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Identification and implications of lithic artifacts starch residues from Fenghuangzui Neolithic site in Central China

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Starch residues on lithics are crucial for exploring the function and use pattern of stone tools and reconstructing the ecological environment, diet, and subsistence strategies of ancient populations. Recent excavations at Fenghuangzui Site (4400–4200 cal BP) revealed abundant Shijiahe Culture remains, especially feature H13, with a large amount of pottery, lithics and ashes were unearthed, which may indicate population gathering and communal activities. This paper analyses starch granules from 23 lithic artifacts (e.g., Stone adze, Core tools and Flake tools) unearthed from H13. The results indicate that the extracted starch granules primarily belong to roots and tubers, demonstrating that these lithic artifacts were used for processing local rhizome plants. Combined with rice and millet, indicated by macro-remains and phytoliths, the finding showed a wide diet of these inhabitants. This paper provides a new case study of starch granules in the Late Neolithic sites of the Middle Yangtze River valley.

Humans have had a close relationship with plants since the beginning of their existence. One scientific method to explore this relationship is through the identification of archaeobotanical remains, which provides insights into how people utilized, managed, and cultivated plants to meet their needs¹. Among the various analytical methods developed for this purpose, starch granule analysis stands out. Starch is a long-chain compound formed by the polymerization of glucose molecules and is stored in the parenchyma of roots, stems, leaves, fruits, and seeds of plants as starch granules². Different plant species have starch granules that exhibit distinct morphological characteristics³.

Numerous studies on starch granules have contributed valuable theoretical insights into the vitality patterns of ancient populations in China and the status of agricultural development. To date, over 150 case studies on starch granules have been reported across more than 130 prehistoric sites in China, focusing on materials such as pottery, lithics, mussels, dental calculus, and soils (Fig. 1). The most frequently discussed topics in these studies include the use of plants as food resources and the actual functions and usage patterns of various artifacts or tools, such as stone knives, grinding stones,

pointed-bottom bottles, and grooved basins^{4–8}. Additionally, starch granule analysis has been employed to investigate the domestication of plants^{9–11}, food processing techniques^{12,13}, and beverage production^{5,14–16}.

The Yangtze River valley is a crucial region for understanding the formation and development of Chinese civilization, with a long history of rice farming supported by archaeobotanical evidence. This has led some researchers to suggest that it may be one of the centers of rice cultivation. While many macro-plant remains have been reported from the area, studies focused on starch granules are relatively scarce. The Late Neolithic Fenghuangzui site, located in Xiangyang City of Hubei Province in the middle reaches of the Yangtze River valley, presents an opportunity to explore the potential and application of starch granule analysis in central China.

During the excavation conducted from 2020 to 2021, a hearth feature (referred to as H13) was uncovered in the southern part of the site, alongside numerous lithic artifacts, pottery, and plant and animal remains. This paper presents the findings from the recent analysis of starch granules extracted from the lithic artifacts found in H13. The goal is to identify the functions of these lithic tools and to investigate the formation process of H13. By

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Fig. 1 | Prehistoric sites with starch granule studies published in China (The red box is the research area of this paper).

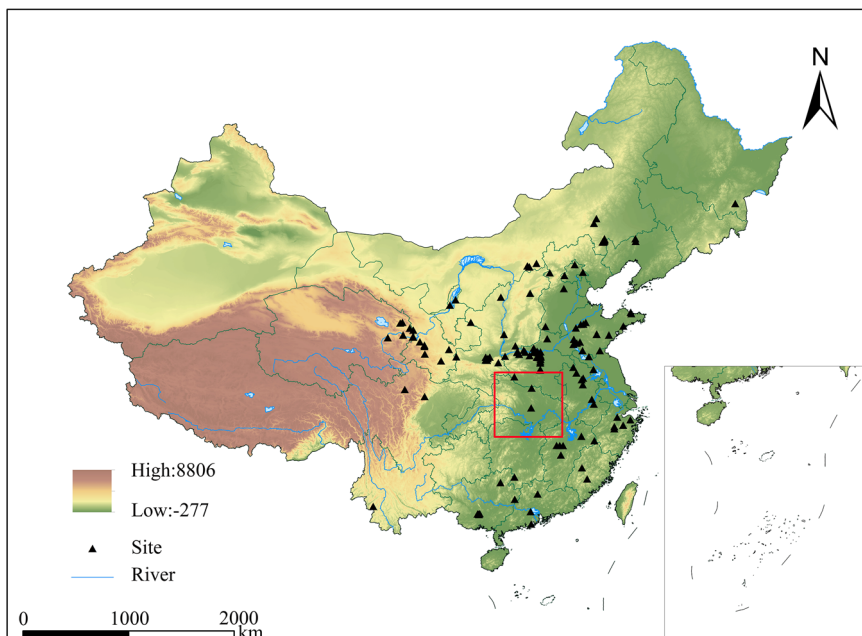
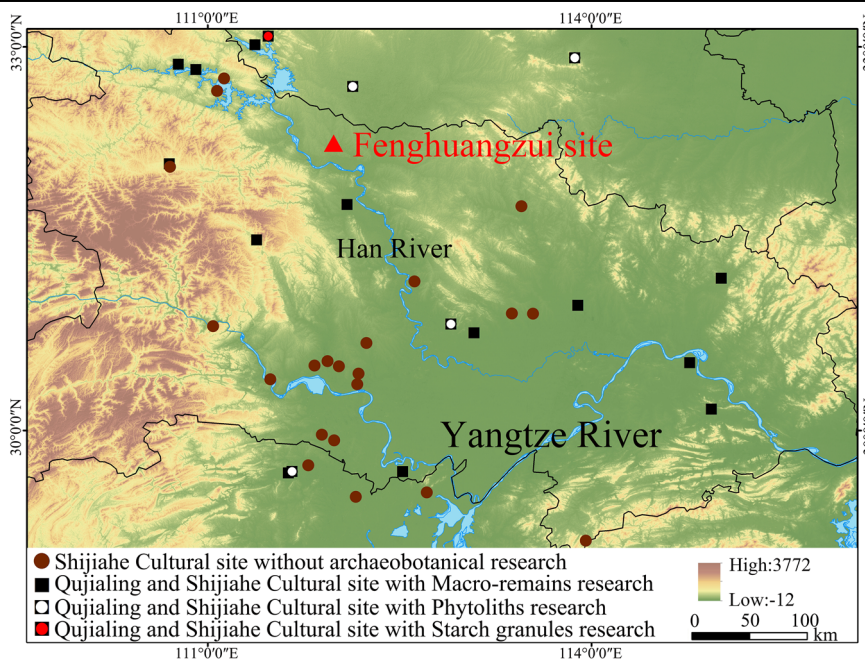


