

Thirty thousand-year-old evidence of plant food processing

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European Paleolithic subsistence is assumed to have been largely based on animal protein and fat, whereas evidence for plant consumption is rare. We present evidence of starch grains from various wild plants on the surfaces of grinding tools at the sites of Bilancino II (Italy), Kostenki 16–Uglyanka (Russia), and Pavlov VI (Czech Republic). The samples originate from a variety of geographical and environmental contexts, ranging from northeastern Europe to the central Mediterranean, and dated to the Mid-Upper Paleolithic (Gravettian and Gorodtsovian). The three sites suggest that vegetal food processing, and possibly the production of flour, was a common practice, widespread across Europe from at least ~30,000 y ago. It is likely that high energy content plant foods were available and were used as components of the food economy of these mobile hunter-gatherers.

flour | Upper Paleolithic | grindstones | diet | starch grains

Currently evidence for the Paleolithic human diet is obtained from bone chemistry, dental microwear, and zooarchaeological and archaeobotanical remains (1, 2). For a variety of taphonomic and analytical reasons, the last form of evidence is rare at Paleolithic sites, and Paleolithic populations are primarily considered as hunters. Previous studies at Dolní Věstonice, Klisoura, Kebara, and Ohalo (3–7) identified plant remains, plausibly representing an important element of the diet, and the last-mentioned site also documents routine processing of wild cereals and effective methods for cooking ground seeds. A number of Upper Paleolithic sites also yielded grindstones (8–10), some of which may have served for grinding plant tissue, whereas others were used for grinding ochre (11). Here we report on starch grains recovered on grinding stones from three Mid-Upper Paleolithic (Gravettian or Gorodtsovian) sites across Europe: Bilancino II in Italy (12), Kostenki 16 in Russia (13), and Pavlov VI in the Czech Republic (14).

The Sites

Bilancino II (Mugello Valley, Italy) is an open-air settlement located on an alluvial terrace along the Sieve River, ~238 m above sea level, in the vicinity of a wetland where substantial numbers of hygrophilic plants were palynologically identified (15). The area was dominated by grasses and sedges (Gramineae and Cyperaceae). Analysis of the spatial distribution of finds throughout the 120 m² of the living floor and the lithic refittings indicate a single period of occupation of the site (Fig. S1), belonging to the Gravettian. This phase fits with the three accelerator mass spectrometry (AMS) ¹⁴C dates, the most reliable of which is the oldest (from a hearth): 28,298 ± 301 calibrated (cal) BC (Beta-106549) (12).

Kostenki 16 (Uglyanka), a part of the Kostenki site complex, is an open-air site located on a small promontory formed by the broad Pokrovsky Valley, Russia, on the main left branch of the valley (Fig. S2). Pollen analysis indicates an unstable climatic al-

ternation during the transition from warmer to colder interstadial conditions and a limited extent of forest (13). On the basis of its stratigraphic position within the upper humic bed, the cultural layer of the site belongs to the middle chronological group of the Kostenki sites. Typologically, the lithic assemblage forms an independent Upper Paleolithic entity called the Gorodtsovian, and it is dated by a series of radiometric dates (16); cal BC radiocarbon dates for Kostenki 16 (Uglyanka) are 28,087 ± 253 (LE-ΠΕ-1431), 30,106 ± 953 (LE-5270), 29,464 ± 562 (GIN-8033), 30,786 ± 520 (GIN-8031), and 31,904 ± 698 (LE-74126).

Pavlov VI (southern Moravia, Czech Republic) is a newly discovered site of the Dolní Věstonice–Pavlov–Milovice complex, located on the northeastern slopes of the Pavlov Hills, at an altitude of ~200 m a.s.l., above what was previously the Dyje River floodplain. Pollen analysis from nearby sites of the same complex and age (Dolní Věstonice, Bulhary) indicates extensive pine and birch forest with Cyperaceae and Gramineae as the dominant herbs (17). Pavlov VI represents an isolated hunting site of ~5 m in diameter, with the remains of two mammoths, a central hearth, and surrounding pits (Fig. S3). This unit belongs to the earlier Gravettian (Pavlovian) as represented at the nearby larger sites. This typology matches with the ¹⁴C dates obtained from Pavlov VI: 28,985 ± 337 cal BC (GrA 37627), 29,078 ± 339 cal BC (GrA 37628), and 29,482 ± 288 cal BC (OxA 18306).

Lithic Use-Wear Analysis. At Bilancino II, two sandstone cobbles were analyzed; the larger artifact was used as a grindstone (passive element) and the smaller one as a grinder pestle (active element) (Fig. 1A). The grindstone “A” (13.6 cm long) has asymmetric deep wear on the surface, which appears abraded and leveled due to resting percussion (8). The grinding was evidently performed using little force and was adapted to the softness of the worked material (mainly cattail rhizomes) (18). Pestle “B” (11.4 cm long) reveals two areas of use wear: surface b, where the top grains are leveled and abraded by diffuse thrusting percussion, and rounded extremity b1, showing percussion impact related to thrusting percussion.

