



Plant use in the Lower and Middle Palaeolithic: Food, medicine and raw materials

Karen Hardy ^{a, b}

^a ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain

^b Departament de Prehistòria, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain

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ABSTRACT

There is little surviving evidence for plant use in the Lower and Middle Palaeolithic periods yet the evidence there is, clearly indicates the importance of plants in the diet, as medicines and as raw materials. Here, the current evidence for plants is summarised, and the way this can be used to enrich perceptions of the Lower and Middle Palaeolithic are explored. The evidence for plant food fits well with basic nutritional requirements while the presence of medicinal plants correlates with plant-based self-medication by animals. Many plant-based technologies are likely to have developed early in the Palaeolithic. Though investigating this is challenging due to a lack of evidence, the extensive evidence for use of plant materials as tools by chimpanzees provides a broad backdrop. The ecological knowledge carried by all hominins would have provided a safety net when moving into new regions, while varying levels of neophobia would have enabled adaptation to new environments as hominin populations moved and climates changed. Recent plant use among traditional societies in high latitudes shows that even in locations with reduced biodiversity, plant resources can fulfil essential dietary requirements.

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1. Introduction

Plants were an integral and essential part of everyday life in the Palaeolithic, just as they are today. They provided nutrients, including essential carbohydrates (Hardy et al., 2015a), raw materials, medicines and, once fire had developed, fuel. The importance of plants in human evolution is such that Australopithecine species are in part defined on the physical and isotopic evidence for the differences in their plant-based diets (e.g. Lee Thorp et al., 1994, 2010; Strait et al., 2009). The earliest appearance of cut marked bones indicating animal butchery is 3.4 million years (McPherron et al., 2010) while the earliest evidence for flaked stone tools dates to 3.5 million years (Harmand et al., 2015). The implications of meat eating and stone tool manufacture are considered so significant in terms of behaviour and brain development that this, together with the limited evidence for plants in the early Palaeolithic, has meant that the roles of plants in the diet and technology has been largely eclipsed in these early periods.

Wide-ranging theories on Palaeolithic hominin behaviour and brain development have focused almost exclusively on the need

for protein (e.g. Kaplan et al., 2000; Morgan et al., 2015; Richards and Trinkaus, 2009; Snodgrass et al., 2009; Snodgrass and Leonard, 2009). The technologies and use of plant-based raw materials have received little attention, while the link between cognition and technological innovation has focused primarily on lithic raw material acquisition patterns and stone tool technologies (e.g. de Beaune, 2004; Stout and Chaminade 2012; Toth and Schick 2018).

Yet it is impossible from the dietary (Hardy et al., 2015a), unlikely from the medicinal (Huffman, 2016) and unrealistic from the technological perspectives, that plants were not a fundamental part of all aspects of Palaeolithic life. There is widespread acknowledgement that plants were eaten, and used in technology, throughout the Palaeolithic (e.g. Klein, 2009; Tyldesley and Bahn, 1983), identification of a profound problem of 'missing' data on the early use of plants (Ambrose, 2001), and the recognition that the vast majority of innovations have probably been lost (Reader, 2004). In archaeological contexts with exceptional survival of plant materials, fibre artefacts outnumber stone tools by a factor of 20 to 1, while in anaerobic conditions 95% of all recovered artefacts are either made from wood or fibre (Adovasio et al., 2007). This largely corresponds with chimpanzee tool use, in which tools made from organic materials/vegetation is far in excess of use of stone for

E-mail address: khardy@icrea.cat.

tools, with proportions ranging from 11 to 18% for stone, against 78–83% for plant based materials (Reader, 2004). Most of the technological items used by chimpanzees today would not enter the archaeological record (McGrew, 2010a).

The use of plants as medicine and for technological items is extensive among higher primates (Huffman 1997, 2001, 2003, 2016; Huffman and Seifu, 1989; Humle and Matsuzawa 2002; Koops et al., 2015; Masi et al., 2012; McGrew, 2010a, 2010b, 2013; Pansini and de Ruiter, 2011; Roffman et al., 2015; Russon et al., 2009; Sanz and Morgan 2007; Van Schaik, et al., 1996), while botanical knowledge has been recorded among chimpanzees (Janmaat et al., 2013). McGrew (2010a) suggests that anything done by a chimpanzee today was within the capabilities of the Last Common Ancestor (LCA), 6–7 million years ago. A broad ecological knowledge, which includes plants as well as other naturally occurring items, would have provided the foundation for adaptation to changing climates and environments as hominins spread into new regions (Hardy and Kubiak-Martens, 2016). Therefore, use of plants needs to be incorporated into perspectives on early Palaeolithic diet, dispersals, and behavioural, technological and cognitive development for, not to do so, results in partial perspectives (e.g. Guil-Guerrero 2017; Hosfield, 2016). For example, the availability and dietary need for carbohydrates should be taken into account when investigating survival limits.

Here, I outline the current evidence for the use of plants in the Lower and Middle Palaeolithic as food, medicine and raw materials and place this within a broader evolutionary perspective. I also examine ways in which this evidence can be used to enrich perceptions of these periods, in terms of diet, the use of non-nutritive plant secondary compounds, technological expertise, occupation of cold environments and pioneer populations.

2. Archaeological evidence for plants

Table 1 summarises the evidence of plant use from the Lower and Middle Palaeolithic. This includes plant and wood fragments, evidence from phytoliths, and chemical and microfossil evidence extracted from dental calculus. It does not include results of use wear or dental microwear studies, these are discussed below. The evidence for fire has not been included. Arguments about the timing of the habitual, controlled use of fire have been extensively discussed elsewhere (Gowlett, 2016; Gowlett and Wrangham, 2013; Roebroeks and Villa, 2011; Wrangham, 2017; Wrangham and Carmody, 2010). Though the timing of the earliest use of fire remains unclear, hearths representing repeated, controlled use of fire are present in the archaeological record from around 400 ka (Karkanas et al., 2002; Shahack-Gross et al., 2014). The evidence for controlled use of fire is extensive in the Middle Palaeolithic (Albert et al., 1999, 2000, 2003, Albert, 2007; Allué et al., 2012; Badal et al., 2012; Cabanes et al., 2007, 2010; Esteban et al., 2017; Goldberg et al., 2012; Madella et al., 2002; Pastó et al., 2000; Vallverdú et al., 2005). The evidence for birch bark pitch, which can only be recovered through heating at high temperatures in an oxygen-free environment, on artefacts from a pre-MIS 6 context (Mazza et al., 2006), is perhaps the clearest indication that complex pyrotechnology was well established by the early Middle Palaeolithic.

3. Plants as food

Use wear traces from the Oldowan site of Kanjera (~2 Ma) were interpreted as the result of processing soft grit-covered plant materials such as underground storage organs (USOs) (Lemorini et al., 2014). USOs include roots, bulbs, tubers, corms and rhizomes, examples eaten today include potatoes, yams, onions and ginger.