Fig. 2 | Location of Fenghuangzui and other Late Neolithic sites in the middle Yangtze River.



categorizing and analyzing the types of starch granules recovered from the lithic tools, this study discusses how the inhabitants of Fenghuangzui may have utilized both wild and cultivated plants.

Methods

Archeological and environmental settings

The Fenghuangzui site, located at coordinates 111°59'20.39" E and 32°14'42.67" N, reaches a maximum elevation of 94 meters above sea level. It is situated between Yanying Village and Qianwang Village in Longwang Town, within the Xiangzhou District of Xiangyang City, Hubei Province, central China (Fig. 2). The site lies in the upper reaches of the Han River, near the southern edge of the Nanyang Basin. It primarily extends across an irregular platform, with a river flowing to the east and behind the platform¹⁷.

Feature H13 was uncovered during the 2020 excavation. The feature has an oval shape, with well-defined walls and a nearly flat bottom. It

measures 6.6 meters in length (long diameter) and 2.1 meters in width (short diameter), with a depth of 0.5 meters. The cultural deposits within H13 have been divided into two strata: upper and lower¹⁸.

The upper stratum, measuring up to 0.21 meters thick, consists of yellow-brown clay with a loose texture, mixed with red burnt clods and charcoal. Artifacts found in this layer include pottery, a few lithics, and animal bones. In contrast, the lower stratum ranges from 0.05 to 0.29 meters thick and contains gray-black soil with a loose texture, along with plant ash, charcoal, and some braised soil. Numerous sherds, lithics, and animal bones were excavated from this lower layer.

Four radiocarbon dating samples (see Table 1) from feature H13 indicate that it dates back to between 4400 and 4200 calibrated years before present (cal BP), placing it firmly within the Shijiahe Culture period¹⁸.

Evidence from plant remains, such as carbonized rice grains and rice husks, suggests that the subsistence economy during the Shijiahe Culture

Table 1 | Radiocarbon dating of H13

Laboratory number	Sample	Unit	Radiocarbon date (BP)	Tree-ring chronology calibration (BP)(95.4%)
Beta-577497	Charcoal	H13①	3850 ± 30	4470–4218 (75.6%) 4209–4155 (19.8%)
Beta-577498	Charcoal	H13①	3880 ± 30	4416–4235 (94.1%) 4196–4185 (1.3%)
Beta-577499	Charcoal	H13②	3880 ± 30	4416–4235 (94.1%) 4196–4185 (1.3%)
Beta-577500	Charcoal	H13②	3870 ± 30	4414–4227 (89.6%) 4200–4178 (4.4%) 4169–4160 (1.4%)

period was primarily based on rice farming. Additionally, fishing, hunting, and gathering wild plants contributed to the diet to varying^{1,19–21}.

Recent archaeobotanical research has made significant advancements regarding the Qujialing and Shijiahe cultural sites in the Jiangnan Plain and nearby regions (see Table 2 for a list of sites where archaeobotanical remains have been excavated and analyzed). These studies indicate that rice and millet agriculture played a crucial role in the local and regional diet of the Jiangnan Plain, incorporating domesticated plants such as *Setaria italica*, *Panicum miliaceum*, *Oryza sativa*, and *Glycine max*. Additionally, various weeds were collected and cultivated, including *Setaria viridis*, *Digitaria sanguinalis*, *Echinochloa Beauv*, and *Perilla frutescens*, along with fruiting plants like *Actinidia* and *Ampelopsis brevipedunculata*, as well as nuts and drupe shells. The findings from macro-remain analysis strongly support these conclusions.

Moreover, plant microfossils have been vital for understanding the diverse methods of food procurement and consumption. Figure 1 illustrates the phytolith and starch granule analyses performed at the Chengtoushan site in Lixian, Hunan²², the Qujialing site in Jingmen, Hubei^{23,24}, and the Gouwan site in Xichuan, Henan²⁵. Phytolith analysis suggests that the Qujialing people began cultivating and utilizing rice approximately 5800 years ago, indicating advanced domestication of rice at that time. These discoveries provide a scientific foundation for understanding late Neolithic human life and rice domestication in the eastern part of the Hanshui River in the Jiangnan Plain²³.

Although starch granule analysis has significant potential to reveal food sources and provide insights into plants used for various purposes, including food processing, medicinal use, and crafting, it has been less frequently applied in Neolithic studies on the Jiangnan Plain compared to other research methods. The present paper tentatively employs starch granule analysis on lithic artifacts from H13, aiming to enhance our understanding of the functions of these tools and to contribute new information about food exploitation and subsistence practices in the late Neolithic middle Yangtze River valley.

