Plant foods in the Upper Palaeolithic at Dolní Věstonice? Parenchyma redux

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The classic image of Upper Palaeolithic hunter-gatherers in Europe envisages them hunting large mammals in largely treeless landscapes. That is partly due to the nature of the surviving archaeological evidence, and the poor preservation of plant remains at such ancient sites. As this study illustrates, however, the potential of Upper Palaeolithic sites to yield macrofossil remains of plants gathered and processed by human groups has been underestimated. Large scale flotation of charred deposits from hearths such as that reported here at Dolní Věstonice II not only provides insight into the variety of flora that may have been locally available, but also suggests that some of it was being processed and consumed as food. The ability to exploit plant foods may have been a vital component in the successful colonisation of these cold European habitats.

Keywords: Czech Republic, Dolní Věstonice, Upper Palaeolithic, Gravettian, archaeobotany, plant foods, parenchyma

Introduction

The subsistence practices of European Palaeolithic hunter-gatherer societies have been a matter of interest and research for decades and yet we still know relatively little about the role of plant foods in their diets. Speculation has centred around powerful theoretical arguments for the likely importance of gathered plant foods in the Palaeolithic diet and

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their possible availability to Pleistocene gatherers (e.g. Speth & Spielmann 1983; Jones 2009; Hardy 2010), and indeed, evidence of such plant foods is suggested by microfossil data in the form of starch grains adhering to stone tools (Revedin *et al.* 2010; Hardy & Moncel 2011), in sediments (Barton 2005) and trapped in dental calculus (Henry *et al.* 2011; Hardy *et al.* 2012). Macrofossil evidence for plant food remains from Palaeolithic contexts are still, however, relatively scarce and archaeobotany remains an under-developed field within Palaeolithic studies (Hather & Mason 2002). This is partly due to obvious problems of taphonomy and preservation for such very ancient organic remains, although, in fact, systematic investigation of archaeobotanical remains through flotation has been reported from very few Palaeolithic excavations (e.g. Koumouzelis *et al.* 2001; Weiss *et al.* 2004).

The Moravian Gate Project (see Svoboda *et al.* 2007; Beresford-Jones *et al.* 2010, 2011) sought to address this lacuna by intensive flotation of newly excavated contexts from the Gravettian sites of Dolní Věstonice II and Předmostí in the Czech Republic (dated between 25 and 30 kya). We were inspired to do so, in part, by a seminal analysis of a hearth context excavated at Dolní Věstonice II in the 1980s (Mason *et al.* 1994). Though only 280ml in size, the small sample taken from this hearth yielded various plant remains, including parenchyma identified as Asteraceae family, which were tentatively interpreted as evidence for the consumption of starchy vegetable plant foods. More recently, Revedin *et al.* (2010) identified starch grains suggestive of *Typha* sp. (bulrush, family Typhaceae) adhering to a putative grindstone from the nearby site of Pavlov VI (dated 25 950±110 BP [GrA-37627] to 26 660±140 BP [OxA-18306]).

Our 2005 investigations at Dolní Věstonice II (DVII-05) floated virtually the entire excavated cultural layer to extract, in contrast with Předmostí, a very large assemblage of charred macrobotanical remains. These included woody charcoals of various conifer species; *Abies* sp. needles; seeds, whose poorly preserved morphology only allowed for identification to the levels of Pinaceae and cf. Apiaceae; and the parenchymous remains of vegetative storage organs of plants (Beresford-Jones 2006; Beresford-Jones *et al.* 2010). Elsewhere, we have reported how these data shed light on various aspects of Upper Palaeolithic human ecology (Beresford-Jones *et al.* 2010, 2011). Here we focus on our investigations of the parenchyma remains from DVII-05. Our results both corroborate and elaborate upon the findings of Mason *et al.* (1994), thereby strengthening the evidence for the importance of plant foods to these early European hunter-gatherer societies. They call too for a renewed effort to develop the neglected methodology of identifying preserved soft plants in archaeological remains.

