







Research Article

Cooking in caves: Palaeolithic carbonised plant food remains from Franchthi and Shanidar

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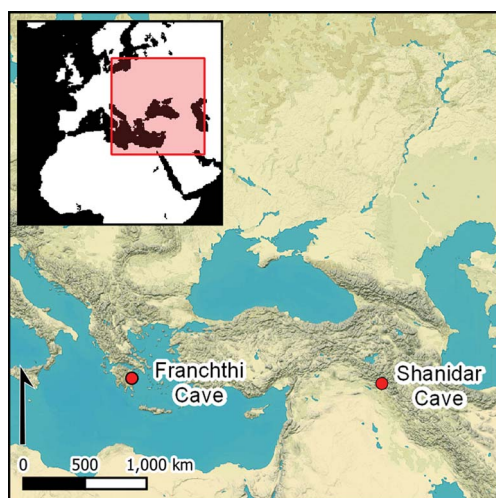
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Research on Palaeolithic hunter-gatherer diet has focused on the consumption of animals. Evidence for the use of plant foods is comparatively limited but is rapidly expanding. The authors present an analysis of carbonised macro-remains of processed plants from Franchthi Cave in the Aegean Basin and Shanidar Cave in the north-west Zagros Mountains. Microscopic examination of the charred food remains reveals the use of pounded pulses as a common ingredient in cooked plant foods. The results are discussed in the context of the regional archaeobotanical literature, leading the authors to argue that plants with bitter and astringent tastes were key ingredients of Palaeolithic cuisines in South-west Asia and the Eastern Mediterranean.

Keywords: South-west Asia, Eastern Mediterranean, Palaeolithic diet, prehistoric food preparation, hunter-gatherers, archaeobotany

Introduction

The dietary choices and food preparation technologies of Palaeolithic hunter-gatherers are the subject of much debate. Palaeolithic peoples have been portrayed, for example, as specialist hunters focusing on large mammals (Richards & Trinkhaus 2009) or as generalist foragers targeting easy-to-gather resources out of necessity, due to pressures on the availability of preferred animal prey (Stiner *et al.* 2000; Speth 2010). In this article, we focus on the dietary contribution of plant foods. In a calorie-driven interpretation of Palaeolithic diet, plants

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are categorised as ‘low-ranked’ resources, due to the time- and labour-intensive nature of gathering and processing them. Consequently, scholarly emphasis has focused on the significance of the more carbohydrate-rich plant foods that were easy to collect and prepare as potential dietary staples (Prado-Nóvoa *et al.* 2017; Hardy *et al.* 2022).

Archaeobotanical data from pre-agricultural sites in South-west Asia and the Eastern Mediterranean, however, indicate a reliance on a much wider range of plant foods than just starch-rich tubers and grasses (e.g. Martinoli 2004; Weiss *et al.* 2004; Lev *et al.* 2005; Asouti *et al.* 2018, 2020; Caracuta *et al.* 2021). Almost all sites from these regions dating to the Middle and Upper Palaeolithic and the Epipalaeolithic/Mesolithic periods, for example, provide evidence for the use of wild almonds, which contain high levels of cyanogenic metabolites that can produce hydrogen cyanide (Asouti *et al.* 2020; Caracuta *et al.* 2021). Several other plants also feature prominently in the regional archaeobotanical record, including tannin-rich wild pistachios (terebinth), wild pulses (some containing neuro-toxic compounds) and astringent wild mustards. Most of these plants require several preparation steps to leach out unpalatable and/or toxic compounds prior to consumption. The long-term and widespread use of almonds, terebinths and pulses therefore suggests that Palaeolithic foragers developed processing technologies and associated food preparation practices that enabled their routine safe consumption.

In this article, we report new evidence concerning the long-term histories of Palaeolithic plant food use and associated food preparation practices from two multi-period sites: Franchthi Cave (Greece) and Shanidar Cave (Iraqi Kurdistan). We focus on the analysis of amorphous, charred plant aggregates retrieved from flotation samples from the two sites; some of these materials represent the earliest remains of their kind discovered to date in South-west Asia and Europe. Such remains, often representing the charred residues of food preparation (hereafter ‘food remains’), can provide direct evidence for the plant species consumed, often combined in multi-component foods, as well as preparation methods (Carretero *et al.* 2017; Heiss *et al.* 2017; Arranz-Otaegui *et al.* 2018; Valamoti *et al.* 2021). Our results highlight the early exploitation of a diverse range of plant foods that required specialised processing techniques, bringing to the fore the significance of food preparation and cooking practices in ancient human dietary practices.

Materials and methods

Franchthi Cave is located in the Argolid peninsula of southern mainland Greece. It was excavated between 1969 and 1976 by T.W. Jacobsen of Indiana University and M.H. Jameson of Pennsylvania University, under the auspices of the American School of Classical Studies in Athens and in collaboration with the Greek Archaeological Service (Farrand 2000). Occupation at the site spans the Upper and Final Palaeolithic, Mesolithic and Neolithic (c. 38 000–6000 cal BP) (Farrand 2000; Asouti *et al.* 2018). Sampling for archaeobotanical remains was carried out by machine-assisted water flotation. The non-wood charred plant macro-remains were previously studied and published by Julie Hansen (1991). The presence of charred, amorphous plant aggregates that potentially represent food remains was noticed during anthracological analyses conducted by Eleni Asouti and Ceren Kabukcu at the University of Liverpool in 2017 (Asouti *et al.* 2018). The four charred plant aggregates from Franchthi

Table 1. Summary of provenance, phasing and corresponding radiometric dates for the analysed food fragments.