Materials and experiments

Twenty-four lithic specimens were excavated from H13, with five originating from the upper stratum and 19 from the lower stratum. Twenty-three of these specimens were included in the current study for starch granule analysis (Fig. 3). The analysis indicates that most artifacts from H13 are Chipped lithic artifacts, while Ground lithic artifacts are rare, represented only by a few stone chisels and ground flake. Chipped lithic artifacts include cores, flakes, tools, and fragments. The tools are core tools and flake tools. Considering the type and function of lithic artifacts, this study selected stone adze, and some tools for the extraction and analysis of starch granules. Figure 3 displays some of the lithic artifacts analyzed in this study.

The extraction of starch granules was conducted at the archaeological laboratories of Wuhan University and the Key Laboratory of Vertebrate Evolution and Human Origins at the Chinese Academy of Sciences in

Table 2 | The sites where archaeobotanical remains were unearthed and investigated

Site	Location	Archeological culture	Type	Reference
Chengtoushan	Lixian, Hunan	Shijiahe	Phytoliths, macro-remains	22
Yangzhuang	Zhumadian, Henan	Shijiahe	Phytoliths	42
Baligang	Dengzhou, Henan	Yangshao, Shijiahe	Macro-remains Phytoliths	43 44
Yejiamia	Xiaogan, Hubei	Late Qujialing, Early Shijiahe	Macro-remains	45
Qinglongquan	Yunxian, Hubei	Yangshao, Qujialing, Third Qinglongquan	Macro-remains	46
Gouwan	Xichuan, Henan	Yangshao, Shijiahe, Qujialing	Macro-remains Starch granules	47 25
Tanjialing, Sanfangwan	Tianmen, Hubei	Late Shijiahe	Macro-remains	48
Xiawanggang	Xichuan, Henan	Yangshao, Qujialing, Third Wangsan	Macro-remains	49
Lishangang	Macheng, Hubei	Shijiahe	Macro-remains	49
Xiajiangjiabianzi	Yicheng, Hubei	Late Shijiahe	Macro-remains	49
Xiezidi	Daye, Hubei	Shijiahe, Late Shijiahe	Macro-remains	50
Dasi	Yunxian, Hubei	Yangshao, Qujialing, Late Shijiahe	Macro-remains	51
Chengzishan	Ezhou, Hubei	Shijiahe	Macro-remains	52
Sunjiagang	Lixian, Hunan	Late Shijiahe	Macro-remains	53
Mulintou	Baokang, Hubei	Qujialing	Macro-remains	54
Jijiawan	Fangxian, Hubei	Yangshao, Qujialing	Macro-remains	55
Qujialing	Jingmen, Hubei	Youziling, Qujialing, Shijiahe	Macro-remains Starch granules Phytoliths	56 24 23
Zoumaling	Shishou, Hubei	Qujialing, Shijiahe, Meishan	Macro-remains	57

Beijing, China. The extraction procedure followed methods outlined by Pearsall et al.²⁶, Ying et al.²⁷, Barton, Torrence and Fullagar et al.^{28–30}. Sample collection involved inspecting the entire surface of each lithic artifact, without sectional sampling. Each specimen underwent three cleaning steps, referred to as Sediment 1, Sediment 2, and Sediment 3. First, the lithic was



Fig. 3 | Main tools investigated in the present study. 1. Stone Adze (H13@:73); 2. Flake Tool 1 (H13@:6); 3. Flake Tool 2 (H13@:72); 4. Flake Tool 2 (H13@:84); 5. Core Tool 1 (H13@:3); 6. Core Tool 3 (H13@:56); 7. Core Tool 2 (H13@:18).

brushed to remove attached soil samples (Sediment 1); then it was washed with distilled water, and the collected liquid constituted wet wash samples (Sediment 2); finally, ultrasonic cleaning was applied, yielding ultrasound samples (Sediment 3). It was anticipated that the various sediments would reveal residues from different sources: Sediment 1 would contain more residues from the soil, and Sediment 3 would consist of materials closely associated with the specimen's surface, and Sediment 2 would include mixed contents from both soil and lithic surfaces. The primary goal of wet cleaning was to separate Sediments 1 and 3 to minimize cross-contamination from soil to lithic surfaces. All three sediments were processed following the same laboratory protocols.

To prevent potential contamination, several measures were implemented before and after extraction:

1. Preservation: Excavated lithic artifacts were placed in sealed bags. Prior to sampling, these artifacts were stored in the warehouse of the Field Archaeological Base at the Fenghuangzui Site, Wuhan University.
2. Experiment protocol: During the experiments, all personnel wore lab clothes, masks, gloves, and other protective gear. All equipment used for sampling was disposable and thoroughly rinsed with pure water before use to eliminate contamination.
3. Decontamination: The topsoil sample served as a control for comparison with the ultrasonic sample.

The starch granule extraction process adhered to the methods detailed in Guan et al.^{27,31}, encompassing the following steps: concentration, deflocculation, and heavy liquid flotation.

- (i) Concentration: A sample was filled with pure water until the liquid reached 50 ml in a test tube, which was then capped and centrifuged at 2000 rpm for 5 min. After centrifugation, the surface liquid was discarded, retaining approximately 5 ml at the bottom. This step aimed to concentrate the sample while removing some clay and impurities.
- (ii) Deflocculation: A 10 ml solution of Disodium EDTA (Na_2EDTA) at a concentration of 0.1% was added to the sample, which was then shaken on a reciprocating shaker for over 2 h to detach starch granules from soil particles. Subsequently, pure water was added for cleaning, and the sample underwent centrifugation at 2500 rpm for 2 min, after which the surface liquid was discarded, retaining about 5 ml at the bottom.

This process was repeated two more times to ensure the complete removal of Na_2EDTA .