Plant taxonomy and tissue types

There are two main plant tissues of interest in our analysis here: vascular tissues and parenchyma, which together comprise the basic tissue types analysed and used to make interpretations in this investigation. Vascular tissues are responsible for transporting water and nutrients around a plant. They may be divided into the xylem, which facilitates movement of water and dissolved nutrients by capillary action only, and the phloem, which facilitates active transport of sugars and nutrients. Taxonomic classification systems for plants divide all seed-bearing plants (spermatophytes) into two main groups, the gymnosperms (with naked seeds), which are primarily represented by the conifers, and the angiosperms (with seeds enclosed in fruits). Some other plants, in particular the pteridophytes (ferns and their allies), occasionally contribute to archaeological assemblages of charred woody tissue. Each group is characterised by xylem constructed in different ways. In pteriphytes and most gymnosperms, xylem is constructed exclusively of tracheid cells—long, thin cells arranged in long cylindrical bundles with each cell overlapping those above and below it. In contrast, the xylem of angiosperms (and a small group of gymnosperms, the gnetophytes) comprises both tracheids and long, tubular vessels. These different tissue types are present throughout the stems and also the roots of vascular plants. Whereas thin-walled phloem cells are usually destroyed by charring to leave a mass of solid carbon, or sometimes a cavity (Hather 1991), xylem elements are commonly preserved at least partially intact, so that their features and arrangement within parenchymous tissues are useful for making broad characterisations regarding the composition of a charred macrobotanical assemblage. The only gnetophyte of temperate zone archaeobotanical significance is the genus *Ephedra*, and so the presence of vessels can often be taken to be indicative of angiosperms.

The second plant tissue of interest is parenchyma, comprising thin-walled, isodiametric cells with a variety of functions including the storage of starch, protein, fats and oils, and water. Parenchyma occurs in most leaves, stems and roots in small deposits that may be only a few cells thick, yet it is the primary component of large stems and fleshy organs specialised for the storage of starch, such as fruits and some seeds, and vegetative underground storage organs (USOs) such as roots, rhizomes, tubers and bulbs, herein collectively termed 'starchy tissues'. Individual parenchyma cells are structurally relatively simple compared with cells of vascular tissues, yet there is a large amount of variation in gross morphology, cell shape and tissue structure between taxa (Hather 1991). Parenchyma tissues may, for instance, frequently show various types of cavity. These include secretory cavities associated with the secretion and storage of different substances (see Hather 2000: 40–41), and air spaces in plant tissue formed through different growth processes (see Hather 2000: 40). An example of the latter is aerenchyma, a specialised type of parenchyma tissue containing continuous intercellular spaces, typical of aquatic plants in which it aids buoyancy and air circulation within submerged parts of the plant. Further characteristics of interest include crystalline structures that are sometimes associated with parenchyma, such as calcium oxalate crystals appearing as needle-shaped 'raphides' and globular stellate 'druse crystals' (see Franceschi & Horner 1980; Hather 2000: 33–35). The specific mechanism controlling calcium oxalate secretion in plants is unclear (Webb 1999), but the oxalate radical is toxic to herbivores (and indeed humans) and may thereby deter predation.

Previous investigations by Hather (1988, 1991, 1993, 2000) explored these and a number of other anatomical and morphological characteristics of modern parenchyma samples using a scanning electron microscope (SEM). These analyses suggested the various features can, in principle, be used together with the structure and arrangement of associated vascular tissues to distinguish different taxa on the basis of soft tissue remains. From this work, archaeological remains of starchy parenchyma have been putatively identified, mainly from Mesolithic and Epipalaeolithic contexts, including, *inter alia*: *Sagittaria* sp. and *Polygonum* sp., *Allium ursinum* (wood garlic), *Conopodium majus* (pignut), *Typha* sp. (bulrush), *Scirpus* sp. (club-rush) and *Dryopteris filix-mas* (male-fern) (Kubiak-Martens 1996, 2002; Perry 1999).

Dolní Věstonice II site and ecology

DVII is one of a cluster of sites scattered along the western and northern slopes of the Pavlov Hills, which overlook the wide valley of the Dyje River near the village of Dolní Věstonice in the Czech Republic. Rescue excavations here in the 1980s revealed three main agglomerations, each containing Gravettian cultural remains including lithic assemblages, animal bones, *in situ* hearths, evidence for possible structures, human burials, ochre, clay figurines and even some evidence of clay firing (Svoboda 1991; Klíma 1995). These have been interpreted as the vestiges of Upper Palaeolithic hunter-gatherer societies, who pursued a largely mobile lifestyle following migratory animal herds through the Moravian Corridor, but who returned continually to certain strategic sites, perhaps according to seasonal rounds (Beresford-Jones *et al.* 2011).