Use-wear analysis of the associated lithic industry revealed organic residue, probably of vegetable origin, on the active edge of some Noailles burins. On the basis of experimental archaeology and ethnoarchaeological analogies, these highly specialized tool types were probably used for the separation of the vegetable fibers from cattail (*Typha*) leaves (12).

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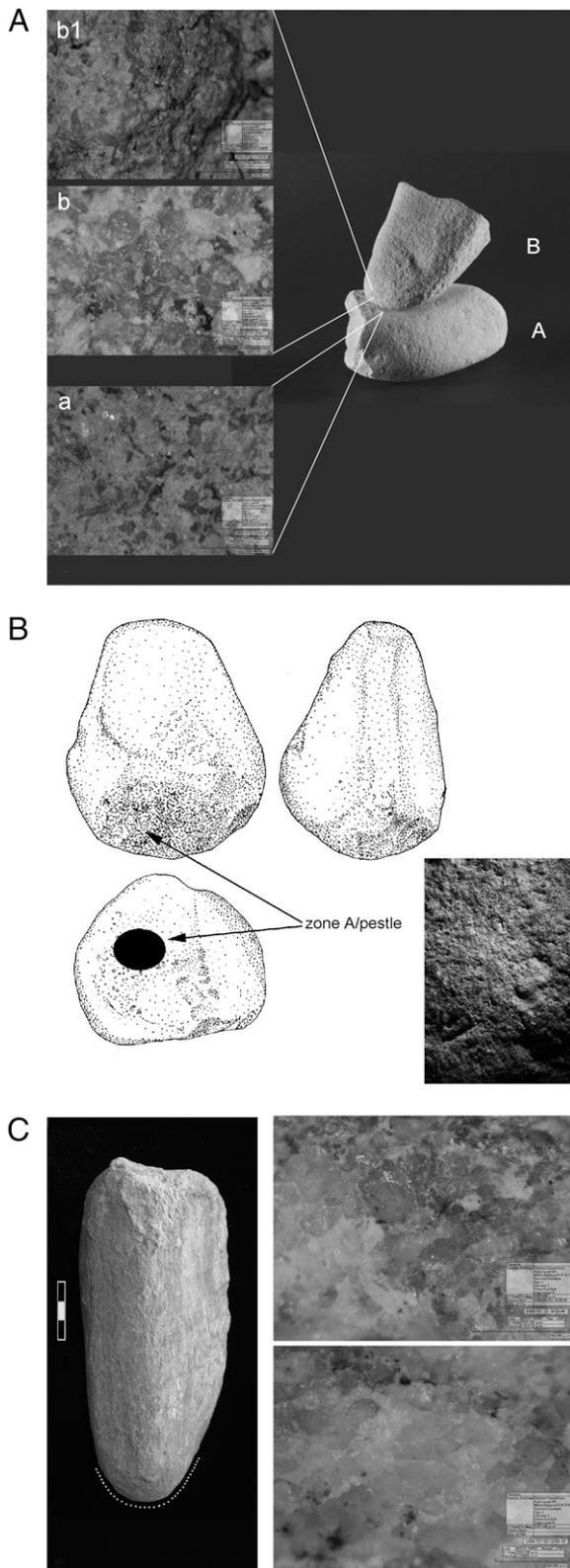


Fig. 1. (A) Bilancino II grindstone and pestle grinder and wear traces. (B) Kostenki 16-Uglyanka, pestle and wear traces (C) Pavlov VI pestle grinder and wear traces.

At Kostenki 16, we analyzed a pestle-like tool made of a coarse-grained cobble with a trapezoid/subpyramidal/flat-convex form sizing $11.1 \times 9.2 \times 7.7$ cm. Use-wear traces identified on this item

are related to three different functions (pestle, anvil, and hammer) (Fig. S4). Zone A (Fig. 1B) shows that the lower broad, slightly convex end of the tool was used for grinding vegetal materials, moving it like a pestle. Traces of use are concentrated mostly on a convex extremity and occasionally occur on the lateral edges. This location suggests that grinding took place on the slightly concave surface of a soft stone slab (not in a mortar, because there are no further traces on the lateral faces).

At Pavlov VI, we analyzed a pestle grinder (Fig. 1C) with a rounded (pointed) end that was worked with a thrusting percussion. On the edge merging toward the lower surface of this rounded end, there is leveling of the top grains, associated with some short striations, as also noted on the Bilancino II pestle grinder (12, 18). Some fissuring and fracturing within the largest grains is also evident. Both grinding and pounding appear to have been used simultaneously during the processing.