- (iii) Heavy liquid flotation: About 10 ml of heavy liquid (sodium polytungstate solution) with a density of 1.85 g/cm^3 was added to the sample, which was centrifuged at 2000 rpm for 5 min. The surface liquid was then poured from the starch granules sample tube. This step was repeated to maximize starch granule recovery. Finally, the starch granule sample (SS) and the original sample (S) were washed by centrifugation in pure water to eliminate the heavy liquid.
- (iv) The starch granule sample (SS) was stored in a cool, dark place to prepare for observation. The slide was placed horizontally on a desk, and the observation sample number was recorded. A drop of 100% pure glycerin was added to the slide's center to improve the consistency of the starch granule sample and minimize the fluidity of the liquid. A pipette gun was employed to extract the starch granule samples during the extraction procedure.

Starch granules were examined under a microscope at a magnification of $\times 200$ and photographed at $\times 400$ using an Olympus BX 53 microscope. During this microscopic observation, various morphological characteristics of the starch granules were recorded, including their integrity, shape, position of fissures, lamellae, location of the central hilum, state and shape of extinction crosses, visibility of umbilical points, and the overall contour of the starch granules.

Results

A total of 111 starch granules were extracted from 22 of the 23 lithic artifacts, of which 101 granules were morphologically identifiable in subsequent analyses (Fig. 4). Each starch granule collected from Sediment 3 (Sed 3) on stone tools was initially compared with modern starch granules. Details regarding the starch granules from stone tools are presented in Table 3.

The classification and identification of starch granules mainly rely on the method used by Guan Ying and Zhang Xi^{32–34}. This method is mainly based on Geometric Morphometrics and Supporting Vector Machine (SVM) in Supervised Machine Learning. And the unknown starch granules are primarily based on the modern starch grain database established by the Archaeological Residue Research Group at the Key Laboratory of Vertebrate Evolution and Human Origins, Chinese Academy of Sciences.

Given the possibility that starch residues from Sediment 2 (Sed 2) may have originated from both the soil and the lithic surfaces, they were excluded from further discussion in this study. It is also believed that Sed 1 has been influenced by taphonomic contamination at the site; thus, it serves as a control sample to eliminate contamination effects. We compared starch granules obtained from Sed 1 and Sed 3 for geometric morphological analysis. Using Canonical Variate Analysis (CVA), we observed a significant difference between the starch granules from Sed 1 and those from Sed 3 ($p < 0.001$), indicating distinct peaks (Fig. 5). This suggests that starch granules from Sed 3 were minimally affected by soil contamination during the deposition process, providing insight into the utilization of the sampled specimens.

CVA results

The CVA of starch granules in the soil (Sed 1) identified four significant canonical variates (Fig. 6). The eigenvalues indicate that canonical variate 1 (CV1) accounts for 66.3%, canonical variate 2 (CV2) for 22.1%, and canonical variate 3 (CV3) for 8.9%, altogether explaining 97.4% of the total variance. The CVA scatter plot shows that starch granules in the soil overlapped with three control groups, suggesting the presence of legumina types in the soil.

CVA of starch granules on lithic artifacts (Sed 3) identified six significant canonical variates (Fig. 6). The eigenvalues indicate that canonical variate 1 (CV1) accounts for 52.5%, CV2 for 25.2%, and CV3 for 11.0% of the total variables, collectively explaining 88.7% of the total variance. The CVA scatter plot shows that the starch granules on lithic artifacts overlapped with six control groups, indicating that these

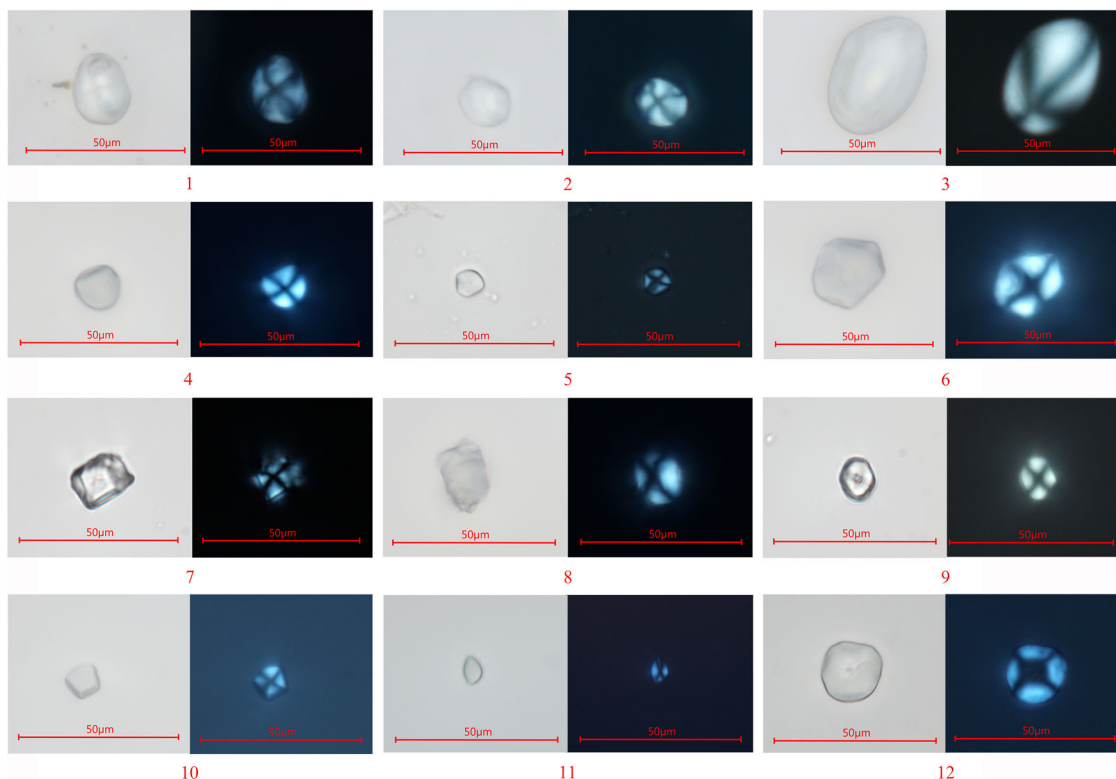


Fig. 4 | Main types of starch granules discovered in the residue sample (scale bar = 50 µm).