These Gravettian occupations took place in the context of generally cold climates, but punctuated by complex and often rapid fluxes towards warmer periods (the so-called Dansgaard-Oeschger cycles). At DVII, for instance, palynological, malacological, geoarchaeological and charcoal evidence (Svoboda 1991; Opravil 1994; Beresford-Jones *et al.* 2011) combine to suggest a unique 'mammoth steppe' environment (Guthrie 2001) of seasonally diverse habitats varying widely across the landscape. Outside river valleys these would have comprised large open areas of natural steppe (*sensu* Guthrie 2001, and not to be confused with today's largely secondary steppe), with continuous vegetation of grasses and herbaceous plants but too dry for trees. Within sheltered river valleys, meanwhile, taiga (boreal woodland) environments persisted, supporting conifers (*Pinus*, *Abies, Larix*/*Picea* spp.), a few other cold-tolerant tree species such as *Betula* sp., and various wetland plants of the riparian and marshy ecologies immediately along the river's edge.

Gravettian hunter-gatherers would have exploited this mosaic of habitats in various ways. Riparian and obligate wetland plants likely offered the most plausible sources of readily available carbohydrates (Revedin *et al.* 2010; Gordon Hillman *pers. comm.*), while steppic regions and boreal woodland would offer more seasonally available resources. Exploiting plant foods from these latter habitats would require considerable "ecological intelligence" (Jones 2009: 173)—a critical feature of the increasingly complex lifeways that allowed humans to expand into these hitherto marginal ecologies. The key expression of an ecological intelligence necessary to exploit plant foods in such landscapes would be that of "timely dextrous unpacking" (Jones 2009: 173)—knowing which plants were safe to eat, at what times of year they could be usefully gathered and how to process these plants to neutralise any toxins while extracting nutrients in a consumable form. Alongside the various types of starchy tissue, other plant foods would also have been available in the environment around DVII, potentially including, for instance, the scales and inner bark of certain pine species (see Hedrick 1919; Östlund *et al.* 2004). Certain essential subsidiary nutrients, such as vitamin C in Rosaceae and/or Ericaceae fruits, were also almost certainly provided by plants (Jones 2009).

Dolní Věstonice II (2005 excavations)

The DVII-05 excavations were carried out on a surviving section of the Gravettian cultural layer, located close to the original position of the famous 'triple burial' site. This uncovered a scattering of lithic and bone debris, and a dense concentration of charcoal up to 200mm thick lying upon rubified loess interpreted as an *in situ* hearth (see Beresford-Jones *et al.* 2010, 2011). Excavation proceeded by 100mm deep spits within 0.5m^2 quadrants, retaining all excavated sediments as flotation samples following the removal by hand of larger finds. A total of 992 spit contexts totalling 3632 litres of deposits were floated in the field, and their light fractions separated using a 500μm and 2mm sieve stack.

Method

Archaeological parenchyma remains

We report here on the analysis of only a small sub-set of the very large assemblage of charred plant remains extracted from the DVII-05 contexts: 19 samples from the charcoal-rich hearth deposit and 10 other samples from across the cultural layer. The >2mm light fraction of these samples was sorted at the University of Cambridge using a light microscope to identify potential parenchyma fragments, following Hather (1993: 3). Visual assessment suggested that between 5 and 10% of the DVII-05 assemblage (depending on sample) was made up of non-woody charred remains. Yet, as Hather (1993: 3) warns, parenchymous remains "are often difficult to recognise and are often wrongly assigned as wood charcoal". Nearly 200 putative parenchymous fragments were further examined by fracturing to expose a clean fresh surface using a scalpel blade (Hather 2000: 76). Just over half were revealed to be wood charcoal: a typical proportion in parenchyma studies. This left a sample set of 83 pieces of confirmed parenchyma tissue for analysis using the SEM, almost all of which had a maximum diameter of between 2 and 8mm. Sixty-one fragments came from the hearth feature, and 22 from other contexts scattered across the cultural layer.

Modern reference materials

Aside from their introduction as plant foods, another pathway through which charred soft plant tissue might enter an Upper Palaeolithic hearth context is via dung burned as fuel. Previous investigations of the DVII-05 hearth have shown unambiguously that the principal fuel was conifer wood (see Beresford-Jones *et al.* 2010). In an environment in which wood may have sometimes been scarce and, for instance, mammoth dung copious (Haynes 1991), it seems almost inconceivable that hunter-gatherers did not occasionally exploit large herbivore dung as fuel, just as they have in more recent contexts (Rhode *et al.* 1992). To gain an approximate impression of how charred plant remains might appear in such an archaeological context, we obtained samples of elephant dung from animals kept at Whipsnade Zoo (England), and fed on a diet of around 80% hay, 15% vegetables and 5% tree wood. Whole boluses of elephant dung were charred in a muffle furnace at 300°C for five hours, in preparation for SEM analysis.