Starch Analysis. At Bilancino II, a large number of starch grains of different sizes and shapes were observed both on the grindstone and on the pestle grinder (Fig. 2 and Figs. S5 and S6) (12). The preservation of the grains is not always good, which can be explained in particular for the grindstone where the traces illustrate intensive and prolonged use. On both artifacts the best represented grains are those referred to as morphotypes a and d (Fig. 2A). The starch grains of morphotype a (Fig. 3A), which are slightly angular to angular without evident centric hila, might belong to Gramineae. Among these, the grains, which are slightly angular, with hardly visible centric, point-shaped hila and adequate dimensions (in the sample measuring $9\text{--}14\ \mu\text{m}$), appeared very similar to those of *Brachypodium* (Fig. 3G) or related genera. These grasses have caryopses that are easy to grind and can grow in environments similar to that of Bilancino II (15). Morphotype d consists of grains in a poor state of preservation, with circular-elliptic contours and without an evident hilum (Fig. 3B). It is not possible to make an attribution, but it could be suggested that these are grains, possibly damaged by grinding, originally belonging to morphotype e. The morphotype e (Fig. 2A) consists of grains of circular-elliptic contours with a centric Y-shaped hilum; in the sample, those ranging from 13 to $18\ \mu\text{m}$ (Fig. 3C) may be attributed to *Typha* spp., which is listed in the pollen spectra of Bilancino II (15) and has starch-rich rhizomes (Fig. 3H and Fig. S5). Considering the size distribution of the morphotype e grains, the mode of the measured values is closer to that calculated for *Typha angustifolia* (narrow leaf cattail) than to that of *Typha latifolia* (broadleaf cattail) (Table 1).

A few small angular-compounds grains recovered on the pestle (Fig. 2A, morphotype c), with single grains ranging from 4 to $6.5\ \mu\text{m}$ in size, could represent *Sparganium* (bur reed) (Fig. 3I). The similarity of the wear traces and the types of the starch grains recovered on the two artifacts at Bilancino (Fig. 1A) confirmed that they were used together.

At Kostenki 16, only a few starch grains were recovered on the surface of the pestle (probably due to previous washing). The majority of the grains were circular/elliptic, and all were in a poor state of preservation (Fig. 2B, morphotype k). They ranged in size from 2.5 to $37\ \mu\text{m}$. The highest frequency is in the range from 5 to $10\ \mu\text{m}$. The latter may be tentatively attributed to *Botrychium* (moonworts), a fern that was widespread around the site (13) and is characterized by a starch-rich root that is easy to grind. Nevertheless, the scarcity of the grains makes it impossible to arrive at a definitive source.

At Pavlov VI, among the various nonflaked stone tools examined, only one of the cobbles (18×8.4 cm) provides evidence of vegetal residues and wear traces. Many starch grains in a good state of preservation (Fig. 3D–F and Fig. S5) were found on the surface of the pestle grinder. The grains vary in size (from 3 to $30\ \mu\text{m}$) and many of them present a well-defined centric hilum (Fig. 2C). Occasionally, lamellae (the strata formed during the starch grain growth, Fig. 3F) could also be observed. Many grains are angular