Site	Fragment context no.	Flotation sample no.	Phase	Chronometric date range	Illustrated in
Franchthi Cave	H1A 167	H1A 167	FGP VI/VII	11.7–11.4 ka cal BP (Early Holocene onset)	Figure 1
Franchthi Cave	H1A 168	H1A 168	FGP VI/VII	11.7–11.4 ka cal BP (Early Holocene onset)	Figure 2
Franchthi Cave	H1A 172	H1A 172	FGP VI	12.9–11.7 ka cal BP (Younger Dryas)	Figure 4
Franchthi Cave	H1A 177	H1A 177	FGP V	13.1–12.9 ka cal BP (Bølling Allerød, GI-1A warm period)	Figure 3
Shanidar Cave	636	4778	Baradostian	~40 ka BP (MIS 3)	Figure 9
Shanidar Cave	1812	5511	Baradostian	>40 ka BP (MIS 3)	Figure 5
Shanidar Cave	1823	5541	Baradostian	>40 ka BP (MIS 3)	Figure 7
Shanidar Cave	1866	5714	Initial Baradostian	>40 ka BP (MIS 3)	Figures 6 & 8
Shanidar Cave	1924	5631	Mousterian	70–75 ka BP (likely MIS 5a)	Figure 10

Cave examined here originate from two chrono-cultural phases: stratum T3, which is assigned to the later phases of the Upper Palaeolithic (Mediterranean Gravettian), corresponding to the Bølling-Allerød warm period (Franchthi General Phase (FGP) V, *c.* 13 100–12 900 cal BP), and the Final Palaeolithic (Epigravettian) strata, which are dated to the Younger Dryas (FGP VI, *c.* 12 900–11 700 cal BP) and the start of the Holocene (FGP VI/VII, *c.* 11 700–11 400 cal BP) (Hansen 1991; Farrand 2000; Asouti *et al.* 2018) (Table 1).

Shanidar Cave, located on the western flanks of the Zagros Mountains of Iraqi Kurdistan, was originally excavated between 1951 and 1960 by Ralph and Rose Solecki of Columbia University and colleagues (Solecki 1971). Since 2015, a team led by Graeme Barker has conducted systematic excavations at the site (Reynolds *et al.* 2015), during which the fragments analysed in this study were collected. Five charred plant aggregates were recovered from Upper Palaeolithic (Baradostian) and one further fragment from the Middle Palaeolithic (Mousterian) deposits. Although the full radiometric dating programme is ongoing, the Baradostian strata date to *c.* 42 000–35 000 years ago (Reynolds *et al.* 2018), which corresponds to the later part of Marine Isotope Stage 3 (MIS 3). Regionally, the Baradostian techno-cultural industry is interpreted as coeval with the Aurignacian of the European Upper Palaeolithic, which is associated with *Homo sapiens* (Reynolds *et al.* 2018; Shidrang 2018). In Iran, the Baradostian industry has been associated with anatomically modern humans at the cave site of Eshkaft-e Gavi (Scott & Marean 2009), where it has been dated to *c.* 42 000–30 000 years ago—somewhat later than the Baradostian assemblage of Kaldar Cave, which is dated to 54 400–46 050 cal BP (Bazgir *et al.* 2017). Meanwhile, the samples recovered from the Mousterian strata at Shanidar Cave probably date to >70 000–75 000 years ago, based on their broad stratigraphic association with the well-known Neanderthal ‘flower burial’ and the recently discovered ‘Shanidar Z’ articulated skeletal remains, dated to *c.* 73 000 BP (Pomeroy *et al.* 2017, 2020).

Charred plant aggregates may take the form of large, recognisable items of food (Heiss *et al.* 2017), carbonised crusts adhering to the walls of pottery vessels (Kubiak-Martens *et al.* 2015) or amorphous lumps, some of which could represent accidentally charred food remains (Valamoti *et al.* 2021; Bates *et al.* 2022); microscopic examination is required to confirm their interpretation as food remains and to identify their plant components. The charred amorphous plant aggregates recovered at Franchthi and Shanidar were sorted using a Leica S8 APO stereo-zoom microscope (magnification $\times 7$ –80). Under the stereo-zoom microscope, the fragments under study here appeared as discrete, non-friable masses, sometimes with visible seed fragment inclusions.

As carbonised dung is frequently found in archaeobotanical samples, it was important to exclude the possibility that the charred, amorphous plant aggregates might be faecal remains. During microscopic examination, charred dung fragments often appear fibrous, with matted/layered stems included in a dense matrix that often contains spherulites (Smith *et al.* 2019; Bates *et al.* 2022). None of the Franchthi and Shanidar fragments contain spherulites, or inclusions of grass stems and leaf fragments and we therefore interpret these amorphous plant aggregates as likely food remains. In addition, they mostly contain fragments of seeds and grain-derived plant cells, and are irregular in form and porous in texture, with voids and cracks of variable sizes. Similar items, interpreted as carbonised food remains and matched by experimentally reproduced examples, have previously been

reported in recent archaeobotanical literature (Carretero *et al.* 2017; Valamoti *et al.* 2021; Bates *et al.* 2022).

All of the charred food remains were further examined under a Meiji MT6500 darkfield/brightfield incident light microscope (magnification $\times 50$ – 500) and subsequently mounted on SEM aluminium stubs and gold sputter coated (to a thickness of 20nm) to allow for more detailed observation (following established analytical protocols: Carretero *et al.* 2017; Heiss *et al.* 2017; Valamoti *et al.* 2021). Identification of plant constituents, including specific plant cell types and patterns, made use of the published literature on plant cell identification, including comprehensive guides on specific genera and families, and comparisons to modern specimens held in the University of Liverpool Archaeobotany Laboratory plant reference collection.