Further reference materials of charred USOs were also prepared as part of this investigation to provide comparisons with the archaeological materials, and will be reported on separately in a future publication.

Scanning electron microscopy

Archaeological samples and the reference materials were examined using a Jeol 820 SEM located in the Earth Sciences Department, University of Cambridge. Samples were prepared for SEM viewing by mounting them on stubs and sputter-coating them with gold under vacuum. SEM photographs were taken at 5–20Kv at a variety of magnifications, allowing the comparison of archaeological samples with reference materials at different resolutions and with published photographs from Hather (1993, 2000). For this purpose, we collected 550 SEM photographs of archaeological parenchyma fragments from DVII-05 and 400 SEM photographs of reference parenchyma from 32 species of modern USOs.

Results

The DVII-05 archaeobotanical assemblage is very large and the precise overall proportion of non-woody charred remains has not yet been assessed. Nonetheless, that proportion is clearly significant: somewhere between 2.5 and 5% depending upon samples (see also Beresford-Jones *et al.* 2010). Under SEM virtually all of the 83 fragments examined were shown to be largely, or entirely, composed of radially-oriented parenchymous tissues that make up non-woody plant structures. Nearly all of the vascular tissue in association with this parenchyma showed the characteristics of xylem vessel elements, typical of angiosperms (Figure 1a and b). Very few instances of tracheid structures were found that would be indicative of conifers and ferns.

A variety of different parenchyma morphologies were evident in the samples. While most fragments showed some destruction of the cellular tissue caused by the expansion of escaping moisture during charring, some pieces preserved visible cellular structure and other characteristics that should, in principle, be useful for characterising this soft-tissue assemblage.

Secretory cavities

Secretory cavities are visible in several parenchyma fragments. One fragment from the hearth, for instance, shows a cavity *c.* 400μm in diameter (Sarah Mason and John Hather *pers. comm.*; see Figure 1c), almost identical in form and size to that used by Mason *et al.* (1994) to identify USO remains from the Asteraceae family in their original DVII analysis (Figure 1d). In each case these secretory cavities have epithelial cells bordering the cavity which have collapsed on charring, leaving their impression on the cell wall lining. They are each also bordered by a smaller (*c.* 200μm × 50μm) cavity of approximately the same size and shape, and by intact parenchyma cells adjacent to the cavity. A number of USOs of the Asteraceae family in our reference collection show similar secretory cavities, including *Inula helenium* and *Arctium lappa* (Figure 1e), supporting the association with this plant family.