Abundant *Celtis* seeds occur on several Lower and Middle

Palaeolithic sites, including Dmanisi, Gran Dolina, Zhoukoudian, Vallonet, Terra Amata, Caune de l'Arago, Grotte du Lazaret, Mas des Caves, Douara Cave (Allué et al., 2015; Chaney, 1935; de Lumley, 1975; Laville and Renault-Miskovsky, 1977; Matsutani, 1984). These are arguably the most common edible plant remains from early Palaeolithic periods, though Dennell (2008) argues for caution suggesting that other animals also eat these seeds. The survival of *Celtis* seeds is largely due to a process of biomineralization that assists in their preservation (Allué et al., 2015).

Further evidence for plants in the Lower Palaeolithic includes starch granules from two different plant sources, one of which may be from grass seeds, recovered from samples of dental calculus from the site of Sima del Elefante (1.2Ma) (Hardy et al., 2017). Fragments of nut shell from 7 species comprising wild almond (*Amygdalus communis* ssp. *Microphylla*; *A. korshinskii*) – this is toxic when raw (Zohary et al., 2012) –, prickly water lily (*Euryale ferox*), Atlantic pistachio (*Pistacia atlantica*), pistachio (*P. vera*), Palestine oak (*Quercus calliprinos*), Mt Tabor oak (*Q. ithaburensis*) and water chestnut (*Trapa natans*), were recovered from the 790 ka site of Gesher Benot Ya'aqov together with pitted basalt and limestone stones, possibly used for opening the nuts (Goren-Inbar et al., 2002, 2004). An additional assemblage of over 100,000 macrobotanical fragments was also recovered (Melamed et al., 2016). Though the assemblage was uncarbonised, and therefore cannot be ascribed with absolute certainty to human agency, Melamed et al. (2016) conducted a comparative study with the natural plant distribution from associated geological layers. This demonstrated a far higher proportion of edible plants in the archaeological layers, suggesting deliberate collection.

Boraginaceae, for which there is evidence from Lower Palaeolithic Dmanisi (Gabunia et al., 2000; Messenger, et al., 2008) as well as Middle Palaeolithic Douara Cave (Matsutani, 1984), comprise a family that has many taxa which are both edible and have a broad range of medicinal properties. Chemical compounds identified as polyunsaturated fatty linoleic and linolenic acids, most probably from pine nuts, were extracted from samples of hominin dental calculus from Qesem Cave (400–300 ka), indicating consumption of food items containing these essential fatty acids (Hardy et al., 2015b). A large assemblage of uncarbonised plant remains comprising edible and medicinal plants were recovered from Schöningen (300 ka). It is not clear though, whether these plants were brought to the site or are the remains of natural deposits (Bigga et al., 2015). Middle Palaeolithic sites where plant remains have been recovered include Theopetra Cave where many edible plant species including seeds, nuts, and fruits were recovered (Mangafa, 2000). At Ehringsdorf, Germany, charred linden tree fruits (*Tilia*) and Kornel cherry (*Cornus mas*) fruits were recovered while at Ributz, Germany charred hazelnuts (*Corylus avellana*) were found (Richter, 2016). Charred seeds from species that are edible, and some that have medicinal properties, were recovered from Neumark-Nord 2, Germany (Pop et al., 2016). A large assemblage comprising charred legume and other fragments of both edible and medicinal plants, were recovered from Kebara Cave, Israel (Lev et al., 2005). A wide range of phytoliths from Amud Cave, Israel (70–55 ka) suggest grass seeds may have been collected for food (Madella et al., 2002). DNA and chemical biomarkers demonstrating ingestion of starchy foods, mushrooms and medicinal plant species were extracted from the dental calculus of Neanderthals from El Sidrón, Spain (49 ka) (Hardy et al., 2012; Weyrich et al., 2017). Starch granules suggesting ingestion of plant food were recovered from dental calculus samples at several other Neanderthal sites (Henry et al., 2011; Power et al., 2018; Salazar García et al., 2013). Finally, charred pine nut and olive fragments were recovered from the late Neanderthal site of Gorham's Cave, Gibraltar (Barton et al., 1999; Barton, 2000).

Table 1

Plant remains from the Lower and Middle Palaeolithic. Column 3. E = edible; T = technological, M = medicinal. The relative age of sites is given according to the original publication. For plant remains from the Middle Stone Age in Africa see [Wadley \(2015\)](#).

