81:845–855.
44. Revedin A, et al. (2010) Thirty thousand-year-old evidence of plant food processing. *Proc Natl Acad Sci USA* 107:18815–18819.
45. Carmody RN, Wrangham RW (2009) Cooking and the human commitment to a high-quality diet. *Cold Spring Harbor Symp Quant Biol*, 74:427–434.
46. Flannery K (1969) *The Domestication and Exploitation of Plants and Animals*, eds Ucko PJ, Dimbleby GW (Aldine, Chicago), pp 73–100.
47. Weiss E, Wetterstrom W, Nadel D, Bar-Yosef O (2004) The broad spectrum revisited: Evidence from plant remains. *Proc Natl Acad Sci USA* 101:9551–9555.
48. Solecki RS (1963) Prehistory in Shanidar valley, northern Iraq. *Science* 139:179–193.
49. Solecki RS, Leroi-Gourhan A (1961) Palaeoclimatology and archaeology in the Near East. *Ann N Y Acad Sci* 95:729–739.
50. Solecki RS (1961) New anthropological discoveries at Shanidar, northern Iraq. *Trans N Y Acad Sci* 23:690–699.
51. Solecki RS (1971) *Shanidar, The First Flower People* (Knopf, New York).
52. Solecki RS (1975) Shanidar IV, a Neanderthal flower burial in northern Iraq. *Science* 190:880–881.
53. Solecki RS (1977) The implications of the Shanidar cave Neanderthal flower burial. *Ann N Y Acad Sci* 293:114–124.
54. Solecki RS (1957) Two Neanderthal skeletons from Shanidar cave. *Sumer* XIII:59–60.
55. Solecki RS (1960) Three adult Neanderthal skeletons from Shanidar cave, northern Iraq. *Annu Rep Smithson Inst*, 1960:603–635.
56. Cowgill LW, Trinkaus E, Zeder MA (2007) Shanidar 10: A middle paleolithic immature distal lower limb from Shanidar cave, Iraqi Kurdistan. *J Hum Evol* 53:213–223.
57. Leroi-Gourhan A (1975) The flowers found with Shanidar IV, Neanderthal burial in Iraq. *Science* 190:562–564.
58. Leroi-Gourhan A (1968) The Neanderthal IV from Shanidar. *Bull Soc Prehist Franc* LXV:79–83.
59. Leroi-Gourhan A (1969) *The Domestication and Exploitation of Plants and Animals*, eds Ucko PJ, Dimbleby GW (Aldine Transaction, Chicago), pp 141–148.
60. de Puydt M, Lohest M (1887) Archaeological and Historical Federation of Belgium. Proceedings of the Congress Held in Namur August 17–19, 1886, ed de Radiguès de Chennevière H (Société Archéologique de Namur, Namur, Belgium), pp 205–240 (in French).
61. Fraipont J, Lohest M (1887) The human race of Neanderthal or Canstadt type in Belgium: Ethnographic research on the human bones found in the quaternary deposit in Spy Cave, and their geological ages. *Arch Biol (Liege)*, 7:587–757 (in French).
62. de Puydt M, Lohest M (1886) Exploration of Spy Cave. *Annals of the Geological Society of Belgium*, 13:34–39 (in French).
63. Semal P, et al. (2009) New data on the late Neandertals: direct dating of the Belgian Spy fossils. *Am J Phys Anthropol* 138:421–428.
64. Otte M (1979) *The early Upper Paleoloithic in Belgium* (Musees Royaux d'Art et d'Histoire, Brussels, Belgium) (in French).
65. Toussaint M, Pirson S, Bocherens H (2001) Neanderthals from Belgium. *Anthropol Praehist* 112:21–38.
66. Reichert ET (1913) *The Differentiation and Specificity of Starches in Relation to Genera, Species, etc* (The Carnegie Institution of Washington, Washington, DC).
67. Seidemann J (1966) *Starch Atlas* (Paul Parey, Berlin) (In German).
68. Lamb J, Loy TH (2005) Seeing red: The use of congo red dye to identify cooked and damaged starch grains in archaeological residues. *J Arch Sci* 32:1433–1440.
69. Samuel D (1996) Investigation of ancient Egyptian baking and brewing methods by correlative microscopy. *Science* 273:488–490.
70. Samuel D (2000) *Ancient Egyptian Materials and Technology*, eds Nicholson PT, Shaw I (Cambridge Univ Press, Cambridge, UK), pp 537–576.
71. Samuel D (2006) *Ancient Starch Research*, eds Torrence R, Barton H (Left Coast, Walnut Creek, CA).