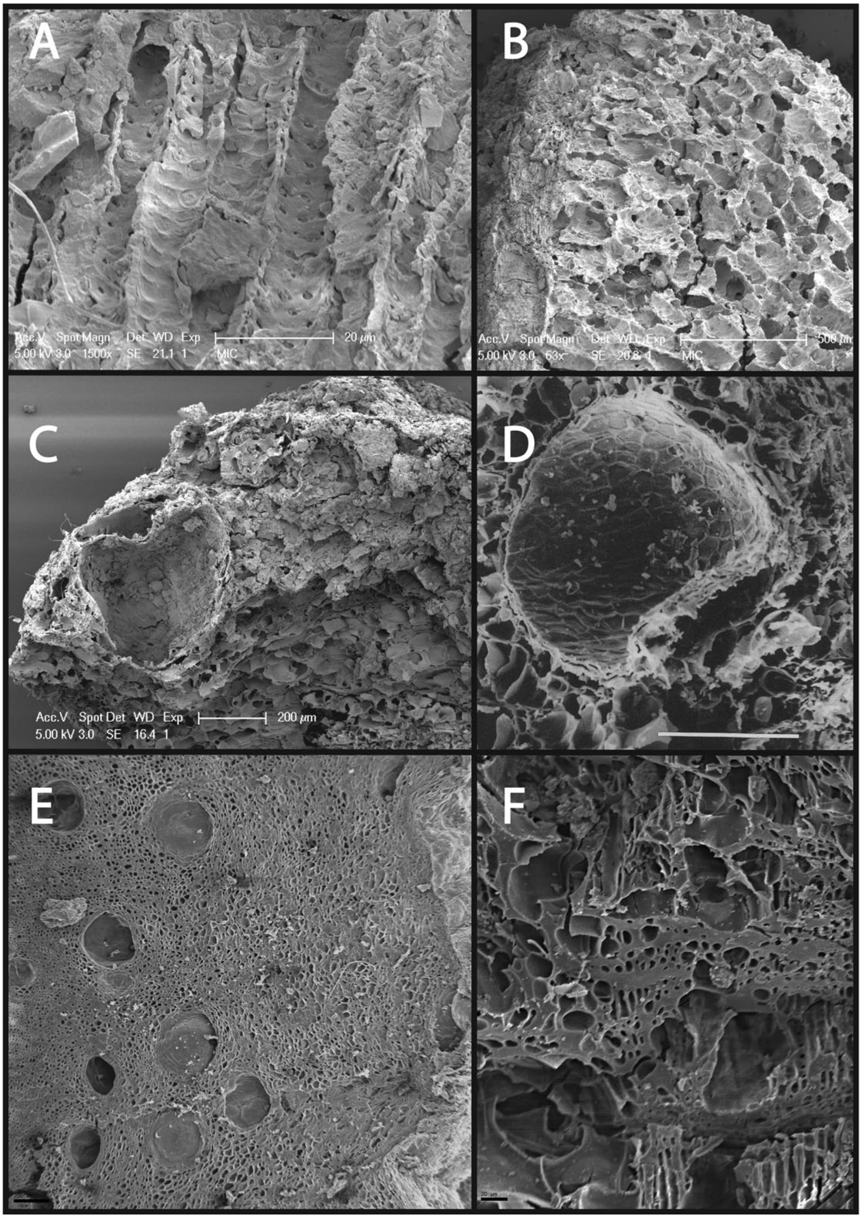

Figure 1. Archaeological parenchyma from DVII. ***a)*** *Xylem vessel elements shown close-up (fragment V0A4-8);* ***b)*** *same fragment as depicted in Figure 1a, with xylem vessel elements shown at lower magnification on left-hand side of the photograph;* ***c)*** *secretory cavity identified in DVII-05 parenchyma (fragment X0A1-2). Preserved parenchyma cells are visible across the lower third of the image;* ***d)*** *secretory cavity identified by Mason* et al. *(1994) in material excavated in the 1980s (photograph reproduced with permission from Sarah Mason);* ***e)*** *examples of secretory cavities in* Inula helenium, *photographed for the reference collection;* ***f)*** *parenchyma cells and vascular tissue degraded into solid carbon, visible as a band across the centre of the photograph (cf. Hather 2000: fig. 85; fragment U3B1-2).*

Aerenchyma

Six fragments from the hearth and cultural layer showed features of what Hather (2000: 36) calls 'type ii' aerenchyma in which "isodiametric cells form chains and plates surrounding large intercellular spaces". These cells have partially collapsed on charring, leaving walls covered with the impressions of collapsed cell outlines and surrounded by large cavities of intercellular airspaces (e.g. Figure 2a and b). This type of aerenchyma is particularly common in aquatic taxa.

Druse crystals

Druse crystals were identified in at least three fragments. These include an aerenchyma fragment from the hearth which showed clusters of crystals *c.* 100μm in diameter with varying numbers of elongated, oblong-shaped crystals in each group (Figure 2c). The crystals appear rounded rather than sharply pointed at each end, and are strongly textured by fissures and pits. This texturing may indicate a long duration and/or high temperature burning period (Canti 2003). The effects of burning on druse, however, are not always consistent (Robyn Veal *pers. comm.*); indeed, a second fragment shows druse of a different morphology which lack this textured surface, with crystal clusters *c.* 250μm × 150μm across composed of many long, pointed crystals. A square prismatic crystal *c.* 10μm across was also noted on a third fragment from the hearth V0D4-2.

Other

Further features observed in the parenchyma fragments included patchy occurrences of solidified parenchyma cells and vascular tissues that had degraded into solid carbon during charring (cf. Hather 2000: fig. 85; Figure 1f). A single amorphous fragment of destroyed plant tissue was also identified from the hearth deposits, lacking cellular structure and covered with a series of depressions (Figure 2d). This is similar in character, although morphologically and texturally different, to amorphous pieces of "finely comminuted plant material" described by Mason *et al.* (1994: 53), interpreted by them as the products of a cooked plant food 'mush' analogous to that obtained in other contexts from wild acorns. Similarities were also noted between fragment V0A3-1 and amorphous charred foodstuffs found in Roman-era contexts (Robyn Veal *pers. comm.*). As a preliminary investigation to further expand the range of available comparisons, we considered inner bark as a potential food source, using samples of *Pinus sylvestris* (Scots pine) processed by a four-stage process of baking, grinding, chewing and charring. The resulting mix preserved a distinctive macrostructure showing many tracheids and fibres that had become broken and tangled together (Figure 2f), bearing no resemblance to the amorphous materials from DVII. While bark processed in this manner can therefore be ruled out as a source for this amorphous material, we continue to interpret these pieces as probable evidence of plant processing activities.