Results

Franchthi Cave

Four charred food fragments, recovered from four flotation samples from Franchthi Cave, were analysed. Three of these contain fused pulse seed, seed coat and other tissue fragments such as macrosclereids, set in a fully or partially gelatinised matrix (Figures 1–3). There is evidence for starch and protein cell deformation, alongside areas of vitrification most commonly associated with the effects of soaking and heating. The smooth edges of the seed fragments embedded in the charred matrix indicate fragmentation before carbonisation. The seed fragment sizes are generally variable and might indicate coarse grinding and/or pounding (as opposed to finely ground flour-like mixtures). The formation of the gelatinised matrix around the fragments of the seeds with adhering seed coats further suggests that preparation of the food item might have started with soaking whole dry seeds, or with the use of fresh seeds that had a high moisture content. The interpretation of pounding prior to charring, as indicated by the smooth edges of the seed fragments and their variable sizes, is based on recent experimental and archaeobotanical research on cereal food preparations, which has established criteria for detecting this sequence of events (Valamoti *et al.* 2021). Further experimental work focusing on pulse processing, including grinding, mashing and soaking, is needed to provide additional reference data for the interpretation of pulse-rich archaeological food remains. The food fragments (Figures 1–3) also contain abundant remains of the papillose seed coat pattern and macrosclereid cells characteristic of the tribe Fabeae (limited to lentil, vetch and grass pea; Butler 1990; see also Figures S1 & S2 in the online supplementary materials (OSM)). The food fragment in Figure 1D, for example, is sufficiently well preserved to permit the identification of bitter vetch (*Vicia ervilia*) (Butler 1990: 493–95, pls 5–7; see also Figure S2). Our observations regarding the presence of pulse species are further supported by previous studies, which report the abundance of charred lentil, vetch and pea seeds in the archaeobotanical assemblage from Franchthi Cave (Hansen 1991; see also Asouti *et al.* 2018).

Unlike the food fragments described above, the fourth fragment of food remains is close-textured and lacks seed fragments, observable seed coat or epidermal cells (Figure 4). Its matrix contains voids and cracks of varying sizes, indicating a heat-affected, expanded

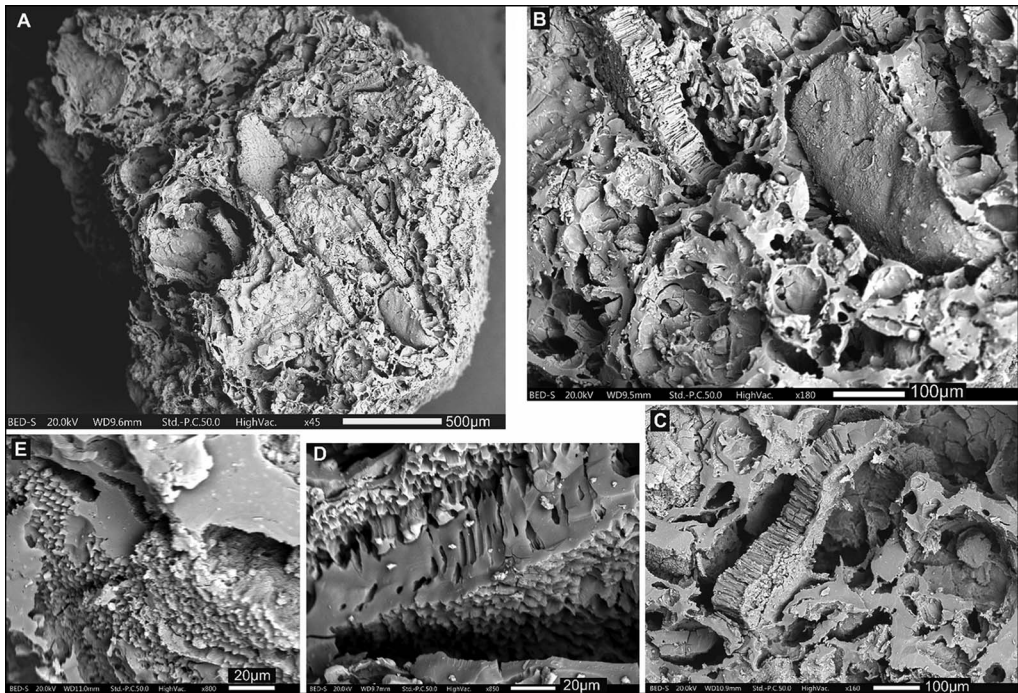


Figure 1. Pulse-rich charred plant food fragment from Franchthi Cave (context no. H1A 167, Final Palaeolithic, Epigravettian): A) overview; B) close-up of pulse seed coat and seed fragment; C) close-up of pulse seed coat surface; D) view of *Vicia ervilia* seed coat papillose cells; E) close-up of pulse seed coat surface (SEM micrographs taken by C. Kabukcu).

starch-rich matrix. This structure strongly resembles experimental preparations and archaeobotanical examples of charred bread-like foods or finely ground cereal meals, such as those reported from various Neolithic and later prehistoric settlements (Valamoti *et al.* 2008; Carretero *et al.* 2017). Probably as a result of the advanced state of vitrification and gelatinisation, the food fragment does not preserve identifiable plant cells or other characteristic components that would permit identification of specific plant species. The presence of starch-rich plant food sources at Franchthi Cave, however, is well established, including grasses (oats and barley) and nuts (almonds and *Pistacia*) documented in the archaeobotanical assemblage (Hansen 1991; Asouti *et al.* 2018).

Shanidar Cave

Five charred food fragments from the Upper Palaeolithic (Baradostian) layers at Shanidar Cave were analysed in detail (Figures 5–9). All contain crushed and fused remains of pulses, including of the genera *Lathyrus* and *Pisum*. The mounded-papillose seed coat pattern (Figure 3C–D) is frequently observed in medium-sized *Lathyrus* species (Butler 1990). The height of the macrosclereids suggests that they probably belong to *L. cassius*, *L. hirsutus* or *L. nissolia* (Butler 1990: 550–51, pls 62–63; Güneş 2013; see also Figure S3).

