Paleolithic human exploitation of plant foods during the last glacial maximum in North China

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Three grinding stones from Shizitan Locality 14 (ca. 23,000–19,500 calendar years before present) in the middle Yellow River region were subjected to usewear and residue analyses to investigate human adaptation during the last glacial maximum (LGM) period, when resources were generally scarce and plant foods may have become increasingly important in the human diet. The results show that these tools were used to process various plants, including Triticeae and Paniceae grasses, Vigna beans, Dioscorea opposita yam, and Trichosanthes kirilowii snakegourd roots. Tubers were important food resources for Paleolithic hunter-gatherers, and Paniceae grasses were exploited about 12,000 y before their domestication. The long tradition of intensive exploitation of certain types of flora helped Paleolithic people understand the properties of these plants, including their medicinal uses, and eventually led to the plants' domestication. This study sheds light on the deep history of the broad spectrum subsistence strategy characteristic of late Pleistocene north China before the origins of agriculture in this region.

ancient starch | late Paleolithic China | plant processing | usewear analysis | stone tool function

t has long been argued that foragers at the end of the Pleistocene broadened their resource base to encompass a wide array of plant and animal foods and that this "broad spectrum revolution" entailed the transition to farming (1). New studies have shown that human exploitation of an extensive range of plant foods can be traced back to much earlier dates in late Paleolithic times in southwest Asia, suggesting a long history of intensive foraging for plants before domestication (2).

Usewear traces and plant residues on grinding stones can provide crucial information for understanding the plant-foraging strategies of ancient people. By applying these methods, several projects have shown evidence of widespread plant use, including wild cereals and tubers, by late Paleolithic populations in many areas of the world, dating to a period between *ca*. 30,000 and 23,000 y ago, including the Near East (3), Europe (4), and Australia (5).

In China, the earliest grinding stones have been uncovered from several Paleolithic site clusters distributed on the Loess Plateau region along the middle Yellow River valley. These include Longwangchan in Shaanxi (6) and Shizitan and Xiachuan in Shanxi (7-9), dating to ca. 25,000-9000 calendar years before present (cal. B.P.). A study of usewear traces and starch residues on grinding stones from Locality 9 (S9 hereafter) in the Shizitan site cluster (ca. 12,700-11,600 cal. B.P.) has demonstrated that people used these tools to process various plant foods, including grasses, tubers, acorns, and legumes (10). Among the grass starch granules uncovered at this site, some from Panicoideae may have been the wild ancestors of domesticated millets (Panicum miliaceum and Setaria italica ssp. italica). Therefore, it is important to investigate the use of plants in an earlier period in this region, to trace possible continuity in a putative plant procurement strategy that may have eventually led to domestication. In this study, we demonstrate usewear patterns and residues on three grinding stones (ca. 23,000-19,500 cal. B.P.) excavated from Locality 14 (S14 hereafter) in the Shizitan site cluster (9), which disclosed the exploitation of Triticeae and Paniceae grasses,

Vigna beans, Dioscorea opposita yam, and Trichosanthes kirilowii snakegourd roots.

Sites and Environmental Contexts

S14 (110°32′40″ E, 36°02′11″ N; 655 \pm 5 m in altitude) is among a series of more than 50 late Paleolithic localities (*ca.* 25,000– 9,000 cal. B.P.), referred to as the Shizitan site cluster, distributed along the Qingshui River, a tributary of the Yellow River in southern Shanxi (Fig. 1). All of these localities are characterized primarily by small flaked tools and a microlithic technology, with no pottery, dwelling structures, human burials, or storage facilities found, suggesting that the occupants were mobile hunter– gatherers (7–9, 11). The long time span of human occupation with abundant material remains provides a wealth of data for study of the transition from the late Paleolithic to the early Neolithic in the middle Yellow River valley.