Moreover, our experiments using elephant dung do not suggest that this amorphous material is the vestige of the burning of elephantid dung for fuel in the DVII-05 hearth. The charring process reduced each bolus almost entirely to ash that crumbled readily into

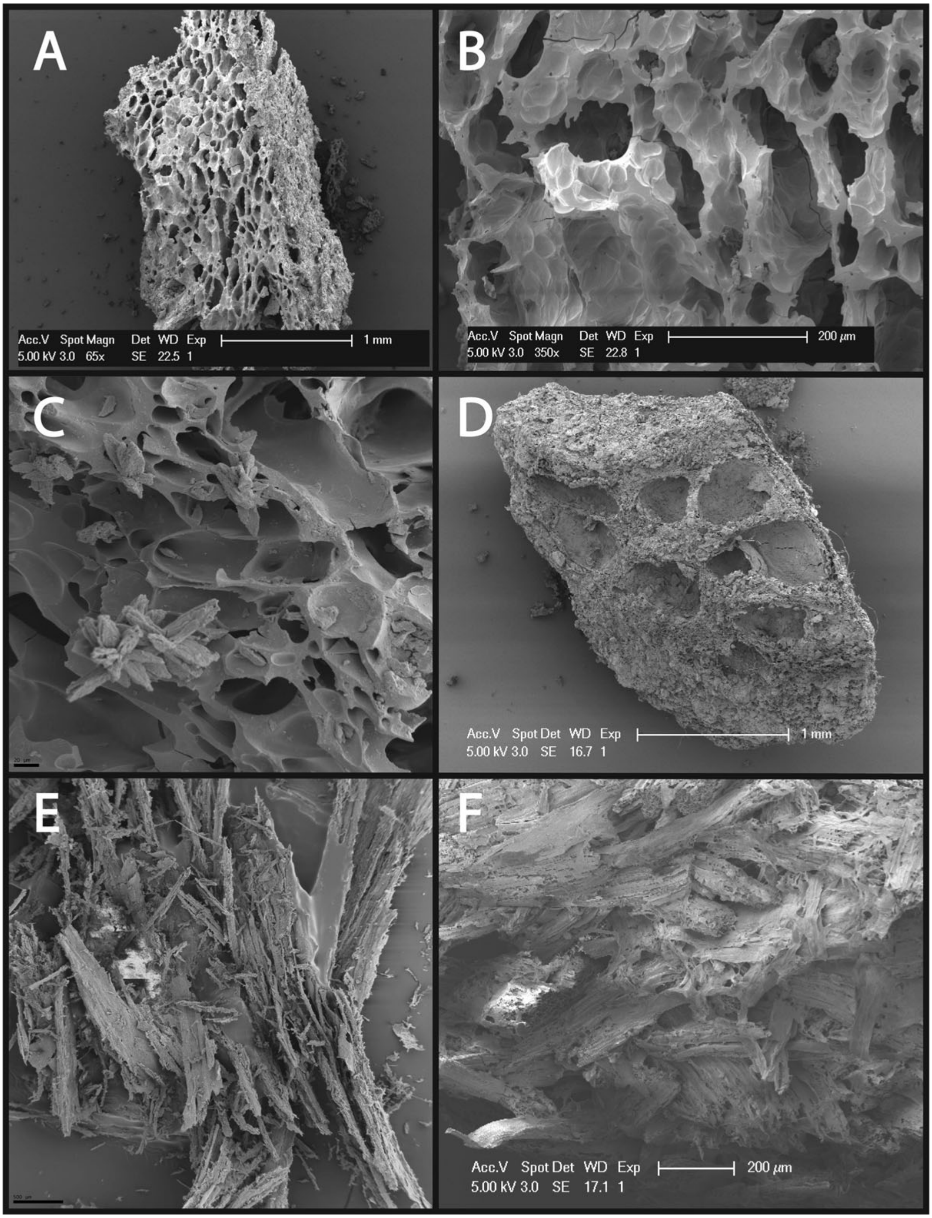

Figure 2. Archaeological parenchyma from DVII. ***a)*** *Fragment of aerenchyma (U4C1-6);* ***b)*** *close up of fragment shown in Figure 2a, showing the outlines of collapsed cells;* ***c)*** *druse crystal from fragment X0B1-6;* ***d)*** *fragment of highly degraded plant matter reminiscent of plant matter processed into 'mush' (V0A3-1);* ***e)*** *remains of charred elephant dung, showing ashy pseudomorphs of grasses;* ***f)*** *bark of* Pinus sylvestris *(Scots pine) processed by baking, grinding, chewing and charring.*

dust under light pressure. SEM analysis was conducted on the fragile ashy pseudomorphs of macrofossils of grasses which remained visible inside the charred dung remains (Figure 2e). Yet no similarities were observed between the charred elephant dung and either the archaeological parenchyma, or the amorphous 'finely comminuted plant material'. Indeed the fragility of the charred dung remains make it unlikely that such evidence would survive in such ancient archaeological contexts.