Table 3 | Lithic samples and effective starch granules of tools from Fenghuangzui H13

No.	Type	Source	Number	Identification results
H13@:73	Stone Adze	Ultrasonic sample	2	<i>Setaria</i> type, <i>Amorphophallus</i> type, and <i>Saururus</i> type
H13@:3	Core Tool 1	Ultrasonic sample	2	
H13@:18	Core Tool 2	Ultrasonic sample	1	
H13@:56	Core Tool 3	Ultrasonic sample	7	
H13@:6	Flake Tool 1	ultrasonic sample	1	
H13@:72	Flake Tool 2	Ultrasonic sample	2	
H13@:84	Flake Tool 3	Ultrasonic sample	1	

Fig. 5 | Frequency plots of canonical variables for Sed 1 and Sed 3.

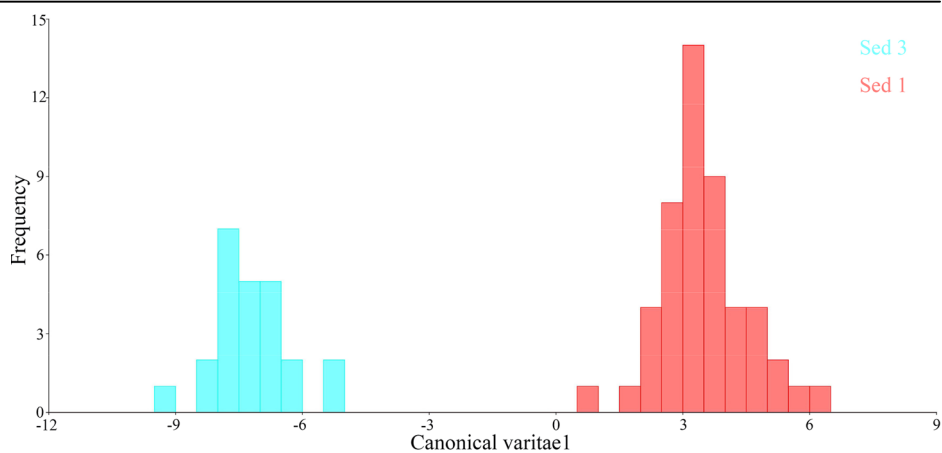
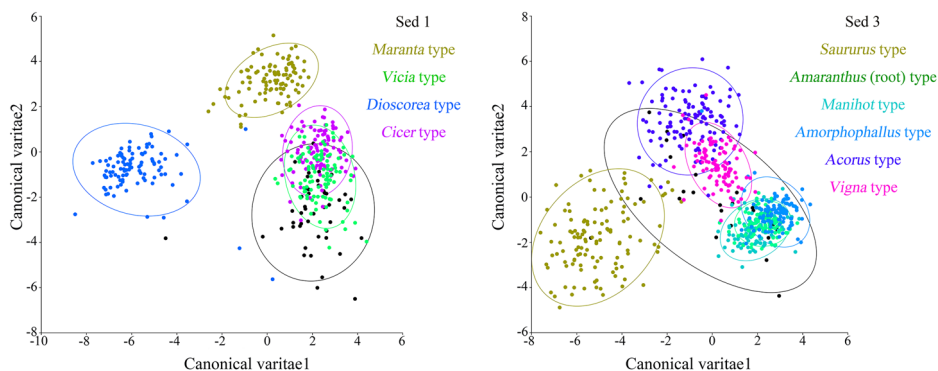


Fig. 6 | Confidence ellipses (probability = 0.9) based on a canonical variate scatter plot of CV 1 and CV 2 for Sed 1 and Sed 3.



granules primarily came from underground storage organ types and legumina types.

SVM prediction

A Support Vector Machine (SVM) analysis was employed to examine and categorize starch granules. The prediction results from the SVM (Table 4) indicate potential sources for the starch granules found in H13 soil (Sed 1), with the analysis suggesting a higher likelihood of these granules originating from *Dioscorea* type, *Maranta* type, *Cicer* type, and *Vicia* type. In contrast, the starch granules identified on H13 lithic artifacts (Sed 3) are most likely associated with *Amaranthus* (root) type, *Dioscorea* type, *Acorus* type, *Manihot* type, *Amorphophallus* type, *Saururus* type, and *Vigna* type. However, it should be noted that these identifications represent probabilistic inferences rather than definitive determinations of plant species. To accurately identify the starch granules and eliminate soil contamination in Sed 3 samples, the SVM model results highlight plant taxa likely derived from soil sediments. The results indicate that *Amaranthus* (root) type, *Dioscorea* type, *Acorus* type, *Manihot* type, *Amorphophallus* type, and *Saururus* type may be considered positive taxa, with model accuracy greater than or equal to 92% (Table 4). It should be noticed that although the *Amaranthus* (root) type, *Dioscorea* type, and *Manihot* type appears in the prediction results of Sed 3, it does not necessarily indicate the existence of *Amaranthus* type, *Dioscorea* type and *Manihot* type, but rather a high degree of similarity between the starch granule morphologies of *Amaranthus* type, *Dioscorea* type and *Manihot* type and these starch granule samples. Therefore, it is necessary to exclude from the discussion the three plants of non-China origin, namely *Amaranthus spinosus* (root), *Dioscorea alata* and *Manihot esculenta* Crantz.