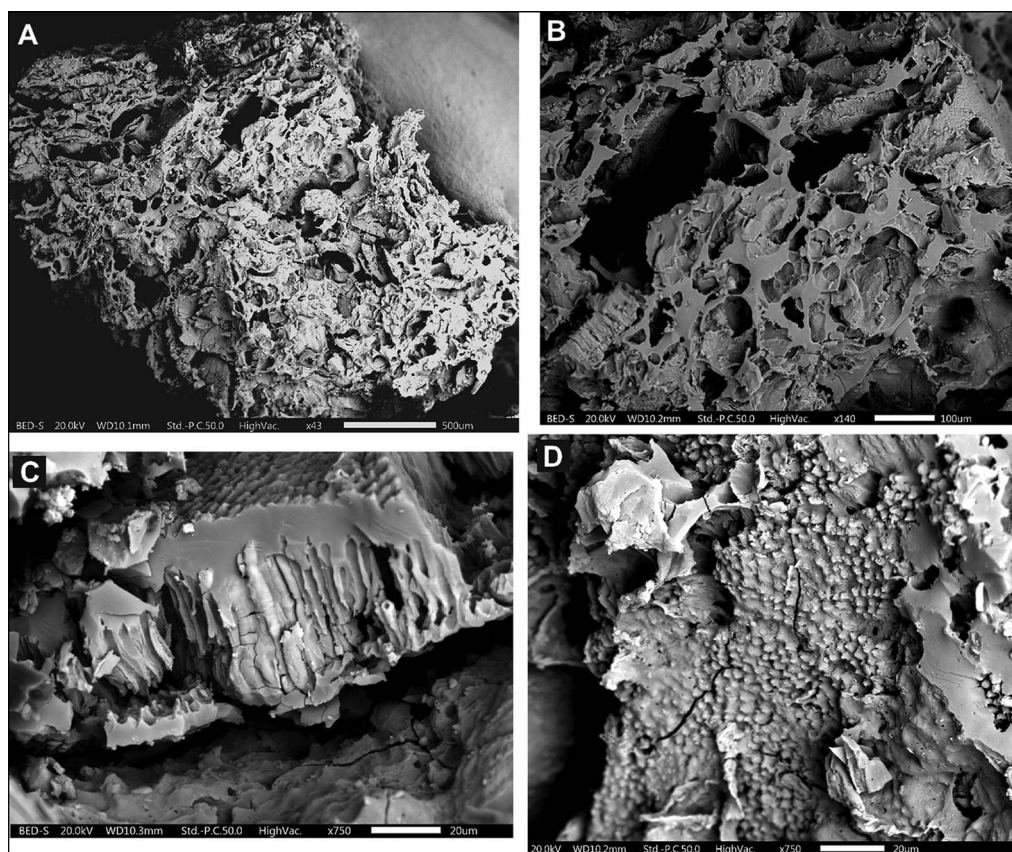


Figure 2. Pulse-rich charred plant food fragment from Franchthi Cave (context no. H1A 168, Final Palaeolithic, Epigravettian): A) overview; B–D) close-ups of pulse seed fragments and seed coat remains (SEM micrographs taken by C. Kabukcu).

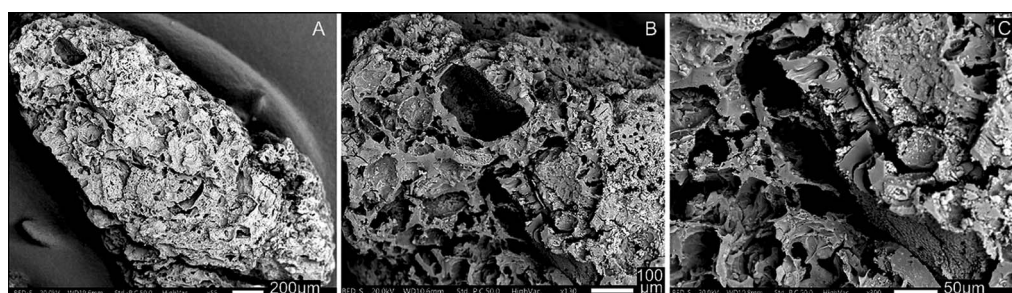


Figure 3. Pulse-rich charred plant food fragment from Franchthi Cave (context no. H1A 177, Upper Palaeolithic, Mediterranean Gravettian): A) overview; B–C) close-up of pulse seed fragments and seed coat (SEM micrographs taken by C. Kabukcu).

Based on the height of the macroscleroid layer and the mounded-papillose pattern, the food fragment shown in Figure 6B–C closely resembles pea (*Pisum fulvum* and *P. sativum* subsp. *elatius*) (Werker *et al.* 1979; Zablatzka *et al.* 2021; see also Figure S4). Additionally,

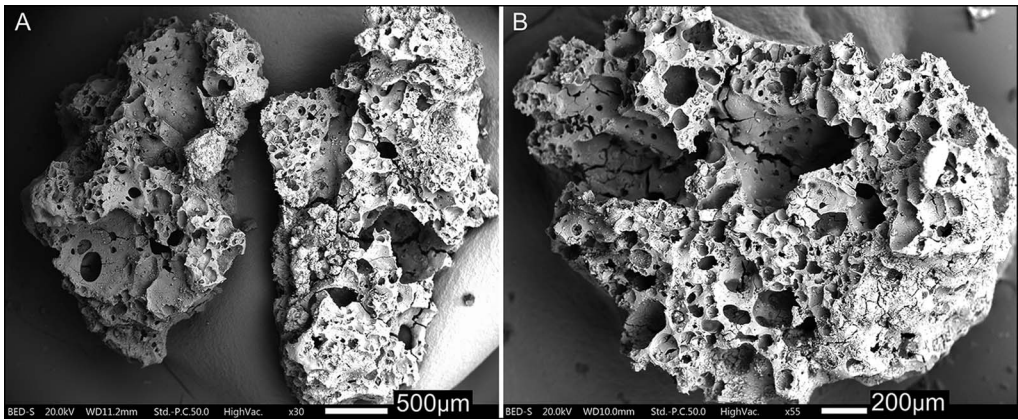


Figure 4. Charred plant food remains from Franchthi Cave, with a homogenised matrix (context no. H1A 172, Upper Palaeolithic, Mediterranean Gravettian): A) overview; B) close-up showing variable sizes of voids (SEM micrographs taken by C. Kabukcu).