Under the SEM one sample was also found to be a wood fragment from a deciduous tree species, only the second such example from the DVII-05 assemblage in which virtually all wood charcoal identified to date comes from conifer species (Beresford-Jones *et al.* 2011).

Discussion

These findings build directly on those of Mason *et al.* (1994), who identified parenchyma in a small 280ml sample from Hearth D in the first settlement unit of the Western Slope at DVII (dated by two independent dates to 25 740±210 BP [GrN-15277] and 25 570±280 BP [GrN-15276]). Our results come from a vastly larger assemblage of charred remains from DVII-05, of which up to 5% are parenchymous materials while the great majority are comprised of conifer charcoals. These parenchymous materials do not originate from conifers, for the xylem tissue directly associated with them is comprised predominately of the vessel elements of angiosperms, with few tracheid structures observed. Thus these parenchymous materials originate from a different class of plants, easily distinguished from the wood used to fuel the DVII-05 hearth; they are not simply the remains of conifer roots burned as fuel, or accidentally *in situ*. Given the *Botrychium* starch identified at nearby Pavlov VI (Revedin *et al.* 2010), it is also interesting to note the absence of structures indicative of ferns.

The presence of parenchymous tissues in the DVII-05 hearth could have arisen through 'accidental inclusion', which might occur, for instance, if the fire had been laid on top of natural growth. Yet the paucity of smaller inedible secondary roots from likely *in situ* plants such as grasses argues against this. Indeed, the occurrence of aerenchyma suggestive of wetland plants in the assemblage further diminishes the likelihood of 'accidental inclusion' because the hearth was plainly not set in a wetland environment (Beresford-Jones *et al.* 2011). SEM analysis also showed no discernible similarities between the charred elephant dung and the DVII-05 fragments. Thus, pending further investigation, we deem it unlikely that either the parenchyma or the 'finely comminuted plant material' found in the hearths at DVII were incorporated through inclusions of animal dung used as fuel. While parenchyma is present in small quantities in most parts of plants, the morphology of the DVII-05 fragments—composed primarily of parenchyma, some showing evidence of gelatinised starch and additional features such as secretory cavities—is instead overwhelmingly indicative of specifically starch-rich plant tissues such as those found in swollen stems and USOs. Taken together, this evidence suggests deliberate human transport to, and incorporation of plant starchy tissues in, the hearth site.

Previous micromorphological investigations of the hearth have demonstrated that the charred remains were deposited during several separate episodes of burning, each separated by long periods of time and probably corresponding to different visits to the site (Beresford-Jones *et al.* 2011). Parenchyma fragments were recovered from each of these individual burning events. This evidence suggests that starchy tissues were utilised by humans on multiple separate visits to the site, and that these resources were available repeatedly during these episodic occupations.

Ethnographic analogies with contemporary hunter-gatherer societies would suggest that soft plant tissues could have been used by Palaeolithic groups for a variety of reasons including as food staples or food flavourings, for medicinal uses or for other purposes (the edible roots of *Inula* may, for instance, also be used as a dye; *Plants for a Future* n.d.). Distinguishing between the archaeobotanical signatures of these different possible uses will require further investigation, including detailed analysis of the spatial distribution of parenchymous remains across different contexts in the cultural layer, and clarification—as far as possible—of the taxa represented. These are both the subject of ongoing research into the DVII-05 assemblage.

Nonetheless, anecdotal evidence that parenchymous remains are a more significant feature of the hearth contexts than elsewhere in the cultural layer, coupled with the high starch content of parenchymous tissues, suggests to us that the most parsimonious explanation is that these represent the remains of plants gathered for consumption as food—an interpretation consistent with those of Mason *et al.* (1994) and Revedin *et al.* (2010), and with theoretical arguments for plant food consumption during the Palaeolithic (e.g. Jones 2009).