Discussions

Lithic artifacts serve as crucial carriers for studying the subsistence practices of prehistoric humans. Residues adhering to stone tool can reflect the ancient humans' use of stone tools and various resources, as well as their livelihood patterns. Extracting and identifying starch granules from stone tools provides direct evidence of ancient tool usage, clarifies the specific functions and purposes of stone artifacts, and offers vital clues for researching the dietary structures of prehistoric populations.

By extracting and identifying the residues from stone tools excavated from H13 of Fenghuangzui Site, combined with the stone tool types, starch granules, and other remains discovered in the ash pit, we can not only gain insight into the specific ways the Fenghuangzui ancestors used stone tools and their utilization of plant food resources at the time, but also understand the formation and characteristics of H13.

Diverse food resources: Experimental results show that the starch granules on the surface of stone tools bear a high degree of similarity to those of root and tuber plants. The discovery of rhizome starch granules reflects the diversity of food sources of residents in the Fenghuangzui site.

Table 4 | Prediction results in Sed 1 and Sed 3

Plant type	Count (Sed 1)	Count (Sed 3)	Model accuracy (%)
<i>Dioscorea</i> type	1		97.5
<i>Maranta</i> type	11		95
<i>Cicer</i> type	7		90.62
<i>Vicia</i> type	2		90.62
<i>Amaranthus</i> (root) type		2	100
<i>Dioscorea</i> type		7	100
<i>Acorus</i> type		2	95
<i>Manihot</i> type		2	94.44
<i>Amorphophallus</i> type		1	92.86
<i>Saururus</i> type		2	92.11
<i>Vigna</i> type		1	90.62

Rhizome plants, including potatoes, yams, and taros, whose edible parts are roots or stems, refer to plants with abnormal underground tuberous parts to store nutrients. Rhizomes are typical edible plant resources that prehistoric people could find in the wild. Although these plant sources are rich in starch, their fragile nature makes them difficult to preserve, which contributes to their rarity in surface flotation collections. Additionally, these plants typically produce fewer phytoliths (according to Piperno)³⁵, making it more likely for starch granules to be preserved and identified in archeological residue samples (as noted by Torrence)³.

In the early and middle stages of the Neolithic Age in China, and even in some areas during the Late Neolithic Age, the practice of gathering coexisted alongside agriculture, forming a crucial part of local livelihoods. The interplay between ecological resources and gathering practices in dietary patterns was shaped by temporal and regional ecological factors. The presence of starch granules from roots and tubers at multiple prehistoric sites across China suggests that these foods played an essential role in Neolithic diets (as documented by Li et al.³⁶; Sun et al.⁷; Wan et al.³⁷; Wu et al.³⁸; Zhang et al.³⁹; Zhao et al.⁴⁰; Liu et al.)⁴¹.

In a word, our analysis of starch granules on the stone tools at the Fenghuangzui site indicates that the economic connotation of agriculture was extremely rich at that time, and wild plants such as tubers were indispensable food resources for the activities of the Fenghuangzui ancestors more than 4000 years ago.

Use of stone tools: Research shows that starch granules were found on several tools with cutting edges, including stone adze (H13②:73), core tools (H13①:3, H13②:18, H13②:56 and H13②:83) and flake tools (H13②:6 and H13①:72). In further analysis, the starch granules in this group were identified as *Acorus* type, *Amorphophallus* type and *Saururus* type. We believe that people at that time primarily used these stone tools with cutting edges as

the main use area to process the wild rhizome plants they obtained, such as harvesting, cutting, and processing *Acorus tatarinowii*, *Amorphophallus paeoniifolius* and *Saururus chinensis*.

Notably, no starch granules were found on the surface of the grinding stone fragment (H13⑤). The extensive weathering of the lithic surface prevents the identification of the raw material type. Three possible explanations exist for the absence of starch granules: the lithic artifacts may have been unused; residues on the surface could have been destroyed during post-depositional processes; or the artifacts may have been used for non-plant materials.

Properties and formation of H13: It can be seen that there is only one lithic artifact (Core tool 1, H13③:3) that was excavated from the upper stratum, while the rest were found in the lower stratum. The research shows that the upper stratum is yellowish brown soil, and most of the unearthened pottery is broken pottery pieces, with few stone tools and animal bones, and the relics are scattered and irregular. There are many complementary pottery unearthened in the lower stratum, and the distribution of these pottery has certain rules. There are also many animal bones and stone tools unearthened in the lower layer. Based on the study of pottery, stone tools and animals and plants, it can be concluded that the formation of H13 lower stratum is the result of multiple dietary activities by ancient people here, and the pottery, stone tools and animal bones used in each activity will be left in the pit, and the upper stratum should be formed after the ash pit was abandoned.

The study of starch granules on the lithic artifacts from the Fenghuangzui Site indicates the diversity of food resources among the residents at that time. In addition to rice and millet, they also collect local wild rhizome plants for consumption, and stone tools are used by them to cut and process these plants. Combined with other artifacts discovered from H13, such as pottery, animal bones, ash, and carbonized plant seeds, it can be concluded that the starch granules obtained from stone tools are related to the food preparation practices of Fenghuangzui residents in their daily lives. These stone tools were discarded in H13 after use. This conclusion helps to improve the understanding of paleobotany in the middle reaches of the Yangtze River, and also provides important clues for understanding human life in the region more than 4000 years ago.

Data availability

All data supporting the conclusions of this article can be obtained from the corresponding authors, Ying Guan and Xin Wang, upon reasonable request.