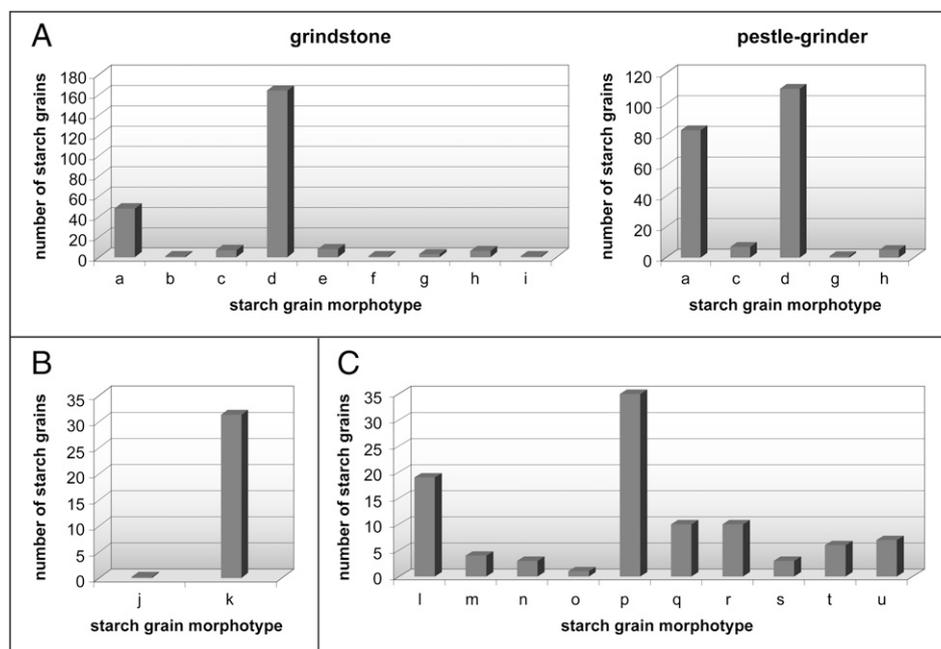


Fig. 2. (A) Bilancino II, starch grains from grindstone and pestle grinder. a: angular, size range 3–22 μm , hilum not evident. b: angular, size 23 μm , hilum star shaped. c: angular–compound, size range 4–32 μm , hilum not evident. d: circular–elliptic, size range 2–42 μm , hilum not evident. e: circular–elliptic, size range 13–25 μm , hilum Y shaped. f: circular–elliptic, size 24 μm ; hilum X shaped. g: elliptic, size range 16–40 μm , hilum linear. h: reniform, size range 10–32 μm , hilum not evident. i: reniform, size 27 μm , hilum V shaped. (B) Kostenki 16–Uglyanka, starch grains from pestle. j: angular–compound, size 7 μm , hilum not evident. k: circular–elliptic, size range 2–37 μm , hilum not evident. (C) Pavlov VI starch grains from pestle grinder. l: angular, size range 3–15 μm , hilum not evident. m: angular, size range 11–14 μm , hilum Y shaped. n: angular, size range 6–11 μm , hilum star shaped. o: angular, size 15 μm , hilum linear. p: circular–elliptic, size range 3–30 μm , hilum not evident. q: circular–elliptic, size range 5–15 μm , hilum Y shaped. r: circular–elliptic, size range 3–17 μm , hilum X shaped. s: circular–elliptic, size range 8–10 μm , hilum star shaped. t: circular–elliptic, size range 8–18 μm , hilum linear. u: circular–elliptic, size range 4–18 μm , hilum circular.

(Fig. 3D) or slightly angular with centric hila, generally hardly visible (morphotype l); this morphotype may be attributed to several taxa and identification is not possible at present because it calls for more extensive archaeobotanical data from the site. Most of the grains are circular elliptic, ranging from 15 to 17 μm . The circular-elliptic grains without an evident hilum (Fig. 3E, morphotype p) most probably also originate from more than one plant. The circular-elliptic grains with a Y-shaped hilum (Fig. 3F, morphotype q) are similar to those of *Typha* (cattail) and might belong to the same species as in Bilancino II; nevertheless, it should be noted that the occurrence of this plant is only occasionally recorded in the area (17). Other starch grains are similar to those of *Botrychium* (moonworts) (Fig. 3J), which is in the pollen spectra of the Mo-

ravian Upper Paleolithic (17, 19). The variety of the starch grains confirms the use of flour of numerous plant species, in accordance with the floral richness of the site.

Discussion and Conclusions

European Paleolithic populations are generally considered to have been predominantly carnivorous, because the evidence for plant subsistence is limited. However, ethnographic analogy and nutritional studies stress the need for a high percentage of nonprotein macronutrients (which can include plant foods) to integrate the diet. We are now able to add evidence for plant food processing, on the basis of the recovery of flour residues on coarse (heavy-duty) tools across Europe up to 30,000 y ago:

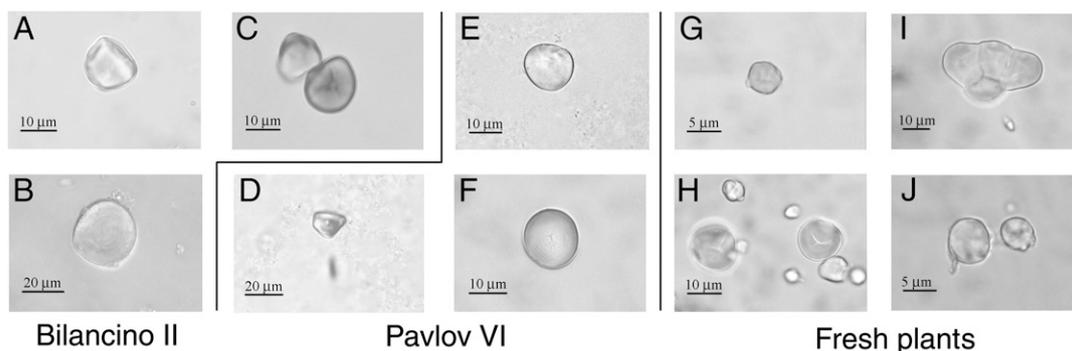


Fig. 3. Starch grains. (A) From Bilancino pestle grinder: morphotype a, angular grain, hilum not evident. (B) From Bilancino pestle grinder: morphotype d, circular–elliptic, hilum not evident. (C) From Bilancino grindstone: morphotype e, circular–elliptic grain, hilum Y shaped. (D) From Pavlov pestle grinder, morphotype l, angular grain, hilum not evident. (E) From Pavlov pestle grinder: morphotype p, circular–elliptic, hilum not evident. (F) From Pavlov pestle grinder: morphotype q, circular–elliptic grain, hilum Y shaped. (G) *Brachypodium ramosum* (fresh plant). (H) *Typha latifolia* (fresh plant). (I) *Sparganium erectum* (fresh plant). (J) *Botrychium ternatum* (fresh plant).