Excavations at S14 in 2000, 2003, and 2005 revealed three continuous cultural strata (II, III, and IV) within a depth of 50–100 cm in an area of 25 m², dating to a time period of *ca.* 23,000–18,000 cal. B.P. (Table S1). Material remains uncovered include 1,643 lithic artifacts and 2,776 animal bone fragments, in addition to 17 ash and burnt surface areas (fireplaces). Several grinding tools (slabs) have been found near fireplaces in all strata (refs. 8 and 9; ref. 12, p. 20), and three of them (all made of sandstone), analyzed here (Fig. 1), were uncovered from Strata III and IV (*ca.* 23,000–19,500 cal. B.P.).

The site is situated in a mountainous region with a temperate climate and a diversity of flora resources today. Pollen data obtained from Shizitan suggest that vegetation coverage in the region was dominated by grasses from 35,100–9,400 B.P. (dating by thermoluminescence analysis) (13). During the last glacial maximum (LGM), the climate was dry and cold, featuring a steppe environment. During the period of *ca.* 18,500–13,200 cal. B.P., this region experienced the last deglaciation, characterized by a mild and arid or semiarid steppe environment with a small amount of deciduous and broadleaf species. This episode was then followed by a dry and cold period dating to 13,200–13,000 cal. B.P. before another era of improved climatic conditions (ref. 12, p. 167).

Results

We collected usewear and residue samples from three grinding stones (GS1, GS2, GS3), which were kept in the Shanxi Museum after excavation. To compare used tools with unused natural stone, we also took samples from a sandstone rock (SS1) in a noncultural deposit near the site (Table S2).

Usewear Analysis. Polyvinyl siloxane (hereafter PVS or peel) was applied to the Shizitan grinding stones to provide portable and

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durable records for microscopic analysis. Previous research, using PVS on usewear patterns from grinding stones in China (10, 14, 15) and other parts of the world (16–19) established valuable reference data for the study of ancient tools. In recent years, we have also conducted a series of experimental studies on grinding stones (20) to produce references for processing seeds, tubers, nuts, wooden objects, minerals, shells, and stone implements. Based on these studies, the analytical variables examined in the current project include: stage of polish development (low, medium, high), polish reticulation pattern, polish topography, striations (furrow, sleek, fine), pitting and pecking, and surface microtopography (Table S3). The results of the analysis of the three grinding stones (GS1–GS3) are as follows.

G51. GS1 is a fragment of a slab (weight, 0.74 kg), and both sides show microscopic traces of use, mainly small areas of polish. On the top side, the microscopic surface is relatively flat, and higher plateau areas show more polish than lower valley areas. In some areas, very fine striations run multidirectionally on the high level of the grain surface; in other areas, crystal grains are clearly flattened with polish (Fig. 2, 1 and 2). Based on our experimental study, similar polish and very fine striations appear on grinding slabs after processing dry tubers (*Dioscorea opposita* yam, *Trichosanthes kirilowii* snakegourd root, and *Pueraria lobata* kudzu-vine root) for 1 h or longer (Fig. S1, 5 and 6).

GS2. GS2 is a small slab (weight, 0.25 kg), and the top surface is slightly concave. Three PVS peels taken from the top surface show similar usewear traces: the microscopic surface is relatively flat, and the high plateau areas show more polish than the lower valley areas. On slightly lower areas, striations are sometimes visible, mostly very fine, faint, short, and running in different orientations (Fig. 2, 3). These patterns are consistent with those from processing plants, including dehusked wheat and millet, in our reference data (Fig. S1, 2 and 3). Grinding movements were multidirectional, probably including linear bidirectional (backand-forth) and circular motions. Pitting is visible in some areas, probably caused by processing hard-shelled seeds or nuts. In rare situations, some wide angular striations (furrows) are present (Fig. 2, 3), resembling the traces of stone-on-stone abrading done in our experimental study (Fig. S1, 1). These furrows, however, may have been caused by unintentional contact with hand stones. GS3. GS3 (weight, 5.64 kg) is the largest one in the assemblage. It was found face-up on top of GS2, situated above a fireplace. Two PVS peels were taken from the used surface. The microscopic surface is rather flat with a few polished areas, and striations are rare. On peel one (P1), some crystal grains show medium-level polish without striations, and on P2, small areas of shallow striations with U-shaped cross-sections (sleeks) are present (Fig. 2, 4 and 5). Compared with the references in our experimental studies, the polish is similar to that from tuber grinding, and the striations resemble traces from large seed processing, such as with beans (Fig. S1, 4).