Site	Age	E/T	Source of material	Interpretation	References
Dmanisi	Lower Palaeolithic ~1.8 Ma	E/M	<i>Celtis</i> seeds Boraginaceae taxa including <i>Anchusa</i> , <i>Lycopsis</i> , <i>Lithospermum</i> , <i>Ephedra</i> .	Edible plants.	Messenger et al. 2008 ; Gabunia et al., 2000 .
Sima del Elefante, Spain	1.2 Ma	E/T	Dental calculus, microfossils from two different starchy plants. Non-edible wood fragment.	Consumption of two starchy plant sources. Possible tooth picking.	Hardy et al., 2017 .
Peninj, Tanzania	Acheulian, 1.7–1.5 Ma	T	Wood phytoliths adhering to tools.	Woodworking.	Dominguez-Rodrigo et al. 2001 .
Vallonnet	~1 Ma	E	<i>Celtis</i> seeds.	Edible plants.	Laville & Renault-Miskovsky, 1977 .
Gesher Benot Ya'aqov, Israel	790 ka	E/M	Over 100,000 macrobotanical items, comprising 78 species and 37 genera.	Food, medicine, raw materials. Uncarbonised but most likely anthropogenic.	Melamed et al., 2016 .
Gesher Benot Ya'aqov, Israel	790 ka	E/T	Edible nut shell fragments and pitted basalt stones. Wood with possible modification marks.	Processing and consumption of nuts. Woodworking.	Goren-Inbar et al. 2002, 2004 .
Gran Dolina	780 ka	E	<i>Celtis</i> seeds.	Edible plants.	Allué et al., 2015 .
Zhoukoudian	Middle Pleistocene	E	<i>Celtis cf. barbouri</i> .	Edible plants.	Chaney, 1935 .
Caune de l'Arago	530-350 ka	E	<i>Celtis</i> seeds.	Edible plants.	Laville & Renault-Miskovsky, 1977 .
Clacton-on-Sea, England	450 ka	T	Spear tip made on yew (<i>Taxus baccata</i>).	Woodworking.	Oakley et al. 1977 .
Qesem Cave, Israel	400-300 ka	E	Dental calculus, Chemical compounds showing ingestion of essential polyunsaturated fatty linoleic and linolenic acids. Microfossils. Pollen, fungal spores, insect fragments, starch granules, microcharcoal.	Consumption of essential polyunsaturated fatty linoleic and linolenic acids, possibly from pine nuts.	Hardy et al., 2015a,b .
Terra Amata	380 ka. Yokoyama et al., 1985 .	E	<i>Celtis</i> seeds.	Edible plants.	Laville & Renault-Miskovsky, 1977 .
Bilzingsleben Germany	MIS 9	T	Possible worked wood.	Possible evidence for woodworking.	Schoch et al., 2015 .
Mas des Caves Schöningen Germany	Lower Palaeolithic 300 ka	E	<i>Celtis</i> seeds.	Edible seeds.	de Lumley, 1975 .
Schöningen Germany	300 ka	E/T/M	66 edible plant species, 32 with medicinal compounds.	Fuel, food, medicine, raw materials. Uncarbonised, possibly natural.	Bigga et al. 2015 .
Cannstatt I, Germany	MIS 7	T	9 spears, lance, double pointed stick, burnt stick.	Woodworking.	Schoch et al., 2015 .
Poggetti Vecchi, Italy	171 ka	T	Possible worked wood.	Possible evidence for woodworking.	Schoch et al., 2015 .
Aranbaltza III, Spain	137-50 ka	T	58 worked pieces of wood including wooden digging sticks.	Woodworking.	Aranguren et al., 2018 .
Grotte du Lazaret, France	190-130 ka	T	Wooden digging stick.	Woodworking.	Rios-Garaizar et al., 2018 .
Campitello Quarry, Italy	Pre-MIS stage 6.	E	<i>Celtis</i> seeds.	Edible plants.	Laville & Renault-Miskovsky, 1977 .
Ehringsdorf, Germany	Middle Palaeolithic.	T	Two artefacts with adhering birch bark.	Pitch and hafting.	Mazza et al. 2006 .
Rabutz, Germany	Middle Palaeolithic	E	Charred fruits of the linden tree (<i>Tilia</i>) and Kornel cherry (<i>Cornus mas</i>).	Edible plants.	Richter, 2016 .
Lehringen, Germany	125 ka	E	Charred hazelnuts (<i>Corylus avellana</i>).	Edible plants.	Richter, 2016 .
Neumark-Nord 2, Germany	~125 ka	T	Spear point made on yew (<i>Taxus</i>).	Woodworking.	Langley et al., 2008 .
Kalamakia Umm el Tlel, Syria	89.5–62 ka	E	Charred seeds from several edible plants.	Edible and medicinal plants.	Pop et al., 2016 .
Inden-Altdorf, Germany	~70 ka	T	Dental calculus. Starches, phytoliths.	Starchy food.	Power et al., 2018 .
Kebara Cave, Israel	60-48 ka. Valladas et al., 1987 .	T	Bitumen adhering to stone tools.	Hafting.	Boëda et al., 2008 .
Theopetra Cave, Greece	MIS 5e.	T	Artefacts with adhering birch bark.	Pitch and hafting.	Pawlik and Thissen, 2011 .
Douara Cave, Syria	60-48 ka. Valladas et al., 1987 .	E/M	Charred legume and other plant fragments.	45 Edible and medicinal plant species.	Lev et al., 2005
Konigsau, Germany	~50 ka	E	Many edible plant species including seeds, nuts, and fruits.	Edible plants.	Mangafa, 2000 .
Hummal, Syria	Middle Palaeolithic.	E	Phytoliths from herbs, fruits, wild grasses and sedges, <i>Celtis</i> sp. and <i>L. arvensis</i>		Tsartsidou et al., 2015
Kalamakia Montmaurin	Middle Palaeolithic.	E/M	Plant remains. <i>Celtis cf. australis</i> and/or <i>Celtis cf. tournefortii</i> , and other species of Boraginaceae.	Consumption of fruits.	Matsutani, 1984 .
Amud Cave, Israel	Middle Palaeolithic.	T	Pitch adhering to stone tools.	Hafting.	Grünberg, 2002 .
Grotta Fossellone	Middle Palaeolithic	T	Bitumen adhering to stone tools.	Hafting.	Monnier et al., 2013 .
Tor Faraj, Jordan	89.5–62 ka	E	Dental calculus. Starches, phytoliths.	Starchy food.	Power et al., 2018 .
Grotta Guattari	Middle Palaeolithic	E	Dental calculus. Starches, phytoliths.	Starchy food.	Henry et al., 2014 .
La Quina	70-55 ka	E/T	Phytoliths.	Edible grass seeds, bedding.	Madella et al., 2002 .
	70 ka	E	Dental calculus. Starches, phytoliths.	Starchy food.	Power et al., 2018 .
	~70 ka	T	Phytoliths.	Bedding.	Henry et al., 2004 .
	67-55 ka	E	Dental calculus. Starches, phytoliths.	Starchy food.	Power et al., 2018 .
	64 ka	E	Dental calculus. Starches, phytoliths.	Starchy food.	Henry et al., 2014 .

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Table 1 (continued)

Site	Age	E/T	Source of material	Interpretation	References
El Salt, Spain.	60–45 ka.	E	Biomarkers in faecal material.	Consumption of mixed diet, including plants.	Sistiaga et al., 2015.
Esquilieu cave, Spain.	58–48 ka	T	Phytoliths.	Bedding.	Cabanès et al. 2010.
Abrijo de la Quebrada, Spain.	MIS5b– MIS4.	T	Phytoliths.	Bedding?	Esteban et al., 2017.
Vindija	45–35 ka.	E	Dental calculus, starches, phytoliths.	Starchy food.	Power et al., 2018.
Kulna	50 ka	E	Dental calculus, starches, phytoliths.	Starchy food.	Henry et al., 2014.
Sima de las Palomas, Spain.	50 ka	E	Dental calculus, starches, phytoliths.	Starchy food.	Salazar García et al., 2013.
El Sidrón, Spain.	49 ka	E/T/M	Dental calculus, chemical evidence for edible and medicinal plants and oil-shale bitumen and pitch. Starch granules. Non-edible wood fragment.	Starchy foods, self-medication. Possible tooth picking. Possible chewing of hafting material.	Hardy et al., 2012, Radini et al., 2016
El Sidrón, Spain.	49 ka.	E/M	Dental calculus, DNA from mushrooms, other edible and medicinal plants.	Starchy food, mushrooms self-medication.	Weyrich et al., 2017
Abri Romanic, Spain.	49–45 ka.	T	Wooden artefacts, some shaped in the form of a scoop. Wood imprints.	Woodworking.	Carbonell and Castro-Curel 1992; Allué et al., 2012.
Shanidar, Iran.	48 ka	E	Dental calculus, starch granules.	Starchy food.	Henry, et al., 2011.
Gorham's Cave, Gibraltar.	45–32 ka	E	Charred plant fragments, wild olive (<i>Olea sp.</i> , stone pine nut, <i>Pinus pinea</i>).	Charred nut fragments.	Barton, 2000; Barton et al., 1999.
Gura Cheii-Râşnov Cave, Romania.	~44.90 ka	T	Bitumen.	Hafting.	Cărciumaru et al., 2012.
Goyet	40.5 ka	E	Dental calculus, starches, phytoliths.	Starchy food.	Henry et al., 2014.
La Ferrassie	39 ka	E	Dental calculus, starches, phytoliths.	Starchy food.	Henry et al., 2014.
Spy II, Belgium.	36.5 ka	E	Dental calculus, starch granules.	Starchy food.	Henry, et al., 2011.
Spy II, Belgium.	36.5 ka	E	DNA mushroom.	Edible/medicinal.	Weyrich, et al., 2017.
La Grotte du Portel, France.	Middle Palaeolithic (Mousterian).	T	Several artefacts with fibres apparently wrapped around the mid-point associated with Clactonian notches.	Fibre technology, hafting.	Prince, 2000.
Grotte-XVI, Dordogne, France.	Middle Palaeolithic.	T	Phytoliths.	Bedding.	Karkanás et al., 2002.