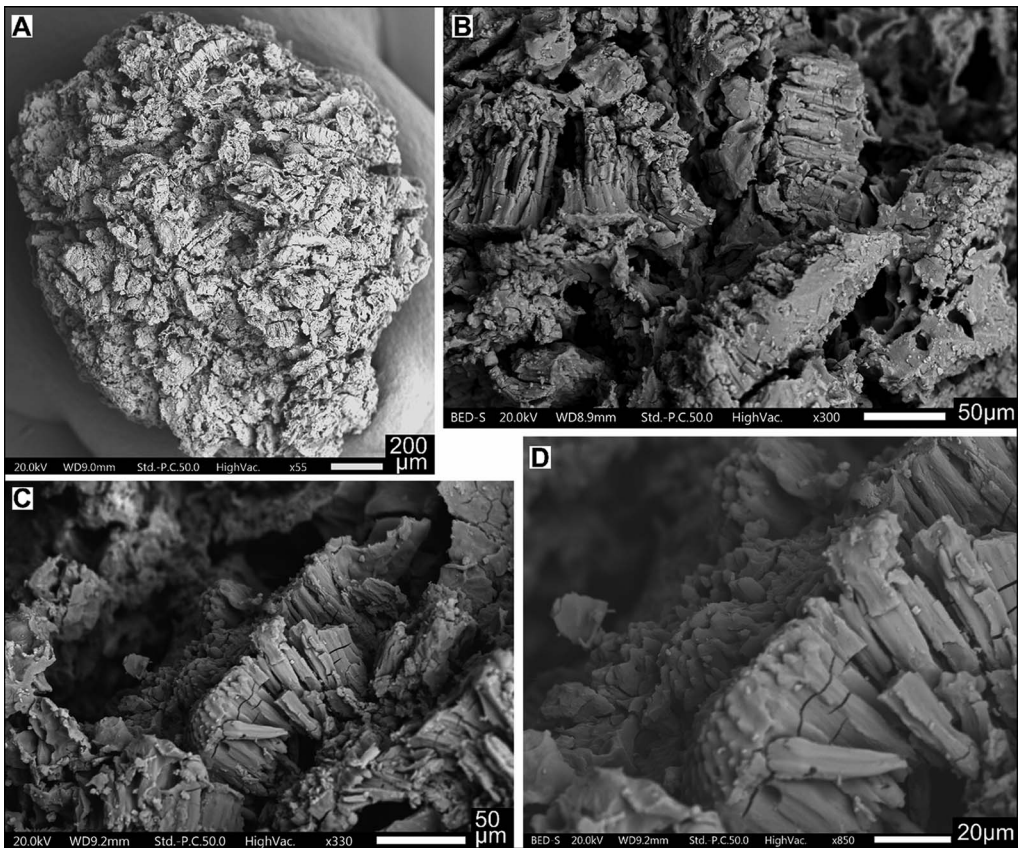


Figure 5. Pulse-rich charred plant food remains from Shanidar Cave (context no. 1812, Upper Palaeolithic, Baradostian): A) overview; B–D) close-up of pulse seed coat surface and mounded-papillose seed coat pattern of *Lathyrus* sp. (likely *Lathyrus cassius*, *L. hirsutus* or *L. nissolia*) (SEM micrographs taken by C. Kabukcu).

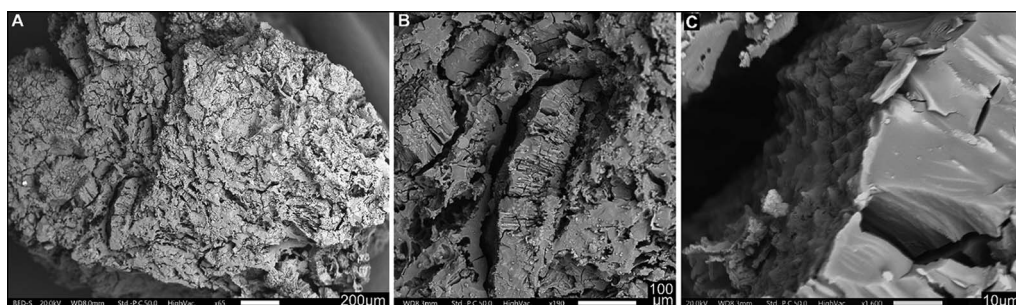


Figure 6. Charred plant food fragment from Shanidar Cave (context no. 1866, Upper Palaeolithic, Initial Baradostian): A) overview; B–C) close-up of wild pea (*Pisum fulvum* or *P. sativum* subsp. *elatius*) seed coat (SEM micrographs taken by C. Kabukcu).

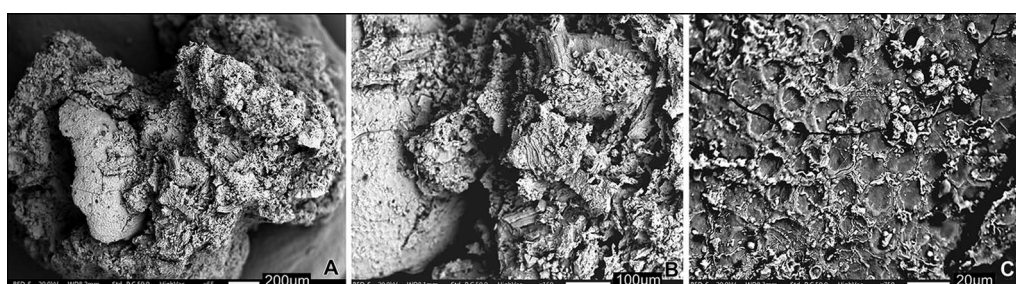


Figure 7. Charred plant food remains from Shanidar Cave (context no. 1823, Upper Palaeolithic, Baradostian) containing wild mustard: A) overview; B–C) close-up of mustard seed fragment and seed coat pattern (SEM micrographs taken by C. Kabukcu).

the fragments with well-preserved reticulate seed coats and globular-shaped cotyledons (e.g. Tantawy *et al.* 2004; Gabr 2018) are probably wild mustards (Brassicaceae). Two of the charred food fragments also contain plant tissues resembling *Pistacia* nutshell and pericarp fragments; these appear heavily deformed, possibly due to the effects of food preparation and/or post-depositional taphonomic processes on the morphology of the plant tissues (see Figures 8B, 8D and 9C–D). SEM images of carbonised modern reference *Pistacia* specimens are included in the OSM (Figure S5).