Summary. Three slabs examined all show usewear traces, which clearly differentiate them from unused stone surfaces (Fig. 2, 6). These slabs were apparently used to process various plant foods, such as seeds, tubers, and nuts. To understand exactly what plants were involved here, we have to rely on residue analysis.

Residue Analysis. Ten residue samples were extracted from the three tools either by applying a small amount of distilled water to the tool and then extracting the sample with a pipette or by removing sediment adhering to the tool surface (21, 22).

Phytolith remains on the S14 grinding implements were minimal and mostly not diagnostic (*Supporting Information* and Table S4). Grass husk phytoliths were not recovered, suggesting that these grinding stones were probably not used to dehusk cereals. Charcoal and/or burnt phytoliths were present on all three tools, perhaps reflecting the location of the implements near fireplaces or food processing areas.





Fig. 2. Usewear patterns from S14 grinding stones. (Magnification: 200×) (1 and 2) GS1, fine striations running diagonally and a polished crystal surface, resembling tuber processing. (3) GS2, small pitting (*right*), short furrows (*lower left*), and very fine and faint striations running vertically (*upper left*), likely related to pounding small, hard objects, abrading stone objects, and processing plants, respectively. (4) GS3-P1, a medium level polished area, similar to tuber processing. (5) GS3-P2, sleeks running vertically, similar to dry bean or large seed processing. (6) Uneven surface of natural crystals on an unused sandstone, for comparison with used tools.

Six of the 10 residue samples yielded a total of 136 starch granules. In general, samples taken from used surfaces tend to produce more starch residues than those from unused surfaces. Two sediment samples (GS1-3 and GS3-4) and one water sample (GS2-3), all taken from unused surfaces, contained no starch. GS1 and GS2 revealed only 10 starch granules (7.4% of the total), likely because the tools were washed after excavation, a situation that apparently affected the survival rate of starch residues. In contrast, 92.6% of total starch granules were found in the samples from GS3, which was unwashed before sampling. Sixty-five granules (48% of the total) show characteristics of damage, many resembling starch granules after grinding, as seen in previous studies (23) and our reference data. The samples taken from a natural rock contain a small number of starch granules with no sign of damage. These observations suggest that the profiles of starch residues recovered from used surfaces of ancient grinding stones are most likely associated with tool function rather than with the enclosing soil matrix, an inference consistent with several previous studies (e.g., refs. 10 and 24-26).

Among over 900 specimens in our modern reference collections, we specifically analyzed those starch-rich and economically important samples relevant to the research area, including 156 samples belonging to 83 species in 45 genera of 18 families. Of the 136 starch granules uncovered from S14, 121 (89% of the total) are identifiable compared with our references. The ancient starch granules are classified into six types on the basis of their morphology and size. The unidentifiable starch granules (15; 11%) lack diagnostic features comparable to available references (Table S5). Because the starch remains from grinding stones are likely to have derived from ground plants, we compared them with starch extracted from ground seeds/tubers in our modern reference samples (*Supporting Information*).