The evidence displayed in Table 1 is not extensive, particularly considering the long period of time it covers, but it demonstrates a broad use of plants that differs from the theoretical frameworks that outline an incremental use of plants through the Upper Palaeolithic (for a full discussion see Zeder, 2012 and Hockett and Haws 2005). The numerous plant species in some assemblages, many of which have relatively low edibility but have other potential benefits such as medicinal properties, suggests that resource selection is likely to be far more complex than a calorie-based cost and benefit equation.

Bringing all the evidence together, it is clear that a wide range of plants were used in the diet, as medicine and as raw materials, throughout the Palaeolithic, including during periods of environmental stress. Richards and Trinkaus (2009) suggest the proposed late development of the broad spectrum use of plants was based on an increased exploitation of energy-rich seeds and nuts which require equipment and time to extract. However, the presence of nuts and pitted stones at Geshert Benot Ya'aqov (790 ka) (Goren-Inbar et al., 2002), and the evidence for ingestion of essential polyunsaturated fatty linoleic and linolenic acids from dental calculus Qesem Cave, Israel (3–400 ka) (Hardy et al., 2015b), suggest that these resources were being exploited in the Lower Palaeolithic. Likewise, the evidence for higher primate use of tools to obtain food suggests that extracting food from hard natural containers, including nuts (e.g. Visalberghi et al., 2007) and shellfish (Perry and Coddling, 2017), was within the capabilities of the LCA (Last Common Ancestor) and therefore early hominins. Though starch granules have been recovered from the dental calculus of Lower (Hardy et al., 2015b, 2017) and Middle (Hardy et al., 2012; Henry et al., 2011; Power et al., 2018; Salazar García et al., 2013) Palaeolithic hominins from several sites (Table 1), the minute numbers involved, the problems inherent in identification to plant source, the many ways plant parts can enter the mouth, and the impact of food preparation methods on the recovered record (Radini et al., 2016), means

interpreting broad dietary trends based on these, is not viable. There has been a significant focus on the reconstruction of protein in Palaeolithic diet, principally through the use of carbon/nitrogen (C/N) stable isotope analysis (Drucker and Bocherens, 2004; Richards, 2002). This has promoted a perspective of Neanderthals as 'top level carnivores' (Richards et al., 2000; Richards and Trinkaus 2009). This perspective has continued to dominate Middle Palaeolithic dietary reconstruction, even when the nitrogen levels ($\delta^{15}\text{N}$) among Neanderthals are inexplicably higher than those of top level carnivores (Speth, 2010). Speth offers two possibilities for this, and suggests that the excessively high nitrogen levels could be due to dietary stress (Speth, 2010), or the consumption of maggots, fly larvae and rotted and fermented meat, as the putrefaction process increases nitrogen levels (Speth, 2017).

The emphasis on stable isotope analysis in hominin dietary reconstruction, has contributed to a perception of diet that may be physiologically unsustainable in the long term (Butterworth et al., 2016; Hardy et al., 2015a). The limit of pure protein in the diet is 35–40%, above this protein toxicity can occur which can cause death quite rapidly (Speth, 2010). The inclusion of fat (Ben-Dor et al., 2011; Speth, 2010) can counter the toxic effects of protein to a certain extent, but there remains an essential need for carbohydrates. Evidence from recent and modern hunter-gatherer populations, suggests they avoid diets that exceed this protein limit (Speth, 1989; Cordain et al., 2000).

Recently, a different approach to stable isotope analysis (based on the nitrogen isotopic composition of glutamic acid and phenylalanine) suggests that the interpretation of data using established methods of C/N stable isotopes is indeed problematic and that there was a greater diversity in dietary composition than previously assumed (Naito et al., 2016). The need for high levels of meat in evolutionary diet has been widely discussed (Brenna and Carlson, 2014; Bunn, 2007; Kaplan et al., 2000; Leonard et al., 2007) but may be overemphasised (Hardy et al., 2015a), while as

much as 25% of the diet can be based on plants without being visible in the isotopic signal (Jones 2009).

There are almost 400,000 plant species across the world, of which about 80,000 are edible (Mora et al., 2011; Joppa et al., 2010), though humans eat only around 200 species today (Warren, 2015). All green plants make starch. Starchy plants comprise between 35 and 70% of the energy intake in the modern human diet (Copeland, 2016). They are thought to have been a key resource in early pre-history (Laden and Wrangham, 2005; Wrangham, 2005; Wrangham et al., 2009; Lee Thorp et al., 2012). Starch, which is the main source of dietary carbohydrates and glucose, is present in plant storage organs. These include USOs, grains and seeds, some nuts, and inner bark (Copeland, 2016). In wild grasses for example, the most accessible storage organs are the seeds, but carbohydrates are also stored in the lower stem (stolon) and rhizomes (White, 1973) which can be an emergency resource, particularly in winter. In some cases, the edible parts need to be unpacked (Jones 2009) or processed (Butterworth et al., 2016) before use. Some processing, such as cooking, make them a more efficient energy source, some require other forms of processing such as leaching to remove toxins, while others can be eaten directly. Plants accumulate and store energy for the spring growth, making USOs a particularly valuable winter resource in high latitudes (Hardy, 2007a; Hardy et al., 2013; Kubiak-Martens, 2006; Moore, et al., 2000). The recommended daily amount of carbohydrate for most populations today is 150 g, while 50–100 g is considered essential to prevent ketosis in adults (Institute of Medicine, 2006). The Arctic diet is sometimes used to argue for a very high focus on animal produce and little to no plant food (Lindeberg, 2009); however, the *CPT1A* gene present in Arctic populations, enables a specific adaptation to a high meat/low carbohydrate diet (Clemente et al., 2014). Yet even here, there is an absolute minimum requirement of 30–50 g of dietary carbohydrate per day (Institute of Medicine, 2006), to keep the brain and body functioning. If hominin populations ate insufficient carbohydrates, they would have needed to rely on gluconeogenesis (Butterworth et al., 2016) which is an energy expensive process whereby glucose synthesis occurs in vivo from non-carbohydrate sources (Copeland, 2016). This could have compromised their energy levels, their efficiency in hunting, their cognitive abilities and their reproductive rates. Additionally, other essential nutrients that can only be obtained from plants include dietary fibre, some essential polyunsaturated fatty acids, vitamin C and certain minerals and phytochemicals.