The carbonisation of plant food fragments and their eventual deposition in a hearth context may further suggest that some swollen stems or USOs were being deliberately processed in the vicinity of the hearth, for instance by roasting, baking or boiling. Indeed, the DVII-05 samples showed possible evidence of plant processing, such as the fragment of destroyed plant material lacking cellular structure in sample V0A3-1 (Figure 2d). In this context too it is notable that the DVII-05 parenchymous materials included several pieces containing calcium oxalate crystals. Calcium oxalate causes irritation to the digestive tract, produces kidney stones and inhibits the absorption of essential minerals, particularly calcium and iron, so that it is toxic to herbivores and humans if ingested in any quantity (Savage *et al.* 2000; Siener *et al.* 2006). Insoluble oxalates cannot be broken down but must be leached out and today most food plants containing large quantities of oxalate are therefore processed by boiling rather than any other method (Savage *et al.* 2000). If the parenchyma containing druse crystals identified at DVII were gathered for consumption, this would imply knowledge of how specific groups of plants should be processed to neutralise toxicity. Precisely such 'ecological intelligence'—an acute knowledge of botany and the ability to extract from plants nutrients that were not readily available—is suggested by Jones (2009) to have been a vital requirement of the groups who moved into new higher latitude European habitats during the Upper Palaeolithic. Indeed, the evidence suggestive of plant processing at DVII (Mason *et al.* 1994 and this study) and Pavlov VI (Revedin *et al.* 2010) is consistent with this argument. Cooking USOs using heat treatments can increase nutrient density, remove toxicity, improve the flavour and edibility, and preserve the USO by removing moisture (Wandsnider 1997; O'Connell *et al.* 1999). It would have expanded the range of food sources accessible to Gravettian peoples.

Further evidence of sophisticated foraging behaviours is provided by the aerenchyma reported in this analysis, which suggests the exploitation of aquatic taxa from riparian or marshy environments. The site of DVII overlooks the Dyje River and there is evidence that damp conditions persisted at the mammoth bone accumulation in its immediate vicinity (Svoboda 1991) and in the pollen records of the nearby site of Bulhary (Rybníčková & Rybníček 1991). Revedin *et al.* (2010) further suggest the harvesting of aquatic taxa *Typha* spp. at the nearby Pavlovian site of Pavlov VI. The Gravettian hunter-gatherers who occupied Dolní Věstonice II thus appear to have exploited a mosaic of different habitats and had a broad familiarity with the plant foods each provided. Wetland plants would have offered the most plausible sources of readily available carbohydrates (Gordon Hillman *pers. comm.*), while steppic regions and boreal woodland would have offered more seasonally available resources.

Conclusion

Although there are powerful theoretical arguments for the importance of gathered plant foods in the Upper Palaeolithic diet (e.g. Jones 2009) and increasing microfossil evidence of various sorts, macrofossil evidence for plant food remains from Palaeolithic contexts is still scarce. The evidence we have presented here builds directly upon the seminal analysis of Mason *et al.* (1994) by conducting large-scale flotation to extract very large quantities of charred plant remains from a hearth deposit and associated cultural layer at Dolní Věstonice II. While dominated by the charcoals of conifers used to fuel the hearth, this ancient archaeobotanical record also contains a significant proportion of parenchymous materials originating from angiosperms. In combination, various features of these parenchyma remains demonstrate the presence of starchy tissues. These suggest, in turn, that the Gravettian hunter-gatherers who occupied the site some 30 000 years ago were indeed consuming plants from various habitats, either as food or to other corporeal ends (e.g. as medicines). Research into parenchyma as a source of palaeobotanical evidence in archaeology has remained under-developed since the work of Hather (1993, 2000; although see e.g. Paz 2001; Wollstonecroft *et al.* 2008). Further investigation of how parenchymous tissues deform and change under different charring conditions, and larger collections of photographed reference materials, are required against which archaeological materials can be compared. Yet despite these current limitations, our findings here argue for further exploration of parenchyma remains as a potentially critical category of evidence for past plant food consumption, particularly during the Palaeolithic, for which there may be few other surviving forms of macrobotanical evidence. Analytical work into the DVII-05 assemblage is ongoing, yet only a tiny fraction of the parenchyma recovered has yet been analysed. That in itself demonstrates the vast amount of evidence that could be recovered if techniques of flotation with appropriate mesh sizes are used at Palaeolithic excavations. Certainly, our findings from DVII-05 demonstrate the potential of this archaeobotanical record—interpreted in conjunction with other data—both for offering proxy evidence of the changing climatic conditions during which humans were first expanding into these hitherto marginal ecologies, and indeed, for shedding new light upon the complexity of the lifeways that enabled them to do so.

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