Type I Starch. Type I starch granules (n = 45; 33%) of the total starch) are round or oval in shape and relatively large in size $(14.56-39.21 \ \mu\text{m})$. The surface is rather flat, the hilum is centric, lamellae are visible on large granules, and the extinction cross is shaped as either "×" or "+." Most of the type I granules appear damaged (33; 74%), showing broken edges, deep fissures, pronounced lamellae, and/or a dark central area on the extinction cross (Fig. 3, *1*–4). These starch granules, in morphology and size, resemble many taxa in the Triticeae tribe of the grass family indigenous to north China and still found in Shanxi today (27). This includes many genera of *Agropyron, Elymus, Roegneria*, and *Leymus* in our references, as well as those reported in other studies (ref. 28, figure 4). The characteristics of damaged granules are also consistent with those found in ground *Leymus* and *Agropyron* from our references (Fig. 4, *1*–4).

It is possible that type I starches belong to more than one genus in the Triticeae tribe, although the large granules are particularly similar to *Agropyron cristatum* and *Agropyron desertorum* in form (Fig. 4, 2 and 3) and size (Fig. 5, 1).

Type II Starch. Type II starch granules (n = 20; 15% of the total starch) are irregularly oval or nearly kidney-shaped and relatively large in size (17.31–40.76 µm). Fissures and lamellae are visible in most cases, and the extinction cross often exhibits many arms. Seven granules (35%) are damaged, characterized by broken edges and/or a large dark area at the center (Fig. 3, 5–8), consistent with bean starch granules damaged by grinding (23). Type



Fig. 3. Starch grains uncovered from Shizitan S14, compared with tuber starch grains from Shizitan S9, Shigu, and Egou (under DIC and polarized filters). (1–4) Type I starch (Triticeae), showing damages (3 and 4). (5–8) Type II starch (*Vigna* sp.), showing damages (7 and 8). (9–14) Type III starch (Paniceae), showing damages. (15–18) Type IV starch (*D. opposita*). (19–21) Type V starch (*T. kirilowii*). (22 and 23) Type VI starch (*T. kirilowii*). (24 and 25) Type VI starch from Shizitan S9. (26–28) Types V and VI starch from Peiligang culture sites at Shigu (26) and Egou (27 and 28). Panels 26–28 are reproduced with permission from ref. 14. (Scales bars: 9–14 and 19–28, 10 μm; others, 20 μm.)



Fig. 4. Modern starch references (under DIC and polarized filters). (1) Leymus secalinus (ground). (2) A. cristatum (ground). (3 and 4) A. desertorum (ground). (5 and 6) V. radiata. (7 and 8) V. unguiculata (ground). (9) S. italica ssp. viridis, showing undamaged granules. (10) P. miliaceum (wild), showing undamaged granules. (11 and 12) S. italica ssp. viridis (ground), showing central depression with a protrusion. (14) E. crusgalli (ground), showing central depressions on most granules. (15 and 16) D. opposita (wild). (17–20) T. kirilowii. (Scale bars: 9–14, 10 μm; others: 20 μm.)

II granules resemble beans in the Phaseoleae tribe, particularly *Vigna* species, in shape and size (Figs. 4, 5–8 and 5, 2), such as *Vigna angularis*, *Vigna unguiculata*, and *Vigna radiata*. It is difficult to identify type II starch to the level of species.

Type III Starch. Type III starch granules (n = 18; 13% of the total starch) are characterized by small sizes $(8.95-18.81 \ \mu\text{m})$ and polygonal shapes. The hilum is centric, with star or Y-shaped fissures often radiating toward the periphery, whereas extinction crosses are mostly "+"-shaped with straight arms. Most starch granules (13; 72%) in type III are damaged, showing a large

central depression with or without a small circular protrusion in the middle, pronounced fissures, widened extinction cross, and/ or visible lamellae on part of the granule (Fig. 3, 9–14). Type III starch granules are similar in shape to several genera within the Paniceae tribe. Some genera in our reference samples, such as *Setaria, Panicum, Echinochloa, Pennisetum,* and *Digitaria,* all exhibit both faceted and spherical granule shapes, the presence of fissures, a centric hilum, and straight cross shape, similar to type III starch granules. However, the damaged type III granules particularly resemble, in morphology, those from green foxtail grass (*S. italica ssp. viridis*), which is the wild ancestor of domesticated foxtail millet (*S. italica ssp. italica*), and barnyard grass (*Echinochloa crusgalli*) Fig. 4, 9–14).