Table 1. Distinctive features of the starch grains of reference plants

Plant	Part of plant processed	General shape	Diameter/main axis, μm			Hilum
			Range	Media	Moda	
Ophioglossaceae: <i>Botrychium ternatum</i> (Thunb.) Sw.	Root	Simple, circular–elliptic in outline, sometimes slightly angular	5–15	7.7	7.5	Generally not evident, centric; rarely X shaped
Rosaceae: <i>Alchemilla vulgaris</i> L.	Root	Simple, circular–elliptic	3–17	6.2	5	Centric, Y shaped
Compositae: <i>Arctium lappa</i> L.	Root	Simple circular–elliptic	5–30	15	15	Not evident; extinction cross radially symmetrical
<i>Lactuca tuberosa</i> A.Chev.			13–21	17.6	17.5	
Gramineae: <i>Brachypodium ramosum</i> (L.) R. et S.	caryopsis	Simple, slightly angular or circular–elliptic	3–16	9.5	5.5	Generally hardly visible, sometimes centric, point shaped or shortly linear; extinction cross radially symmetrical
<i>Bromus secalinus</i> L.		Simple, circular–elliptic	4–10	5.7	5	Generally not evident, sometimes linear and extinction cross bilaterally symmetrical
Umbelliferae: <i>Anthriscus caucalis</i> M. Bieb.	Root	Simple, subangular	7–21	13.2	15	Generally not evident; rarely star shaped, centric; crosses radially symmetrical or asymmetrical; extra arms sometimes present
Cyperaceae: <i>Cyperus badius</i> Desf.	Seed	Simple, slightly angular or subangular	4–20	10.1	7.5	Not evident; extinction cross radially symmetrical
<i>Scirpus lacustris</i> L.			3–9	5.2	4.5	
Polygonaceae: <i>Polygonum hydropiper</i> L.	Root	Simple, subangular or angular	3–9	5.4	5	Not evident; extinction cross radially symmetrical
Sparganiaceae: <i>Sparganium erectum</i> L.	Rhizome	Compound; individual grains angular, easily separable	4–16	7.7	7	Hardly visible, centric or subcentric
Typhaceae: <i>Typha angustifolia</i> L.	Rhizome	Simple, circular–elliptic or subcircular; compound grains, 2–4 grains per group, sporadically occur. Lamellae visible in some of the larger grains	4–18	8	5	Centric, Y shaped, sometimes not evident, very rarely X shaped or linear; extinction cross radially symmetrical
<i>Typha latifolia</i> L.			3–18	10.1	11	

a grindstone and the related pestle grinder from Bilancino II (Italy), a pestle grinder from Pavlov VI (Czech Republic), and a multifunctional tool from Kostenki 16 (Ugryanka) (Russia). Investigations using starch analysis and use-wear analysis of all of these implements show that the grinding and pounding of wild food plants were performed relatively early in the Upper Paleolithic.

A large number of plant families are likely to have been involved in the diet. Generally, the reasons for choosing a plant for food are dictated by its dominance in the local vegetation, as well as by its size and appearance (20). The wide size range and the different morphologies of the starch grains recovered on the grindstone and

the pestle grinders at both Bilancino II and Pavlov VI suggest that they were used for grinding more than one plant species and possibly for other purposes.

The starch grains recovered on these objects appear to be mostly of cattail and fern. Both of these have underground storage organs (USOs) (4), they are rich in starch and, as such, they represent a significant source of carbohydrates and energy. The best-preserved grains, and hence those that are easier to identify, most likely derive from the last grinding episode. Consequently, the best-preserved grains do not necessarily belong to the most used species. On the basis of our experiments in terms of energy availability (12), the composition of cattail rhizome flour is similar

Table 2. Energy and proximate composition of *Typha* and *Triticum dicoccon* meals (per 100 g wb, standardized at 14.5% moisture)

Energy and proximate composition	<i>Typha</i> : Ryzome flour	<i>Triticum dicoccon</i> (29)	
		Whole meal	Refined flour
Energy (kcal; kJ)	266–1,128	307–1,302	329–1,394
Protein	9.1	11.9	11.0
Lipid	2.2	2.8	1.7
Total dietary fiber	17.3	10.4	4.7
Insoluble	14.1	8.2	3.0
Soluble	3.2	2.2	1.7
Soluble/total	0.18	0.21	0.36
Available/digestible carbohydrates	52.5	58.7	67.3

to that found in emmer whole meal (21) (cattail flour, kcal/kJ 266/1, 128; emmer flour, kcal/kJ 307/1,302, per 100 g wet basis (wb), standardized at 14.5% moisture) (Table 2 and *SI Methods*).

The flour would have undergone a multistep processing involving root peeling, drying, and finally grinding using specific tools (Fig. S7). After this, the flour needed to be cooked to obtain a suitable and digestible food. Studies of current human diets suggest that cooking is essential because raw food, as such, cannot supply sufficient calories (22). More specifically, the practices that we can reconstruct demonstrate knowledge in the Gravettian populations of Europe (Fig. S8) of the starch-rich portions of edible plants, combined with the ability to transform them to produce a complex dried product (flour). This would have allowed them greater independence from environmental and seasonal fluctuations.