Though the actual evidence for plant food in the Lower and Middle Palaeolithic is not abundant, it fits well with basic dietary requirements. It is highly unlikely that Lower and Middle Palaeolithic hominins, who were immensely successful in terms of longevity and adaptability, would have achieved this based on an inefficient diet. If, as is assumed, their primary resource was hunted animal produce, this is likely to have involved endurance running and probably rapid bursts of speed. Glucose is the only source of energy that can be used for sustained running speeds above 70% of maximal oxygen consumption (Romijn et al. 1993).

4. Medicines and poisons

The diversity of different plant species that occur on some Palaeolithic sites cannot be easily explained only in terms of dietary necessity (Hardy, 2018). Plant secondary compounds (PSCs) are complex chemicals that are responsible for plant defences. They act as pesticides, anti-grazing and chemical agents (Fraenkel 1959). These compounds, which include alkaloids, flavonoids, and terpenoids, provide aroma, pigments and flavour are the sources of the medicinal, poisonous, psychoactive and hallucinogenic properties in plants (Kennedy, 2014). PSCs are widely used in cooking, but

there are also many toxic PSCs (Engel, 2002) which are also sometimes used including in traditional fishing practices (Neuwinger, 2004). The use of poisons in the African Middle-Late Stone Age has been suggested by Bradfield et al. (2015) and d'Errico et al. (2012), though detection of poisons on Palaeolithic archaeological artefacts is challenging (Borgia et al., 2017).

Toxic plants are so abundant that in order to be able to exploit plants, the means to identify poison is essential; knowing what not to eat is crucial to survival. Poisons are often detected through their bitter taste. The gene *TAS2R38* which identifies the bitter compound phenylthiocarbamide (PTC), is present in the El Sidrón Neanderthal population (Lalueza Fox et al., 2009). As the only known purpose of this gene is bitter taste perception, it may be linked to plant eating (Miller, 2011), as bitter taste can warn of toxicity (Kim and Drayna, 2004).

Recovery of plants with medicinal properties from several Lower and Middle Palaeolithic sites (Hardy, 2018 and references therein), and DNA and biomolecular evidence for medicinal plants recovered in two separate studies of Neanderthal dental calculus from El Sidrón (Hardy et al., 2012, 2013, 2016; Weyrich et al., 2017), suggest that medicinal properties of plants were used and recognised in the Palaeolithic. When this is contextualised within animal self-medication practices, it is unsurprising. Self-medication is practised widely among animals from higher primates (Huffman, 1997, Huffman and Seifu, 1989) to insects (Abbott, 2014; de Roode et al., 2013; Singer et al., 2009). Chimpanzees habitually use 2–300 species of plant in their diet and use at least 36 different species of medicinal plant, while gorillas use at least 26 (Huffman, 2001). Correlations between parasite infestation and deliberate consumption of specific medicinal plants by chimpanzees has been extensively studied (e.g. Huffman, 2016; Huffman and Seifu, 1989; Masi et al., 2012).

The potentially evolutionary role of self-medication and the need for medicinal plants has been highlighted before (Johns, 1990). An evolutionary basis for the intense attraction of medicinal drugs (pharmophilia) displayed by modern humans has been suggested (Sullivan et al., 2010) and it has been argued that medicinal foods (Johns, 1990) used to be a normal part of our diet (Etkin and Ross, 1982), playing a preventative as well as curative role. It is highly unlikely that any hominin species could have evolved without knowing what to eat to sustain health, what to avoid and, as an absolute minimum, how to eliminate intestinal parasites. While it is not possible to prove deliberate self-medication as a reason for collecting specific plants, it is implausible to suggest that all plants, including those that are relatively low-quality food sources and which often have medicinal compounds, were collected as food or reached a site by accident, even when better quality nutritional plants were abundantly available and extensively collected (Hardy, 2018).

5. Technology

Wynn et al. (2011) compared chimpanzee stone tool manufacture and activities linked to this, to the Olduvai archaeological record, and found little to differentiate them. Though the earliest hominin uses of plant materials to construct tools or as raw materials is lost, the perspective outlined by Wynn et al. (2011) demonstrates the contribution the primate, and in particular, chimpanzee (*Pan troglodytes*) organic technological record provides as a baseline for consideration of early Palaeolithic organic technology. Higher primates use a wide range of plant materials as tools, including leaves, bark, wood, fibres and vines, sticks, saps and resins, nut and large seed shells, unmodified sticks, twigs and leaves for tasks including termite and honey collection, oral hygiene, other grooming tasks and obtaining drinking water (Humble

and Matsuzawa, 2002; Koops et al., 2015; McGrew, 2010a, 2010b, 2013; Pansini and de Ruiter, 2011; Roffman et al., 2015; Sanz and Morgan 2007; Van Schaik, et al., 1996). Chimpanzees use digging sticks to unearth tubers (USOs) (Hernandez-Aguilar et al., 2007), spears to catch small mammals (Pruetz and Bertolani, 2007), cleavers to open fruits (Koops et al., 2010), and tool composites, notably hammerstones with anvils, to open nuts (Carvalho et al., 2009; Matsuzawa, 2006). They have tool kits (Carvalho et al., 2012; McGrew, 2010a) with up to 22 different items (Sanz and Morgan, 2007) and display multifunctionality (McGrew, 2013). They also modify tools when they need to (Bania et al., 2009; Hopper et al., 2015).

6. Oral hygiene

Possibly the earliest evidence for use of plants as raw materials or technological items, is in the form of evidence for oral hygiene activities. The presence of a non-edible wood fragment found in dental calculus in association with an interproximal groove in a sample of dental calculus from Sima del Elefante (1.2 Ma) (Hardy, et al., 2017) and another fragment from El Sidrón (49 ka) (Radini et al., 2016), may be physical evidence of tooth picks. Oral hygiene activities, including use of sticks as tooth picks, have been widely observed among non-human primates including chimpanzees (McGrew and Tutin, 1973), bonobos and orangutans (Russon et al., 2009). Long-tailed macaques and Japanese macaques have been recorded using hair to floss between their teeth (Watanabe et al., 2007; Leca et al., 2010). Interproximal grooves, thought to be the result of tooth picking (Brothwell 1963; Ubelaker et al. 1969; Ungar et al. 2001), have been found on *Homo habilis* teeth and all subsequent hominin species (Dąbrowski et al. 2013; Estalrich et al. 2011; Formicola 1988; Frayer et al., 1987; Lozano et al. 2008; Lukacs and Pastor 1988; Puech and Gianfarani 1988; Ryan and Johansen, 1989; Urbanowski et al. 2010; Villa and Giacobini, 1995).