In general, wild Paniceae starch granules (approximately <14 μ m) are smaller in size range than those from domesticated millets (ref. 10, figure 4; refs. 28–30). However, type III starch granules from S14 show sizes greater than 14 μ m in half of the cases examined (9 of 18). These large granules only overlap well with the size ranges of domesticated foxtail millet and a ground green foxtail sample from Zhengzhou (Henan) in our references (Fig. 5, 3).

Based on our experimental study, starch granules from several wild and domesticated Paniceae species become larger in size after grinding, with the maximum length of granules increasing 27–56% among several reference samples of *Echinochloa*, *Panicum*, and *Setaria* spp. It is known that milling can cause structural change in starch granules (31), and in several cases, ancient Paniceae starch granules from grinding stones appear larger than those from the modern corresponding species (ref. 28, p. 254). Given that grasses taken from 23,000-y-old tools at S14 are unlikely to be domesticated species, it is possible that some type III starch granules belong to wild Paniceae grasses, including *Setaria* and other genera, and that their large sizes may have been caused by grinding (*Supporting Information*).

Type IV Starch. Type IV starch granules (n = 24; 18% of the total) are characterized by a large granule size range (19.33–59.05 µm), irregular triangular or oval shapes, an extremely eccentric hilum, the presence of lamellae in most cases, and an extinction cross with bent arms (Fig. 3, 15-18). One granule appears to be damaged, showing broken edges, rough surface, and a dark area in the center of the extinction cross. These starch granules most resemble the *D. opposita* yam, which has many cultivated and wild variations in north China (Fig. 4, 15 and 16). Among five *D. opposita* samples we collected from Henan, the domesticated ones show smaller granule size ranges (8.83–33.16 µm, 14.01–53.16 µm, 11.16–48.22 µm) than those of two wild ones (16.27–63.08 µm, 22.9–70.62 µm). Type IV starch is more comparable with wild yam in morphology and size (Fig. 5, 4).

Types V and VI Starch. Type V starch granules (n = 4; 3%) of the total) are characterized by a bell shape, medium size (14.75-22.96)



Fig. 5. Ancient starch types I–VI compared with modern references after grinding (all reference samples are wild forms unless indicated as domesticated).

µm), an eccentric hilum, absence of lamellae, and an extinction cross with bent arms (Fig. 3, 19–21). Type VI starch granules (n = 11; 8% of the total) are regularly round or regularly oval in shape, and medium in size (11.47–29.72 µm). The hilum is eccentric in most cases, lamellae are visible on large granules, and the extinction cross has bent arms (Fig. 3, 22 and 23). One granule appears damaged, as indicated by its broken edges.

Types V and VI starch are most comparable in morphology and size with the root of snakegourd (*T. kirilowii* in the Cucurbitaceae family) in our reference data. Starch granules from modern *T. kirilowii* are varied in shape, and include spherical, oval, bell-shaped, and polygonal morphologies. The hilum is eccentric in most cases, fissures in various forms are sometimes present, lamellae are visible on some large granules, and the extinction cross often has bent arms (Fig. 4, 17-20). When sizes are compared, types V and VI also fall into the range of *T. kirilowii* (Fig. 5, 5). Types V and VI particularly resemble the large granules in *T. kirilowii*, which are often regularly oval and bell-shaped.

Summary. The recovery rates of starch from the three tools are uneven, partly relating to whether or not the artifact was washed in the postexcavation process. GS3 (unwashed) yielded the most starch granules (126) with all six types present. Taken as a whole, the S14 starch assemblage is dominated by Triticeae grasses (33%), followed by yam (18%), beans (15%), Paniceae grasses (13%), and snakegourd root (11%). Although the percentage of starch granules from certain plants cannot be used to determine the proportion of plant use in the foraging strategy, they help us to understand, in a broad view, the components of starchy food in the hunter–gatherers' diet.