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References

- Zhao, Z. Origin of agriculture and archaeobotanical works in China. *Agric. Hist. China* **39**, 3–13 (2020).
- Yang, X., Lu, H. & Xia, Z. Zhiwu Dianfenli Fenxi zai Kaoguxue zhong de Yingyong. *Archaeol. Cult. Relics* **3**, 87–91 (2006).
- Torrence, R. & Barton, H. *Ancient Starch Research* (Left Coast Press, 2006).
- Ma, Z. et al. Plant microremains provide direct evidence for the functions of stone knives from the Lajia site, northwestern China. *Chin. Sci. Bull.* **59**, 1151–1158 (2014).
- Wang, J. et al. Revealing a 5,000-y-old beer recipe in China. *Proc. Natl. Acad. Sci. USA* **113**, 6444–6448 (2016).
- Liu, L. et al. Harvesting and processing wild cereals in the Upper Palaeolithic Yellow River Valley, China. *Antiquity* **92**, 603–619 (2018).
- Sun, Q. et al. Starch grain analysis of the grooved basin from the Lingjatan site, Hanshan County, Anhui Province. *Acta Anthropol. Sin.* **38**, 132–147 (2019).
- Liu, L. et al. Analysis on pottery residue of the Late Yangshao culture in Xinjie Site of Lantian, Lantian: new evidence of Guya beer brewing. *Agric. Archaeol.* **1**, 7–15 (2018).
- Wang, Q., Wang, Q. & Li, M. The phytophagous diet has been revealed by starch grain analysis from stone tools and pottery at Xijincheng Site, Bo' ai County, Henan Province: the cultivation of the tribe Triticeae. *Agric. Hist. China* **34**, 3–11 (2015).
- Ma, Z. et al. Early millet use in West Liaohe area during early-middle Holocene. *Sci. Sin.* **46**, 918–925 (2016).
- Song, Y., Shi, J. & Liu, L. The origins of millet agriculture in North China from the evidence on the grinding stones at Locality S9 of Shizitan Paleolithic Site in Shanxi Province. *Agric. Hist. China* **32**, 3–8 (2013).
- Yang, X. & Jiang, L. Starch grain analysis reveals ancient diet at Kuahuqiao Site, Zhejiang Province. *Chin. Sci. Bull.* **55**, 596–602 (2010).
- Yang, Y. et al. Plant resources utilization at the Tanghu Site during the Peiligang Culture period based on starch grain analysis, Henan Province. *Quat. Sci.* **35**, 229–239 (2015).
- Liu, L. et al. The origins of specialized pottery and diverse alcohol fermentation techniques in Early Neolithic China. *Proc. Natl. Acad. Sci. USA* **116**, 12767–12774 (2019).
- Liu, L., Wang, J. & Liu, H. On the brewing function of the Early Yangshao period Jiandiping pointed-based bottles from the Banpo and Jiangzhai Sites. *Archaeol. Cult. Relics* **2**, 110–122 (2021).
- Zhao, Y. & Liu, L. On the brewing technique of the Yangshao culture in the Longdong area. *Cult. Relics Cent. China* **1**, 49–63 (2021).
- Li, Z., Wu, T. & Tian, H. Neolithic site of Fenghuangzui in Xiangyang, Hubei Province. *Pop. Archaeol.* **1**, 12–15 (2021).
- Shan, S. et al. Brief excavation report on Ash Pit H13 of Shijiahe culture at Fenghuangzui Site in Xiangyang of Hubei Province. *Jiangnan Archaeol.* **6**, 57–71 (2024).
- The Institute of Archaeology, Chinese Academy of Social Sciences. *Chinese Archaeology: Neolithic* (China Social Sciences Press, 2010).
- Luo, Y. et al. The means of livelihood economy in the Pre Qin Period, in the middle reaches of the Yangtze River. *Cult. Relics South. China* **4**, 205–220 (2019).
- Zhao, Z. Origin of agriculture and archaeobotanical works in China (Continuou). *Agric. Hist. China* **39**, 3–9 (2020).
- Gu, H. Hunan Lixian Chengtoushan yizhi chutude xinshiqishidai shuidao jiqi leixing. *Archaeology* **8**, 81–89 (1996).
- Yang, Y. et al. Phytolith evidence for the prehistoric agriculture development at the Qujialing Site in Jingmen, Hubei Province. *Quat. Sci.* **40**, 462–471 (2020).
- Khan, M. et al. Plant foods consumed at the Neolithic site of Qujialing (ca. 5800–4200 BP) in Jiangnan Plain of the middle catchment of Yangtze River, China. *Front. Plant Sci.* **13**, 1009452 (2022).
- Zhao, J. *Analysis of Starch Residues from Stone Excavators Excavated from Gouwan Site*. Master's thesis, Zhengzhou University (2018).
- Pearsall, D. M., Chandler-Ezell, K. & Zeidler, J. A. Maize in ancient Ecuador: results of residue analysis of stone tools from the Real Alto site. *J. Archaeol. Sci.* **31**, 423–442 (2004).
- Guan, Y. et al. Plant use activities during the Upper Paleolithic in East Eurasia: evidence from the Shuidonggou Site, Northwest China. *Quat. Int.* **347**, 74–83 (2014).
- Barton, H., Torrence, R. & Fullagar, R. Clues to stone tool function re-examined: comparing starch grain frequencies on used and unused Obsidian artefacts. *J. Archaeol. Sci.* **25**, 1231–1238 (1998).
- Kealhofer, L., Torrence, R. & Fullagar, R. Integrating phytoliths within use-wear/residue studies of stone tools. *J. Archaeol. Sci.* **26**, 527–546 (1999).
- Barton, H. & Torrence, R. Cooking up recipes for ancient starch: assessing current methodologies and looking to the future. *J. Archaeol. Sci.* **56**, 194–201 (2015).
- Guan, Y. et al. Plant residue analysis method of stone artifacts in the laboratory: based on the Shuidonggou lithic materials. *Acta Anthropol. Sin.* **29**, 395–404 (2010).
- Guan, Y. et al. Plant diet during the Pleistocene-Holocene transition in northwest China: evidence from starch remains from Pigeon Mountain site in Ningxia Province. *Quat. Int.* **559**, 110–118 (2020).