The single fragment of charred food remain from a Mousterian layer at Shanidar Cave (Figure 10) contains pulse seed and seed coat fragments. Unlike the Baradostian food fragments, however, it also includes the long cells characteristic of grasses (Poaceae) (Figure 10D).

Discussion

The food remains from Upper/Final Palaeolithic strata at Franchthi Cave and Middle/Upper Palaeolithic strata at Shanidar Cave reported here currently represent the earliest direct macrobotanical evidence of Palaeolithic plant food processing in the Eastern Mediterranean and South-west Asia. They represent a significant addition to an accumulating body of archaeobotanical data from these regions that points to selective plant foraging by Palaeolithic

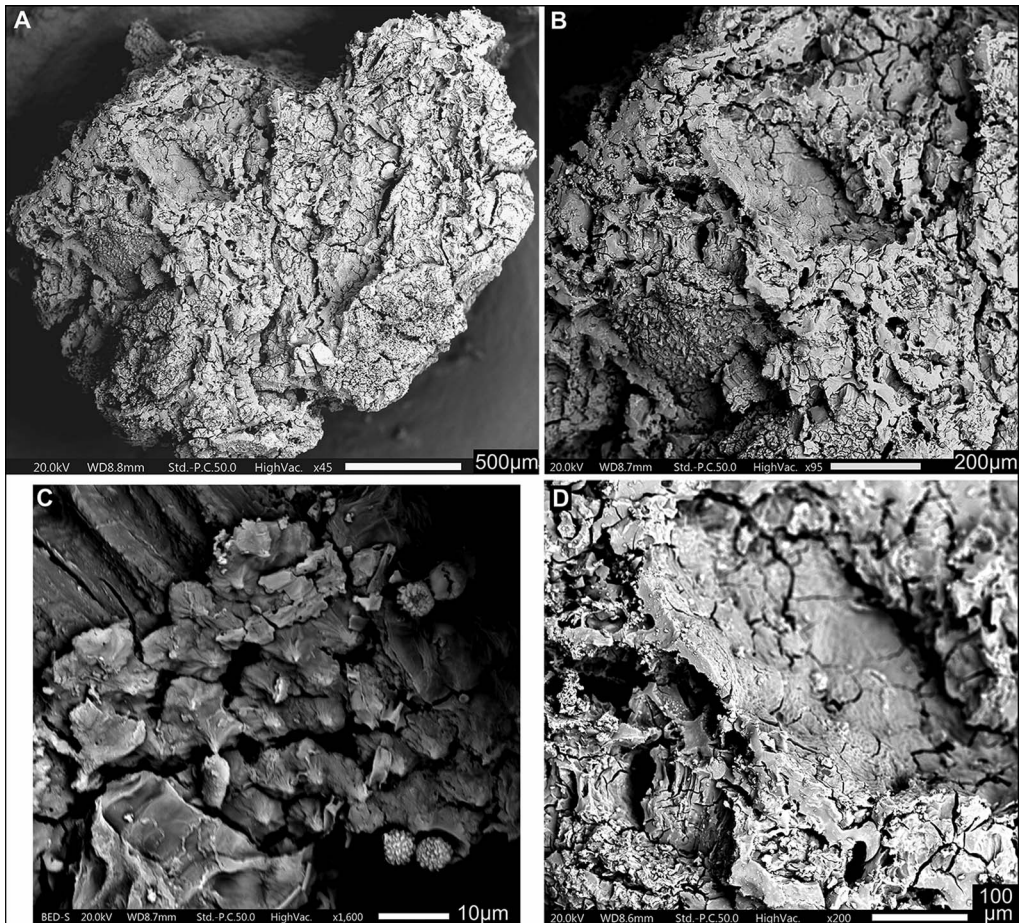


Figure 8. Charred plant food remains from Shanidar Cave (context no. 1866, Upper Palaeolithic, Initial Baradostian): A) overview; B) & D) close-up of *cf. Pistacia nutshell/pericarp* remain; C) close-up of pulse seed coat pattern (*Fabeae*) (SEM micrographs taken by C. Kabukcu).

hunter-gatherers. At Middle Palaeolithic Kebara Cave (Mount Carmel, Israel), for example, pulse seeds (vetches, grass pea and lentils) constitute the majority of the charred plant macrofossils (Lev *et al.* 2005). The Epipalaeolithic occupation at El Wad (also in Mount Carmel) similarly contains an archaeobotanical assemblage dominated by pulses, with a significant proportion of vetches (Caracuta *et al.* 2016). Epipalaeolithic Palegawra Cave (Iraqi Kurdistan) provides evidence for a more diverse range of foraged plants, including wild pulses, grasses, nuts, tubers and mustards (Asouti *et al.* 2020). In the Levantine Epipalaeolithic, there is also increasing evidence for the use of tubers (e.g. Shubayqa I, Jordan; Arranz-Otaegui *et al.* 2018) and mustards (e.g. Kharaneh IV, Jordan; Bode *et al.* 2022). The remarkably well-preserved assemblage from Ohalo II (Israel) also provides evidence for the use of wild grasses during this period (Weiss *et al.* 2004).

Other notable Epipalaeolithic sites in South-west Asia from which archaeobotanical data are available, including the Karain and Öküzini Caves (Martinoli 2004) and the Pınarbaşı