Such a capacity for complex food plant processing could be a part of a Mid-Upper Paleolithic behavioral package (2, 23, 24), with consequences for diversified subsistence strategies and demographic changes in these populations (25).

Methods

For the use-wear analysis, selected artifacts from the three sites were analyzed using both low power and high power approaches (LPA and HPA), in addition to digital microscopy. The recognition and description of use-wear traces were carried out by means of LPA [Leika MZ6 (10–40x)] and HPA via the application to wear-trace analysis of the combined potential of the digital microscope (Hirox KH-7700), metallographic microscopy, and SEM. The terminology applied has been used in recent studies (12). The study of functioning (kinematics) and their function (processing systems) was performed

combining wear traces, experimental reconstruction, and residue analyses on the active surfaces of the four grindstones used.

For the starch grain analysis, small surfaces of each stone were selected according to the macroscopic wear traces, and they were sampled using running distilled water to remove sediment. The residues were processed following Barton et al. (26), using zinc chloride for the heavy liquid separation. Starch grains were observed through light microscopy after iodine/potassium iodide (IKI) staining (27) or under a polarizing microscope (Fig. S5). For the identification, literature (6, 28, 29) and reference materials were used, including portions of fresh plants and *exsiccata* (Table 1). However, the identification of plant starch grains is not easy, due to the scarcity of reference material and literature. When studying new environments, new reference material including all of the potential plants of interest needs to be established. The choice of the reference plants was made on the basis of all available data, particularly the pollen results from Bilancino (15) and Kostenki (30) and in the vicinity of Pavlov (17). When the identification of the pollen grains did not reach the species level, plants currently common in the environmental contexts documented in the pollen spectra were considered, following the available literature (31–45).

We used different names (letters) to indicate the morphotypes from the sites even when they were very similar. This decision was dictated by the fact that the sites are located in different areas of Europe, where the flora was possibly not the same.

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Supporting Information

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SI Methods

An experiment was carried out to check the technique for using the Bilancino grindstone and pestle grinder. We used two fragments of sandstone of a similar size and shape to the archaeological tools to grind the dried rhizomes of cattail. Flour obtained in this way is a fine, white–beige powder with a slightly sweet aroma (1).

The analysis (Table 2) shows the proximate composition of different meals of *Typha* and emmer (*T. dicoccon* Schrank) (per 100 g wb, standardized at 14.5% moisture).

Hulled wheats (einkorn, emmer, spelt), known in Italy by the common name of *farro*, are among the most ancient Triticeae cultivated in the world and have long represented a staple food.

The composition of rhizome flour is similar to the composition of emmer meal (in particular, whole meal). However, rhizome flour has a lower protein and digestible carbohydrate content and a higher dietary fiber content than emmer kernel meals.

An indirect evaluation of protein quality can be obtained through the determination of the amino acid composition, taking the essential acids in particular into consideration.

The amino acid pattern of rhizome is characterized by high levels of valine (12.1 g/100 g protein), glutamic acid (15.2 g/100 g protein), and aspartic acid (25.6 g/100 g protein) and low levels of essential amino acids such as lysine (3.4 g/100 g protein), leucine (5.7 g/100 g protein), and sulfur amino acids (1.4 g/100 g protein). From a nutritional point of view, the limiting amino acids are lysine and sulfur amino acids (chemical score 0.56–0.58, respectively). In emmer and in wheat species, the most widely represented amino acids are glutamic acid (30.0 g/100 g protein), proline (10.0 g/100 g protein), and leucine (6.5 g/100 g protein), and the limiting amino acid is lysine (chemical scores 0.47 and 0.38 for whole meal and refined flour, respectively).

The principal fatty acids of rhizome flour are linoleic (C18:2) (40% of total fatty acids), palmitic (C16:0) (35% of total fatty acids), stearic (C18:0) (9% of total fatty acids), oleic (C18:1) (6% of total fatty acids), and linolenic (C18:3) (5% of total fatty acids). This fatty acid composition presents an unsaturated/saturated fatty acid ratio close to 1, providing a higher stability versus oxidation phenomenon than emmer with an unsaturated/saturated fatty acid ratio of 4.6–4.8.