33. Zhang, X. et al. Ancient starch remains reveal the vegetal diet of the Neolithic Late Dawenkou culture in Jiangsu, East China. *Front. Ecol. Evol.* **9**, 722103 (2021).
34. Zhang, X. et al. Plant consumption by Early-Middle Neolithic Peoples in Guangxi, South China: archaeobotanical evidence from the Dingsishan Site. *Front. Earth Sci.* **10**, 879908 (2022).
35. Piperno, D. R. & Holst, I. The presence of starch grains on prehistoric stone tools from the humid neotropics: indications of early tuber use and agriculture in Panama. *J. Archaeol. Sci.* **25**, 765–776 (1998).
36. Li, M. et al. Ancient starch grains from ash pits of Fengtai Site Qinghai Province and their application in archaeology. *Quat. Sci.* **30**, 372–376 (2010).
37. Wan, Z. et al. Plant resource utilization at Sheshangtou Site in Jiangxi Province based on starch grain analysis. *Prog. Geogr.* **31**, 639–645 (2012).
38. Wu, W. et al. Shandong Zhucheng Liuji Zhuangzi Yizhi Mopan, Mobang Dianfenli Fenxi Chubu Jieguo. *Cult. Relics South. China* **4**, 201–206 (2017).
39. Zhang, Y. et al. Identification and analysis of starch granules on the surface of the slabs from Peiligang Site. *Quat. Sci.* **31**, 891–899 (2011).
40. Zhao, Z., Dang, H. & Jun, G. Analysis of starch grain from stone tools and plant utilization of plant food research at Yuhuangding Site, Jining. *Agric. Hist. China* **40**, 45–55 (2021).
41. Liu, L. et al. The origins of specialized pottery and diverse alcohol fermentation techniques in Early Neolithic China. *Proc. Natl. Acad. Sci. USA* **26**, 12767–12774 (2019).
42. Archaeology Department of Peking University, Zhumadian Municipal Office for the Preservation of Ancient Monuments. *Yangzhuang, Zhumadian—Cultural Remains and Environmental Information of the Middle Holocene in the Upper Reaches of the Huaihe River* (Science Press, 1998).
43. Jiang, Q. & Zhang, J. Phytolith evidence for rice cultivation during prehistoric periods at Baligang Site of Baizhuang, Dengzhou City, Henan Province. *Acta Sci. Nat. Univ. Pekinensis* **34**, 66–71 (1998).
44. Deng, Z. & Gao, Y. Analysis of plant remains excavated from the Baligang Site in Dengzhou, Henan Province. *Cult. Relics South. China* **1**, 156–163 (2012).
45. Wu, C., Liu, H. & Zhao, Z. Discussion prehistoric agriculture of Jiangnan Plain from flotation results of Yeji Temple Site in Xiaogan. *Cult. Relics South. China* **4**, 65–69 (2010).
46. Wu, C. *Analysis of Plant Remains from Qinglongquan Site in Yun County, Hubei Province*. Master's thesis, Graduate School of Chinese Academy of Social Science (2011).
47. Wang, Y. et al. 2007 Flotation results and analysis of Gouwan Site of Henan Xichuan. *Sichuan Cult. Relic* **2**, 80–92 (2011).
48. Deng, Z., Liu, H. & Meng, H. Analysis of plant remains excavated from Sanfangwan and Tanjialing Sites of Shijiahe Ancient City, Tianmen City, Hubei Province. *Archaeology* **1**, 91–99 (2013).
49. Tang, L. *Archaeobotanical Observations on the Dynamics of Agricultural Production from the Late Neolithic to Bronze Age in the Jiangnan Area*. PhD thesis, Graduate School of Chinese Academy of Social Science (2014).
50. Tang, L. et al. Research on charred plant remains from the Xiezidi Site in Daye City, Hubei Province. *Quat. Sci.* **34**, 97–105 (2014).
51. Tang, L. et al. Research on the neolithic agriculture in the region of the northwest of Hubei Province and the southwest of Henan Province from the flotation results of Dasi Site, Yun County, Hubei Province. *Xibukaogu* **2**, 73–85 (2016).
52. Tang, L., Luo, Y. & Zhao, Z. Research on charred plant remains from the Chengzishan Site. *Ezhou. Jiangnan Archaeol.* **2**, 108–115 (2017).
53. Fan, X. & Wu, R. Analysis of botanic remains from Sunjiagang Site, Li County. *Jiangnan Archaeol.* **3**, 104–109 (2018).
54. Tang, L. et al. Research on the mode of mountain subsistence in the period of Qujialing culture—an example of Mulingtou Site in Baokang, Hubei Province. *Cult. Relics South. China* **5**, 189–199 (2019).
55. Tian, J. et al. Research on the charred plant remains unearthed from the Jijiawan Site in Fang County, Hubei Province. *Cult. Relics South. China* **5**, 180–188 (2019).
56. Yao, L. et al. Analysis of charred plant remains from the Qujialing Site in Jingmen, Hubei Province. *Jiangnan Archaeol.* **6**, 116–124 (2019).
57. Tang, L. et al. The identification and study of prehistoric plant remains from the Zoumaling Site in Shishou, Hubei. *Jiangnan Archaeol.* **3**, 109–115 (2021).

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Author contributions

Yinghua Li, Ying Guan and Xin Wang conceived the study. Wentai Lou, Feng Wang and Xuan Wei conducted the experiments and analyzed the data. Wentai Lou was a significant contributor to the writing of the manuscript. Yinghua Li, Ying Guan and Xin Wang revised the manuscript. All authors reviewed and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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