7. Woodworking

Hoffecker (2018) remarks that during the Palaeolithic, most artefacts were most probably in fact, made from wood. Certainly, the most abundant evidence for plant use in early Palaeolithic is for woodworking and wooden artefacts (Table 1). Several Lower and Middle Palaeolithic sites have artefacts with use wear suggesting wood working (Anderson-Gerfaud, 1990; Keeley, 1993; Keeley and Toth, 1981; Lemorini et al., 2014). Possible evidence for woodworking was identified through detection of phytoliths adhering to Acheulian tools (1.7–1.5 Ma) (Dominguez-Rodrigo et al., 2001). At Geshert Benot Ya'aqov (790 ka), a piece of wood with possible modification marks was recovered (Goren-Inbar et al. 2002; 2004). A spear tip made from yew (*Taxus baccata*) was recovered from Clacton-on-Sea (450 ka) and interpreted as a thrusting spear (lance) (Oakley et al., 1977). Nine spears, a lance, a double pointed stick, and a burnt stick made on spruce (*Picea* sp.) were recovered from Schönningen, dating to around 300 ka (Schoch et al., 2015). Analysis of the wooden artefacts from Schönningen demonstrate consistency suggesting sophisticated understanding of wood and technological expertise (Schoch et al. 2015). The wood (mostly spruce) was deliberately selected. The hardest, basal wood was used for the point which was off centre, thus avoiding the weaker central pith. Based on extensive experimental work, Schoch et al. (2015) suggest the spears were used as throwing spears. Fifty-eight pieces of worked wood were recovered from the 171 ka site of Poggetti Vecchi, Italy (Aranguren et al., 2018). These include 39 pieces in boxwood (*Buxus sempervirens* L.) that have been identified as digging sticks. Some of the sticks have naturally pointed ends, while others have been shaped using abrasive stone working.

Several also show working to create a blunt end, or handle. Several of the tools have evidence of charring, possibly as part of the manufacturing process and to remove the outer bark (Aranguren et al., 2018). A pointed wooden artefact made from yew (*Taxus baccata*) was recently recovered from the Middle Palaeolithic site of Aranbaltza III, Spain (137–50 ka) (Rios-Garaizar et al., 2018). Use-wear traces on the tip suggest these were made by a repetitive mechanical activity which has been interpreted as digging (Rios-Garaizar et al., 2018). Possible digging sticks have been recovered from several sites in South and East Africa (Wadley, 2015). The use of digging sticks to harvest tubers has been widely recorded ethnographically (Gott, 1982; Hardy and Sillitoe, 2003; Nelson, 1899; Rudenko, 1961; Vincent, 1985).

A spear point from Lehringen (125–120 ka), has been attributed to Neanderthals (Langley et al., 2008). Several wooden artefacts, some of which were shaped in the form of a scoop, were found at Abri Romanic, Catalunya (Spain) (49–45 ka) (Carbonell and Castro-Curel, 1992). Two possible spears were found at Cannstatt I, Stuttgart (MIS 7) and Bilzingsleben Germany (MIS 9) though in both cases the finds were very fragmentary (Schoch et al., 2015). Several use wear analyses on Middle Palaeolithic stone tools from a range of sites have detected evidence for wood working (Anderson-Gerfaud, 1990, Anderson et al., 1993; Beyries, 1987; Claud et al., 2013; Hardy et al., 2001; Karkanas et al., 2002; Rots, 2013).

8. Composite technology

The development of composite technology is considered a key indicator of cognitive development as attaching one thing to another, requires the ability to plan and to conduct a suite of sub-tasks (Ambrose 2001). Based on use wear traces that identified hafting on MSA Sangoan artefacts (Rots and Van Peer, 2006), it is thought to have developed by at least 300 ka (Ambrose, 2001; 2010). More recently, possible evidence for hafting has been identified on artefacts from Kathu Pan 1 (KP1), South Africa which dates to approximately 500 ka (Wilkins et al., 2012). Hafting traces become relatively common in the Middle Palaeolithic (Rots, 2009; Rots, 2013, 2015) and Middle Stone Age (MSA) (Klein, 2009; Rots et al., 2011; Villa and Lenoir, 2006; Wadley et al., 2004).

The easiest way to bind one item to another, is in the use of bitumen which needs little preparation to make it usable. However, in addition to bitumen, fibres and pitch have also been recovered from Middle Palaeolithic contexts. While it is not clear whether the fibres are twisted (Prince, 2000), pitch preparation and fibre use are both based on complex technologies that require a high degree of technical understanding and expertise.

9. Plant fibres

There is very little evidence for the use of plant fibres in the early Palaeolithic. The earliest direct evidence for fibres yet known, was recovered from Mousterian levels at La Grotte du Portel, Ariège, France, where several artefacts were recovered with fibres wrapped around the mid-point. In each case these fibres were associated with Clactonian notches (Prince, 2000). It is not until the 30th Millennium BC that further evidence for fibres appears in the archaeological record in the form of needles, bodkins, other items related to weaving and clay impressions of figurines with plant-based woven material (Adovasio et al., 1996; Soffer, 2004; Soffer et al., 2000, 2001). Apart from the fibres from La Grotte du Portel, all other evidence for flexible fibres in the early Palaeolithic is currently indirect, notably for the use of water-going craft and hung beads.

The earliest known hominin occupation of islands not connected by a land bridge at any point during the Palaeolithic, is the

island of Flores, one million years ago (Brumm et al., 2010). While a constructed raft requiring fibres to bind it is a possibility, Dennell et al. (2014) suggest it is more likely that hominins reached there inadvertently, carried on natural rafts or pieces of floating vegetation. Lower and Middle Palaeolithic artefacts have been recovered from several Eastern Mediterranean islands that were not connected to the mainland at any time during the Pleistocene. Several sites have minimum ages of 100 ka while in Crete a site has been geologically dated to a minimum of 130 ka (Runnels, 2014). There is considerable uncertainty about how hominins reached these locations, but a fibre-lashed a raft is a possibility (Howitt-Marshall and Runnels, 2016). People had reached Australia by 65 ka (Clarkson et al., 2017) and New Ireland and Timor by 40 ka. McDonald and Veth (2010) suggest that such voyages could only have been accomplished through the use of fibre-lashed watercraft owing to the long distances and strong currents that had to be negotiated.