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Bilancino lithic assemblage: spatial distribution

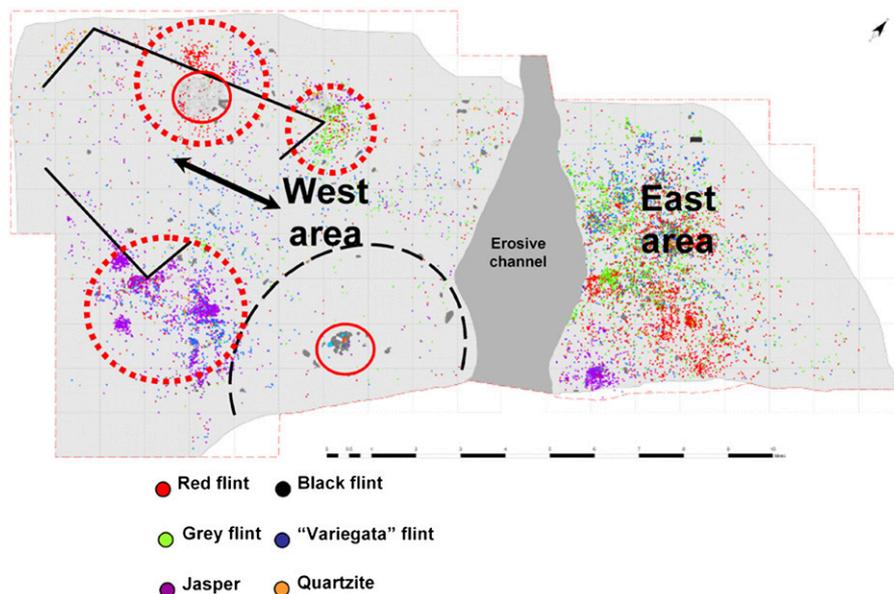


Fig. S1. Bilancino II. Spatial distribution of the lithic assemblage and the activity areas on the living floor.

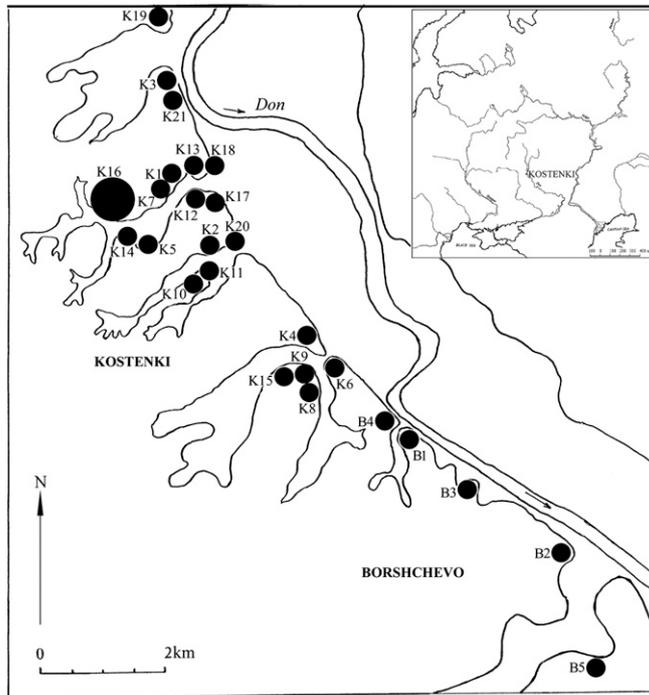


Fig. S2. Kostenki 16 (Uglyanka) in the context of Kostenki-Borshchevo sites.



Fig. S3. Pavlov VI. The living floor.

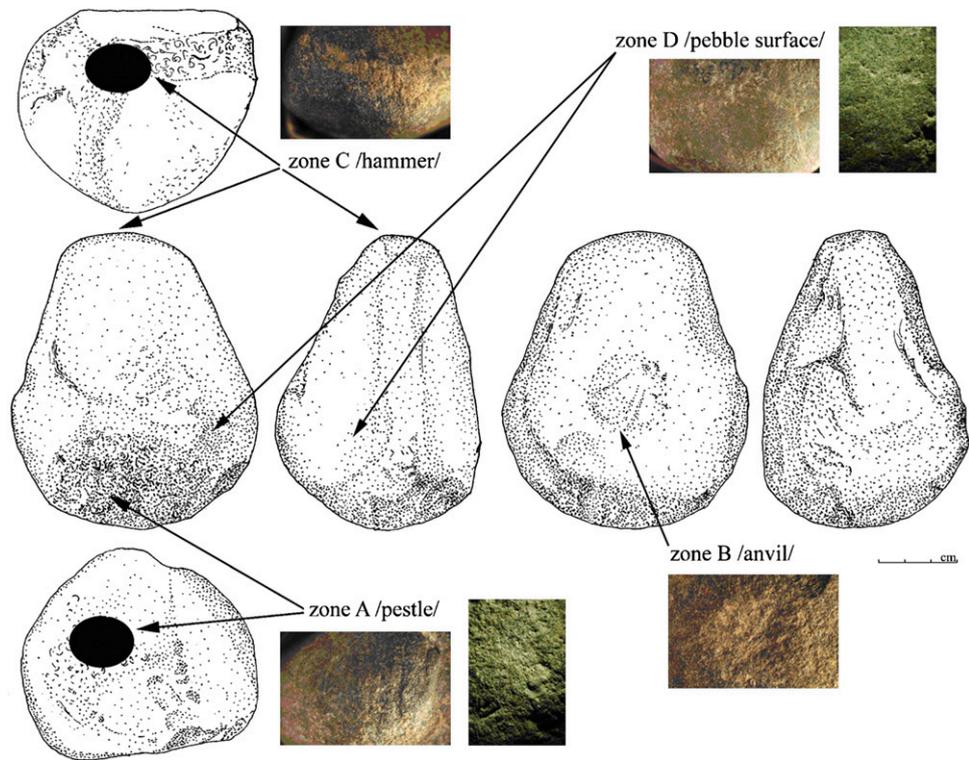


Fig. S4. Kostenki 16 (Uglyanka). The pestle grinder wear traces.