Among the damaged starch granules, a majority comes from seeds (grasses and beans), and granules with apparently enlarged sizes occur mostly in Paniceae tribe grasses. These observations are consistent with our experimental grinding of plants, in which Paniceae starches demonstrate the highest percentages of damaged granules and greatest increase in granule sizes among various seeds and tubers after grinding (Tables S6 and S7).

Discussion

The presence of a high percentage of grass starch (46% of the total) on S14 grinding tools, as the direct evidence for human use of these grasses for food, is consistent with the grass-dominated ecosystem of the region suggested by pollen analysis (13). Paniceae starch on S14 grinding stones constitutes the earliest direct evidence for human consumption of these types of grasses. Starch granules identifiable to Panicoideae subfamily grasses also have been found on grinding stones from Shizitan S9 (10), suggesting a tradition of foraging these small seeds long before their domestication during Neolithic times in the region.

Triticeae starch residues on grinding stones have also been found in the late Paleolithic site at Shizitan S9 (10). Despite a long history of exploitation of Triticeae grasses in northern China, these plants have never gone through a domestication process in this part of the world.

Legume starch granules, including *Vigna* sp., have been found on grinding stones in many sites along the Yellow River region, including the Late Paleolithic site at Shizitan S9 (10), and Neolithic sites at Egou (14) and Shangzhai (32). Beans appear to have been one of the earliest plant foods used by hunter–gathers in north China, but their taxonomy cannot be determined to the level of species based on starch data only. The earliest known macrobotanic remains of *Vigna* beans in China have been identified as Adzuki (*V. angularis*), dating to the late Neolithic in Shandong (33). Beans rich in starch from genera other than *Vigna* have not been found in the archaeological contexts in prehistoric north China. However, the use of *Vigna* for food before 2,500 BC in China still awaits confirmation by macrobotanic discovery in the future.

The most interesting funding of this study is the presence of starch from two taxa of tuber (yam and snakegourd root), with a significant percentage in the starch assemblage (together 29%).

Tubers rarely survive identifiably in macrobotanic remains; therefore, starch analysis is the most effective method by which to recover them from their archaeological contexts. Starch granules identifiable to *Dioscorea* yam have been uncovered from chipped stone tools dated to as early as 28,000 cal. B.P. (34), and from grinding stones (10, 14), and pottery vessels (35) found across north China, dating from the late Paleolithic, through the Neolithic, to the Bronze Age. This plant was apparently widely used very early as an important source of food.

The presence of starch from snakegourd root provides the earliest evidence to date that this tuber was used for food in China. Starch granules from this tuber have previously been found from grinding stones in a late Paleolithic site at Shizitan S9 (10), as well as in early Neolithic sites at Shigu and Egou in Henan (ref. 14, figures 7D and 8 F and H), but they were unidentifiable at the time of discovery, because of a lack of comparative references (Fig. 3, 24–28). Like yam, snakegourd root seems to have been widely foraged by both hunter–gatherers and early farmers in the middle Yellow River region.

Yam and snakegourd today are distributed widely in north China, and both are used as traditional medicine (ref. 36, pp. 218 and 244-245; ref. 37, pp. 103-105). Whereas yam has been commonly cultivated and cooked as food, snakegourd root has not been regularly consumed in north China except when used as famine food. The traditional method of processing and cooking snakegourd root can be found in Jiuhuang Bencao (Herbal for Relief of Famines), written by Zhu Su (1361–1425). Snakegourd roots were skinned, cut into slices, and soaked in water for 4 to 5 d, with the water changed each day. The roots were then ground with tools and sieved with textile to produce very fine flour. Alternatively, the roots were dried and ground before being leached more than 20 times to make very fine flour. The flour then could be used to make cakes or noodles (ref. 38, pp. 64-65). It is important to note that snakegourd root needs to be ground to flour for consumption, a scenario in line with the starch found on grinding stones in ancient sites. We can now trace the use of snakegourd root back to 23,000 y ago, and such a long tradition of use may have helped people to recognize its medicinal properties long before the historical period. We are currently unable to distinguish cultivated yam and snakegourd from wild ones, based on starch. This is a topic worthy of further research.