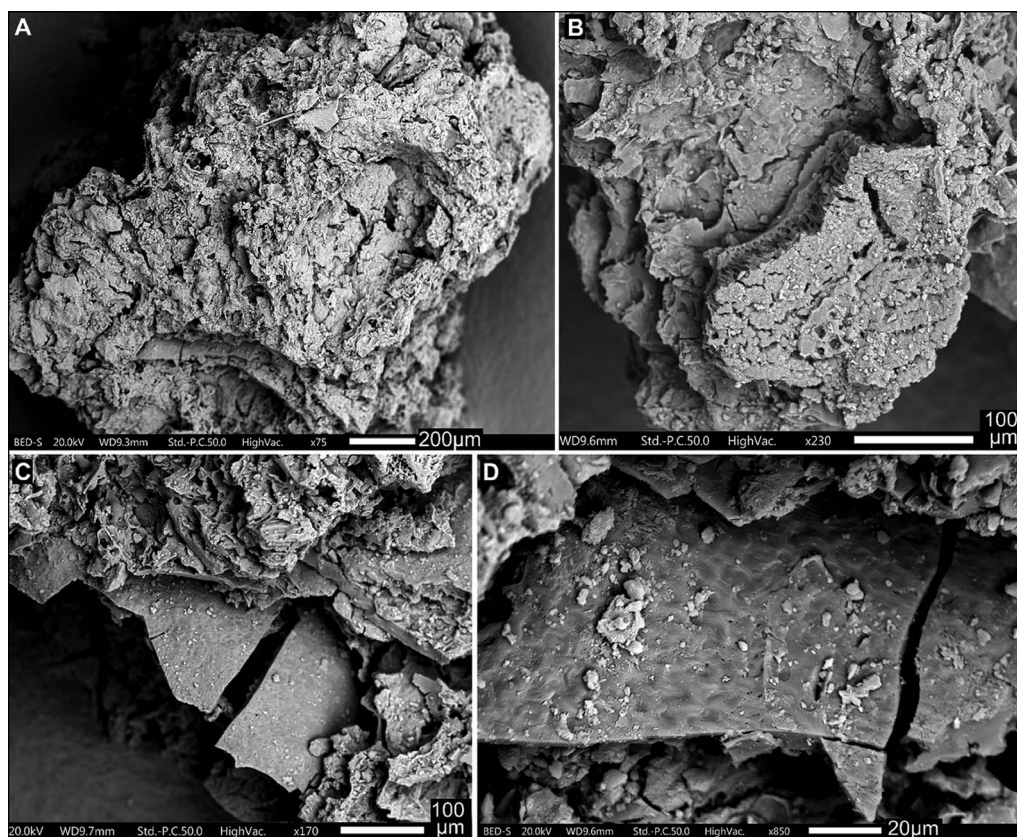


Figure 9. Charred plant food fragment from Shanidar Cave (context no. 636, Upper Palaeolithic, Baradostian): A) overview; B–D) close-up of *cf. Pistacia nutshell/pericarp* fragment (SEM micrographs taken by C. Kabukcu).

rockshelter (Baird *et al.* 2013) in Anatolia, demonstrate an emphasis on nuts (almonds and terebinth), pulses and various wild fruits. The broadly contemporaneous occupation at Haua Fteah in north-east Libya similarly provides evidence for the use of pine nuts and wild vetches (Barker *et al.* 2010). Several European Upper Palaeolithic sites attest to the use of wild grasses and tubers. At Klisoura 1 Cave in Peloponnese (Greece), phytolith and micromorphological data from Upper Palaeolithic clay-lined hearths indicate grass seed roasting (Karkanas *et al.* 2004). Starch and ground stone use-wear data from the Gravettian occupation at Grotta Paglicci in southern Italy suggest the cooking and processing (grinding/crushing) of wild oats and the processing of tannin-rich oak acorns (Lippi *et al.* 2015). Similarly, starch and use-wear evidence on grinding stones from the Late Stone Age occupation at Haua Fteah, dated to c. 31 000 years ago, point to the regular processing of goat grass (*Aegilops* sp.) (Barton *et al.* 2018).

Most of the carbonised food remains reported here contain variously sized fragments of pulse seeds, probably representing processing by coarse grinding, cracking and/or pounding. This type of preparation differs from the finer grinding required for flour and does not necessitate the use of flat grinding stones. It could have been undertaken using only percussive tools

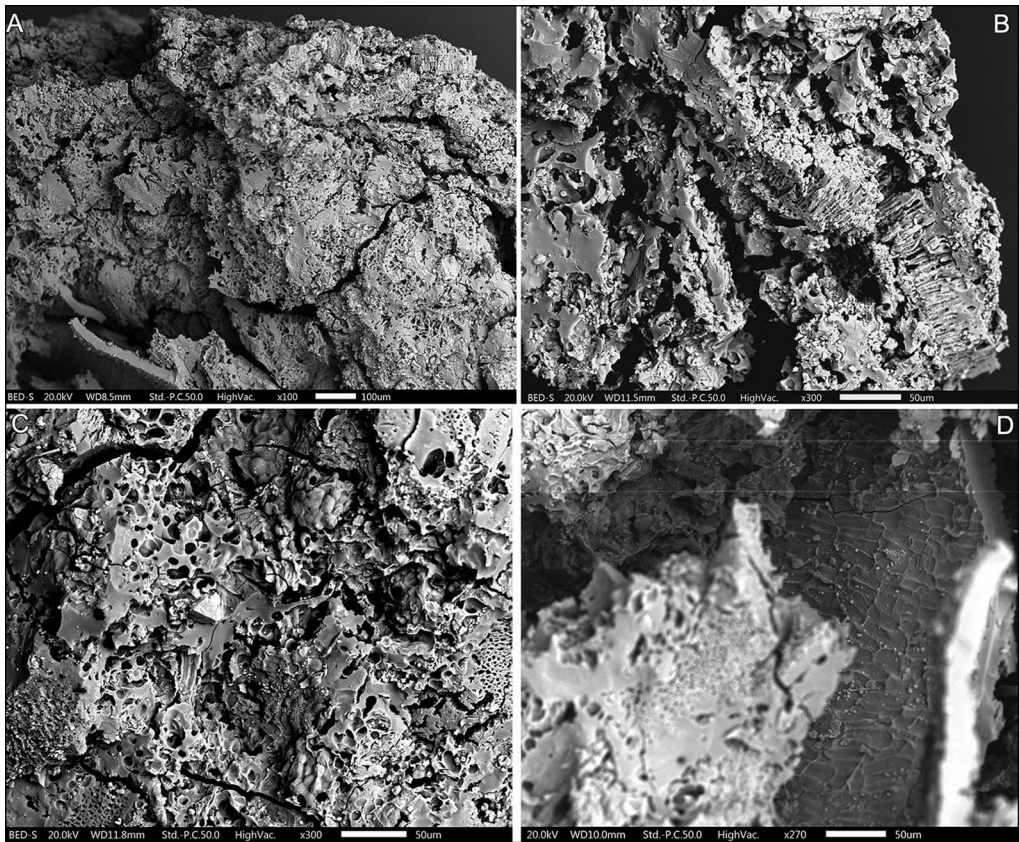


Figure 10. Charred plant food remains from Shanidar Cave containing pulses and grasses (context no. 1924, Middle Palaeolithic, Mousterian): A) overview; B–C) close-up of pulse seed coat and seed fragments; D) close-up of long cells of Poaceae seed (SEM micrographs taken by C. Kabukcu).