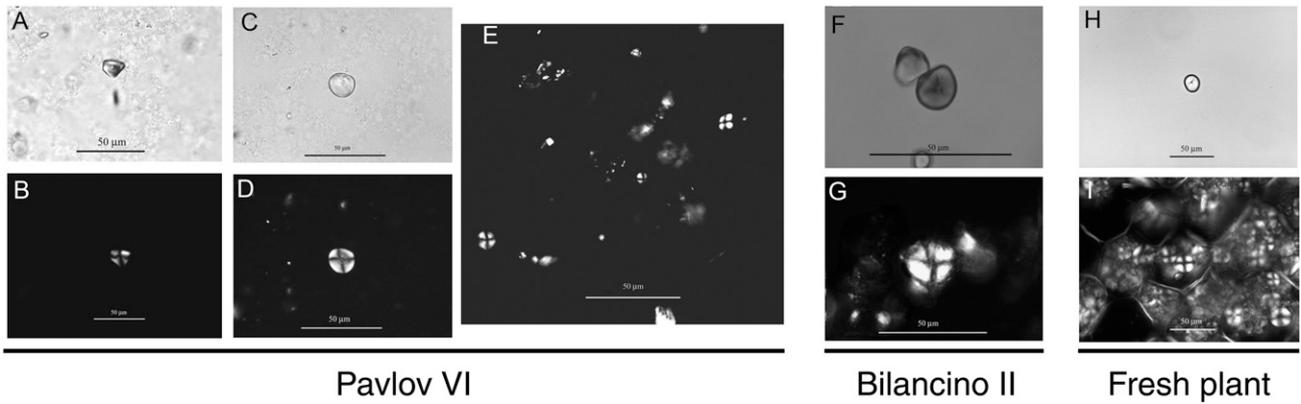


Fig. S5. Starch grains. (A) From Pavlov pestle grinder, morphotype l, angular grain, hilum not evident, polarized light. (B) From Pavlov pestle, morphotype l, angular grain, hilum not evident, polarized light. (C) From Pavlov pestle, morphotype p, circular-elliptic, hilum not evident. (D) From Pavlov pestle, morphotype p, circular-elliptic, hilum not evident, polarized light. (E) From Pavlov pestle, various circular-elliptic grains, polarized light. (F) From Bilancino grindstone, morphotype e, circular-elliptic grain, hilum Y shaped, polarized light. (G) From Bilancino grindstone, morphotype e, circular-elliptic grain, hilum Y shaped, polarized light. (H) From *Typha angustifolia* (fresh plant). (I) From the rhizome parenchyma of *Typha angustifolia* (fresh plant), polarized light.

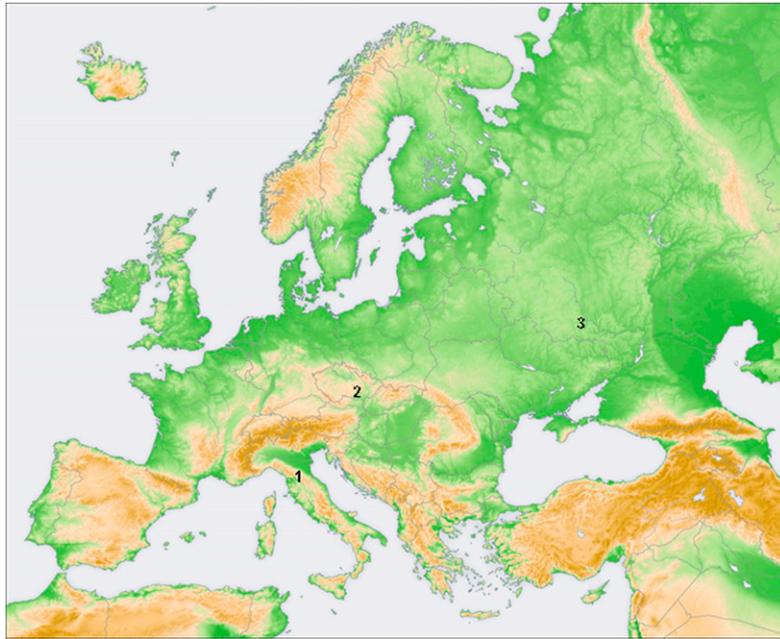


Fig. S8. Location of the three Upper Paleolithic sites in Europe: 1, Bilancino II; 2, Pavlov VI; and 3, Kostenki 16–Uglyanka.