Other indirect evidence for string of some sort may be the naturally perforated fossil sponges, *Porosphaera globularis*, that have been found on several Acheulean sites. These have ambiguous evidence for artificial enlarging and use wear around the holes (Rigaud et al., 2009). Perforated shells, believed to be beads, have been recovered from several Middle Palaeolithic sites, dating to between 125 ka and 100 ka (Vanhaeren et al., 2006). Analysis of traces detected on eagle talons from the 120 ka Neanderthal site of Krapina suggest they were formed by use wear and represent evidence for stringing into a necklace (Radović et al., 2015). Perforated beads with clear evidence for having been strung date to around 75 ka from Blombos Cave (Henshilwood et al., 2004), and Border Cave (D'Errico et al., 2012), South Africa. Perforated beads become common in the Upper Palaeolithic (Adovasio et al., 2007; Ambrose, 1998; d'Errico et al., 2012; Gilligan, 2010; Kuhn et al., 2001; Sinityn, 2003). Use wear traces on tools from the Lower Palaeolithic sites of Hoxne and Clacton identified hide-scraping and boring of bone tools (Keeley, 1993) which may be potentially significant in terms of the possible utilisation of fibres. However, while beads need fibres to be strung, this could have been done using animal based fibres such as sinew in addition to or instead of plant fibres.

Another indirect way to identify possible use of fibres, is in the need for clothing, though again, animal materials could also be used. The physiological limits of survival in cold climates among modern humans is -5°C (Gilligan, 2017) though whether Lower Palaeolithic hominins might have had different tolerances is not known (Gilligan, 2017; Hosfield, 2016). In this respect, it is interesting to note that the people of Tierra del Fuego dealt with cold in various ways including by covering themselves with animal grease (Bridges, 1948).

Flexible plant fibres are only useful as a composite. They need to be knotted, joined, twisted, or added to, an individual plant fibre is of little use on its own. Multiple fibres twisted and added together, make cord. Cord or string can be used alone, looped or knotted, to manufacture artefacts such as bags, nets or clothing (e.g through knitting and weaving) or it can be used as part of a composite, in snares, to haft or to bind, and to make items such as rafts and rope bridges. The timing of the technological breakthrough that led to twisting and extending fibres into cord or string is unknown but is likely to have developed over long timescales. Though fibres are normally invisible in the Palaeolithic record, they are implicit in the construction of much composite technology (Hardy and Sillitoe, 2003, Hardy, 2008, Sillitoe, 1988). The technological expertise (MacKenzie, 1991; Sillitoe, 1988) and conceptual understanding required to twist and link fibres has rarely been investigated (Hardy, 2007b, 2008) though the development of twisting fibre has been called 'the unseen weapon that allowed the human race

to conquer the earth" (Barber, 1995:45).

Fibre for twisting can come from a wide variety of sources. The earliest identified fibre is bast (Soffer et al., 2000), which is collected from inner bark, a well-known example used today is jute. In the Mesolithic, cord has been recovered made from lime, elm, juniper, willow and rowan bast, as well as bilberry and willow roots (Hardy, 2007b, 2016 and references therein) and bulrush (*Scirpus lacustris*) (Clemente Conte et al., 2016). Historical records include the use of mosses, grasses, heather, lime, birch, hazel, beech, yew, pine and spruce (Myking et al., 2005). Though flax and nettle are well known sources of fibres, they do not appear in the archaeological record until much later (Harris et al., 2017). The fibres from Dzudzuana Cave, Georgia (30 ka) claimed to be flax (Kvavadze et al., 2009) have been discounted (Bergfjord et al., 2010).

The best bast is obtained from young trees cut in early summer, though collecting it at this time implies a retting process lasting several weeks, to degrade the soft tissues and separate the bast from the outer bark. Bast can be processed more quickly in early spring as the sap is rising, or in winter, in which case the bast can be separated rapidly over a fire (Myking et al., 2005). In terms of a mobile Palaeolithic population, raw material preparation could therefore be relatively rapid. However, the actual manufacture of twisting fibres is laborious and can only be done when stationary. Sillitoe (1988) recorded that rolling and looping string comprised 85% of women's manufacturing time in Papua New Guinea, while MacKenzie (1991) estimated that to roll and loop enough string to make one string bag, took between 160 and 240 h and that women's fingers are 'perpetually working'. In recorded ethnographic contexts, twisting fibres is learned from a very young age and becomes an innate skill (Hardy, 2008; Hardy and Sillitoe 2003). Though the timing of this remains unclear, once twisting fibre technology developed, there is likely to have been a constant demand for it and it is likely that it was one of the most time-consuming and constant activities in manufacturers' lives.

10. Bitumen and pitch

Bitumen and pitch are two distinct materials that were used during the Palaeolithic as adhesives in hafting. Though only one, pitch, is plant based, bitumen is also discussed here, to eliminate the potential for confusion between the two materials. In most cases, either bitumen (natural tar) or (plant-based) pitch are found, though in one case, evidence for both materials were found in the dental calculus of a Neanderthal (Hardy et al., 2012; Radini et al., 2016; Hardy and Buckley 2017) suggesting these had been chewed, possibly in preparation for hafting.

Bitumen, also referred to as oil-shale or tar-shale, is a natural petroleum product that seeps from underground deposits, and can be found in places, on the surface. Over time the more volatile constituents disappear and a bituminous residue is left, which can become soft, pliable and adhesive when heated (Speight, 2005). Each natural deposit of bitumen is different and can sometimes be identified to source (e.g. Boëda et al., 2008; Hardy et al., 2012). Several bitumen-coated artefacts and small fragments were recovered from Mousterian site of Umm el Tlel, Syria, in two archaeological layers dating to 40 ka, and 70 ka respectively (Boëda et al., 2008). Analysis of the 11 artefacts from the 70 ka layer showed that the bitumen traces were opposite and parallel to the working edge, and clearly represent the remains of hafting material (Boëda et al., 2008). Artefacts with residues chemically identified as bitumen were recovered from the nearby Mousterian site of Hummel (Monnier et al., 2013) and from the Middle Palaeolithic site of Gura Cheii-Râşnov Cave, Romania, (Cărciumaru et al., 2012).

Pitch is recovered from bark through a complex technological process called dry distillation pyrolysis, or oxygen-free fire. It was

also widely used as hafting material and is soft and pliable when heated. Rolls of birch bark can be used as torches, as the tree resin holds the fire, but the extraction of pitch in quantities usable for hafting requires expert fire management skills. There has been significant interest in the early Palaeolithic presence of pitch, and several experimental studies have been conducted to determine the feasible methods of production in the Middle Palaeolithic. Two methods, the use of ash or earth mounds, and the use of controlled burning of bark rolls, both produce usable quantities of pitch (Groom et al., 2015; Kozowyk et al., 2017; Schenck and Groom, 2016; Wragg Sykes, 2015).