and/or perishable implements. Use-wear data from the Acheulian site of Gesher Benot Ya'qov (Israel) point to the early use of stone tools for nut cracking and plant food preparation (Goren-Inbar *et al.* 2015). In the Upper Palaeolithic starch-rich charred food fragment from Franchthi Cave (Figure 4), the absence of large particles and the high degree of homogenisation of the matrix suggest that the plants were processed via fine grinding and/or boiling and mashing. Similar charred plant aggregates comprising fine-ground starch plant tissue and occasionally no identifiable plant cells have also been reported from Epipalaeolithic, Mesolithic and Neolithic contexts in South-west Asia and Europe, and have been interpreted as 'breads' or 'porridges' (Kubiak-Martens *et al.* 2015; Carretero *et al.* 2017; Arranz-Otaegui *et al.* 2018).

Pulse seeds, especially bitter vetch (*Vicia ervilia*) and grass pea (*Lathyrus cassius*, *L. hirsutus* and *L. nissolia*), contain notable quantities of alkaloids and tannins, resulting in a bitter and astringent taste. These compounds are concentrated in the seed coats. While cooking techniques, such as soaking and boiling, can remove a large portion of tannins and other bitter, astringent and toxic compounds (Ressler *et al.* 1997), hulling (the removal of the seed coat)

would have been a far more efficient method. This technique is commonly practised today (Ressler *et al.* 1997), as well as in the past (Melamed *et al.* 2008; Valamoti *et al.* 2011), for processing vetches and grass pea. The soaking of wild pulses, as indicated by the Franchthi and Shanidar charred food fragments, would have enabled their safe consumption and improved their palatability by removing most of the bitter-tasting compounds. The presence of seed coat fragments, however, suggests that a low level of plant chemicals, including some tannins and alkaloids, may have been intentionally retained in plant food preparations. This evidence adds to an increasing body of archaeobotanical studies suggesting a persistent reliance on, and tolerance of, bitter- and astringent-tasting plant foods such as pulses, mustards, almonds and terebinths, from as early as the Middle Palaeolithic through to the later prehistoric periods. Beyond the Eastern Mediterranean and South-west Asia, archaeobotanical studies at sites such as Niah Cave (Sarawak, Borneo) have revealed evidence for the processing of the highly toxic *Dioscorea* (yam) and *Pangium edule* nuts from as early as 50 000 years ago, underscoring the complexity and deep ancestry of such food preparation practices (Barker *et al.* 2007; Barton *et al.* 2016).

Apart from detoxification, food preparation practices such as soaking and pounding would also have improved the bioavailability of bulk nutrients. Multi-proxy data from Early Upper Palaeolithic sites in the Pontic steppe, derived from starch residue extraction, spectroscopic and spectrometric techniques, point to the processing by pounding of a diverse group of tubers, possibly with the aim of tenderising them for consumption (including some less commonly observed C_4 carbon-fixing plant species; see Longo *et al.* 2021). Other aspects of plant resource choice and use, including raw materials and medicinal uses, have also been highlighted with regard to Lower and Middle Palaeolithic foraging (Hardy *et al.* 2012, 2022; Hardy 2018).

Conclusion

The evidence presented here supports previous hypotheses regarding the diversity and complexity of Palaeolithic plant use. It provides direct evidence for previously undocumented food preparation practices and brings into focus the diversity of specialised cooking practices developed by Middle and Upper Palaeolithic hunter-gatherers, which involved multiple preparation steps and different plant components (*sensu* Jones 2009). Our results reinforce current understanding that the use of plants in the Palaeolithic regularly relied on starch-rich tubers and grasses (Henry *et al.* 2011; Hardy *et al.* 2022) and further demonstrate that the labour-intensive processing of a broad spectrum of plant foods, including bitter, astringent and potentially toxic plants for human consumption, was an integral part of hunter-gatherer resource management strategies. The use of plant food preparation techniques was prevalent across the Eastern Mediterranean and South-west Asia from as early as the Middle Palaeolithic and appears to be independent of fluctuations in forage and prey ceilings due to climatic conditions (Hardy 2018; Power & Williams 2018). Crucially, our results demonstrate that food choices and preparation practices traditionally associated with the intensification of plant resource use that is linked to climatic amelioration at the Pleistocene–Holocene boundary and the origin of farming (Smith & Zeder 2013) clearly have a deep history that precedes the earliest evidence for plant cultivation by several tens of thousands of years.

Acknowledgements

C.K. designed the study, carried out the analysis and produced the original draft. All authors contributed to writing, review and editing of the final draft. E.A. provided access to the Franchthi Cave samples; E.H., C.H., E.P., T.R. and G.B. designed and carried out sampling for archaeobotanical remains at Shanidar Cave and provided access to the samples. We thank the Kurdistan Regional Government for inviting G.B. to plan and direct new excavations at Shanidar Cave, and the Kurdistan General Directorate of Antiquities for granting excavation permits and permission to analyse the finds. Additional modern plant reference materials were made available to C.K. by the USDA Agricultural Research Service, Plant Germplasm Introduction and Testing Unit.

Supplementary materials

To view supplementary material for this article, please visit <https://doi.org/10.15184/aqy.2022.143>.

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Data statement

Archaeological and modern plant reference specimens are archived at the University of Liverpool Archaeobotany Laboratory, Department of Archaeology, Classics and Egyptology. All data are available in the main text and the OSM.

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