When both usewear patterns and starch residues found on these tools are compared, they provide supporting evidence for one another in most cases. It is particularly interesting to note that starch granules from yam and snakegourd root occur in high frequency on the used surface of GS3. Usewear traces from this surface (GS3-P1) show a unique polished pattern, resembling tuber grinding in our experimental study.

Usewear traces on GS2 include pitting, probably related to processing seeds with hard shells; however, we did not uncover any starch from nuts, such as acorn. Given the absence of broadleaf trees in the pollen profile during the LGM in the region (13), it is possible that nonstarchy shelled seeds other than acorn were processed on this tool.

Conclusions

Around 23,000–18,000 y ago during the LGM, the Qingshui River valley appears to have been an area with a wide range of faunal and floral resources, which attracted small hunting-gathering groups. In addition to hunting, people collected and processed many types of plants, including grass seeds of Triticeae and Paniceae, *Vigna* beans, *D. opposita* yam, and *T. kirilowii* snakegourd roots, among others.

All of these plants from S14 seem to have been continuously exploited by hunter–gatherers for the next few millennia to the beginning of the Holocene in the Shizitan area (S9), as well as by early farmers in Neolithic times over a much broader region. The major difference between the starch assemblages of S14 and other later sites is the presence of *Quercus* starch in the latter, likely resulting from the onset of the Holocene, when broadleaf trees began to be distributed in the region. Acorn needs to be processed by grinding and leaching before human consumption (39). Such food-processing techniques appear to have developed much earlier, as shown by this study's demonstration that the consumption of certain tubers such as snakegourd root, which requires grinding and leaching, can be traced back to 23,000 y ago.

Northern China is considered the area where foxtail and broomcorn millets were first domesticated (40, 41). Recent studies on macro- and microbotanical remains from Donghulin (Beijing) have suggested that millet cultivation/domestication may be traced back to *ca*. 11,000–9,450 cal. B.P. at this site (30, 42). The presence of starch likely from *Setaria* and other Paniceae seeds at S14 suggests that these wild grasses were probably used for at least 12,000 y before their cultivation/domestication recognizably affected seed morphology.

A broad-spectrum subsistence strategy was already practiced by people at Shizitan during the LGM. The intensive exploitation of Paniceae grasses and tubers for more than 10 millennia before the Neolithic would have helped people to develop necessary knowledge about the properties of those plants, which eventually led to millet's domestication and medicinal uses of tubers.

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Materials and Methods

PVS samples were taken from different locations on the tool to document both used and unused surfaces. The PVS peels were examined under a compound (reflected light) Olympus microscope at magnifications of 50×, 100×, 200×, and 500×. Images were collected with a Zeiss Axiocam ICc3 digital camera and Zeiss Axiovision software Version 4.7.

Residue samples were processed for starch and phytolith extraction using the heavy liquid sodium polytungstate (in a specific gravity of 2.35). Extractions obtained from residue samples were mounted in 50% (vol/vol) glycerol and 50% (vol/vol) distilled water on glass slides and scanned under a Zeiss Axio Scope A1 fitted with polarizing filters and differential interference contrast (DIC) optics. Images were taken using a Zeiss Axiocam MRc5 digital camera and Zeiss Axiovision software Version 4.7.

Most images of usewear and starch from modern references used in this research were also produced with the same microscopy to make the ancient and modern samples comparable.

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