Chemical evidence for birch bark tar (also called pitch) was identified on several flint flakes from the Campitello Quarry site, Italy, which dates to before MIS 6 (Mazza et al. 2006). At Inden-Aldorf, Germany (MIS 5e), numerous artefacts had black residues that has been identified as birch bark pitch (Pawlik and Thissen, 2011). Several lumps of birch bark pitch were found at the Middle Palaeolithic site of Königsau, Germany, one with a finger print and one with the imprint of wood (Grünberg, 2002). Though they date to the Middle Palaeolithic, their specific age is unclear, and both 43–48 ka (Grünberg, 2002) and over 80 ka (Koller et al., 2001) have been proposed. An ‘amorphous black substance’ was noted on the proximal end of an artefact from the Neanderthal site of Starosele (Hardy et al., 2001), this may also be bitumen or pitch.

11. New environments, high latitudes and knowledge acquisition

There is widespread evidence for social learning and cultural transmission in animals (Whiten, 2017a). Among chimpanzees, this includes food choice, self-medication and tool use (Cousins and Huffman, 2002; Hobaiter et al., 2014; Huffman, 2003; Kendal et al., 2015; Van Leeuwen, et al., 2013; Whiten, 2017b). This suggests that knowledge transfer mechanisms were well established in the Palaeolithic. But unlike chimpanzees and many higher primates, hominins spread into new climates and environments. Possibly their greatest challenge was the need to adapt to these new environments (Wells and Stock, 2007) and food sources (Jones, 2009). Successful adaptation would require a population with a reluctance (neophobia) -curiosity (neophilia) balance to enable expansion of the diet while limiting inadvertent poisoning, something that has been well studied among primates (Gustafsson et al., 2016 and references therein). A wide range of neophobia exists in animals, not dissimilar to human degrees of shyness (Cavigelli, 2005) and is also present among chimpanzees (Addessi et al., 2006; Visalberghi et al., 2002). In experimental conditions, chimpanzees are cautious and socially influenced (Gustafsson et al., 2016). Several studies (Addessi et al., 2006; Ueno and Matsuzawa, 2005) have shown that among higher primates, young are less neophobic than older individuals. Masi et al. (2012) suggest this may be adaptive as sub-adults are more likely to disperse at puberty. Neophobia is advantageous where heavy predation and easily located resources are common (Cavigelli, 2005), which may correspond to the circumstances of expanding hominin populations. The variation in neophobic behaviour among animals and humans is likely to have been similar among hominins and would have provided an underlying mechanism that facilitated expansion or adaptation to new environments and new plant populations.

The nature and availability of plant resources changes according to climate, altitude and latitude; however, edible plants are present in most environments. Ethnographic studies of plant use in high latitude environments consistently record long lists of plants used as food and raw materials in the Arctic and sub-Arctic (Kuhnlein and Turner, 1991, Nelson, 1899, Porsild, 1953, Rudenko, 1961). Even in Baffin Island (ETf- Köppen climate classification cold, continental

tundra), plant foods comprising a combination of chyme (from animals), kelp, berries, sorrel and willow, is available (Kuhnlein and Soueida, 1992). There are detailed records of the large numbers of usable plants and the ways that they were used as food and in material culture by the Fuegians (Berihuete-Azorín, 2013, Berihuete et al., 2009; Orquera and Piana, 1999) who lived in a climate classified as ‘mild tundra’ (ET- Köppen climate classification). The Yupiks of the Southeastern Chukchi peninsula, Beringia (subarctic -Dfc Köppen climate classification), continue to exploit a wide range of plants for food. Plant diversity here is between 2–300 species and the whale hunters of Novoye Chapino utilise around 30 different plant species including berries, leaves, roots, mushrooms and seaweeds in their diet. They have access to plant food all year round, because they dig up the roots and collect the plant foods in the autumn which then freeze and are available during winter (Ainana and Zagrebina 2014). In the high latitude grasslands of Inner Mongolia, a dry steppe environment known for its traditions of animal herding and consumption of animal products, there is also an abundant record of plants that are integrated into the traditional diet, and also used as medicine and for raw materials (Khasbagan and Pei, 2000; Khasbagan and Hui, 2011).

For the early hominins of northern Europe there was a wide variety of plant foods available (Hardy, 2010). Even in winter, plant food is always available in the form of mosses, grasses, plant storage organs, carbohydrate-rich tree barks where there were trees and, along coastlines, the large numbers of seaweed species as well as edible aquatic plants (often with edible USOs) which are normally present at the edges of most lakes and rivers, in addition to the partially digested stomach contents of hunted animals (Sinclair, 1953; Speth, 2010).

Humans, are very flexible in their diet. They can survive by eating a wide range of different foods in varying proportions though, while humans can be vegetarians, they cannot survive only on animal produce. Hominins lived in widely varying environmental zones and dental microwear of Neanderthal individuals suggests their diet varied accordingly (Ungar and Hublin, 2011). Dental calculus analysis at Spy (Belgium) (Weyrich et al., 2017) supports results that suggest a greater concentration on animal products among northern European Neanderthals (El Zaatari et al., 2011). Conversely both Hardy et al. (2012), and Weyrich et al. (2017) recorded consumption of plants in dental calculus samples, but no evidence for animal produce at the Spanish site of El Sidrón, also supporting El Zaatari’s (2011) conclusions about higher consumption of plant foods in more temperate regions. Other causes of dietary change and flexibility such as that recorded by Bocherens et al. (2016) at Payre, suggests that changes in subsistence could also be unrelated to climatic change and may be linked to other factors.

12. Conclusion

The amount of evidence for plant use in the Lower and Middle Palaeolithic is small but important and suggests plants were integral to both the diet and technology. Humans have a minimum requirement of glucose-providing plant based dietary carbohydrates, a diet that consistently fell below this would have had negative implications in terms of energy, cognitive function and reproductive rates. If, as is assumed for most hominin populations, they had an animal hunting-based economy and therefore high aerobic requirements, carbohydrates would have been even more important to sustain the levels of energy required.

The evidence for chimpanzee self-medication and organic technology provide basic structures which are useful to contextualise the small amount of archaeological evidence for these in the Lower and Middle Palaeolithic. In terms of material culture, the

Lower Palaeolithic evidence for wooden objects displays a knowledge of its structure and material qualities as well as technological expertise. The earliest clear circumstantial evidence for sea-crafts dates to at least 130 ka which suggests the use of fibres as lashing by this time as well as an understanding of the floatable properties of wood. The use of plant fibres is likely to be very ancient and twisting fibres technology, which requires several conceptual and technological steps, is likely to have developed over an extensive time period. Fibre manufacture is labour intensive and the demand for fibres will have had a significant impact on the lives of the manufacturers, in terms of their mobility and their activities, most probably from the Middle Palaeolithic onwards. The manufacture of pitch requires an understanding of pyrotechnology, including production and management of high heat fires, as well as the properties of the tar-producing barks.

It is unlikely that a lack of edible plants significantly restricted population movement into higher latitudes. Edible plants exist in virtually every environment, and hominin populations carried with them a very broad ecological knowledge that would have given them the mechanisms for adaptability and the flexibility to survive and thrive in most environments. It is clear from the geographically broad archaeological record for the Lower and Middle Palaeolithic periods that they achieved this.

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