



“Founder crops” v. wild plants: Assessing the plant-based diet of the last hunter-gatherers in southwest Asia

Amaia Arranz-Otaegui ^{a, *}, Lara González Carretero ^b, Joe Roe ^a, Tobias Richter ^a

^a Centre for the Study of Early Agricultural Societies, Department of Cross-Cultural and Regional Studies, University of Copenhagen, Denmark

^b Institute of Archaeology, University College London, United Kingdom

ARTICLE INFO

Article history:

Received 16 August 2017

Received in revised form

9 February 2018

Accepted 10 February 2018

Keywords:

Natufian

Archaeobotany

Founder crops

Underground storage organs

Neolithic

southwest Asia

ABSTRACT

The Natufian culture (c. 14.6–11.5 ka cal. BP) represents the last hunter-gatherer society that inhabited southwest Asia before the development of plant food production. It has long been suggested that Natufians based their economy on the exploitation of the wild ancestors of the Neolithic “founder crops”, and that these hunter-gatherers were therefore on the “threshold to agriculture”. In this work we review the available data on Natufian plant exploitation and we report new archaeobotanical evidence from Shubayqa 1, a Natufian site located in northeastern Jordan (14.6–11.5 ka cal. BP). Shubayqa 1 has produced an exceptionally large plant assemblage, including direct evidence for the continuous exploitation of club-rush tubers (often regarded as “missing foods”) and other wild plants, which were probably used as food, fuel and building materials. Taking together this data we evaluate the composition of archaeobotanical assemblages (plant macroremains) from the Natufian to the Early Pre-Pottery Neolithic B (EPPNB). Natufian assemblages comprise large proportions of non-founder plant species (>90% on average), amongst which sedges, small-seeded grasses and legumes, and fruits and nuts predominate. During the Pre-Pottery Neolithic, in particular the EPPNB, the presence of “founder crops” increases dramatically and constitute up to c. 42% of the archaeobotanical assemblages on average. Our results suggest that plant exploitation strategies during the Natufian were very different from those attested during subsequent Neolithic periods. We argue that historically driven interpretations of the archaeological record have over-emphasized the role of the wild ancestors of domesticated crops previous to the emergence of agriculture.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

The Late Epipaleolithic Natufian (c. 14.6–11.5 ka cal. BP) represents the last hunter-gatherer society in southwest Asia prior to the development of plant food production. The characterization of the plant-based subsistence during this time period is therefore key to understand the transition from foraging to farming. Until now, there has been an emphasis on the idea that Natufians relied on the intensive exploitation of large-seeded grasses such as cereals. “... Natufian communities practiced intensive and extensive harvesting of wild cereals ...” (Bar-Yosef, 1998, p. 167), and they probably practiced small-scale wild cereal cultivation (Hillman et al., 2001;

Ibañez et al., 2014). Ground-stone tools, sickle blades and threshing floors were “significant inventions of the Natufian culture, all essential for exploiting wild cereals” (Eitam et al., 2015, p. 7). The cereal-based plant diet has been directly connected to the conceptualisation of the Natufian as a complex hunter-gatherer society characterised by sedentism, incipient social complexity, and a delayed return-economy (Bar-Yosef and Belfer-Cohen, 1989; Bar-Yosef and Kislev, 1989; McCorriston and Hole, 1991). Unfortunately, however, the limited archaeobotanical evidence has hampered the understanding of the economic role that the wild ancestors of domesticated cereals and legumes played prior to the emergence of agriculture in southwest Asia.

In this work we review the available evidence for plant exploitation during the Natufian and we contrast this information with new data from Shubayqa 1, a Natufian settlement located in northeast Jordan (Richter et al., 2012, 2014, 2017; Richter, 2017a,b; Yeomans and Richter, 2016; Yeomans et al., 2017; Pedersen et al., 2016). The archaeobotanical evidence from Shubayqa 1 is

* Corresponding author. University of Copenhagen, Department of Cross-Cultural and Regional Studies, Centre for the Study of Early Agricultural Societies, Karen Blixens Plads 8, Bygning 10 2300 København S. Denmark.

E-mail address: kch860@hum.ku.dk (A. Arranz-Otaegui).

currently unparalleled since it derives from well-dated, stratified deposits, and has yielded one of the largest plant macroremain assemblages dated to the Natufian. Moreover, the assemblage is unique in that provides solid evidence for the exploitation of underground storage organs, often regarded as “missing foods” due to their low archaeological visibility. Taking into account this new data, we evaluate the composition of archaeobotanical assemblages from the Late Epipaleolithic to the Pre-Pottery Neolithic B (c. 15–9.7 ka cal. BP), comparing the proportional representation of the wild ancestors of domesticated crops (“founder crops”) and other wild plant species. We argue that the available data provides a very different perspective on Late Epipaleolithic plant-based subsistence strategies, which highlights the *broad spectrum* of plants exploited by Natufian hunter-gatherers. Historically driven interpretations of the archaeological record have therefore over-emphasized the economic role of the wild ancestors of domesticated cereals and legumes before the development of agriculture.

2. Characteristics of Epipaleolithic archaeobotanical assemblages in southwest Asia

Although more than 400 Natufian sites have been recorded in southwest Asia to date (see Fig. 1), only a handful have yielded plant macroremains (e.g. seeds, wood charcoal etc.), and yet fewer of these have produced substantial assemblages (e.g. >10000 remains) (see Table 1). In recent years phytolith analyses have started to provide new insights about Natufian plant use (Albert et al., 2003; Rosen, 2004, 2007, 2010, 2011, 2012, 2013; Portillo et al., 2010; Power et al., 2014, 2016), but our knowledge is still patchy. The reasons for this unsatisfactory situation can be summarised as follows:

- 1) Although plant remains are essential to address key research topics such as subsistence, they have, more often than not, been overlooked in many archaeological projects. Whilst archaeological sediments are commonly sieved thoroughly to retrieve flint and human/animal bones, systematic sampling for plant macroremains has less often been carried out (see Fig. 1). This is despite the fact that archaeobotanical recovery techniques such as flotation were implemented around the 1970s, and many Natufian sites have been excavated since then. If plant remains were not observed or recognised during excavation, it was commonly assumed that they were absent (e.g. Hole et al., 1969). The result has been that there are few Late Epipaleolithic sites, in comparison to the total number of excavated sites, in which thorough archaeobotanical sampling has been carried out. This has in turn led to a low overall numbers of sites with analysed and published archaeobotanical assemblages.
- 2) In some cases where plant macroremains were recovered, only those identified by naked eye during the excavation were retrieved (e.g. Hopf, 1983; Hopf and Bar-Yosef, 1987). Plant macroremains recovered this way commonly comprise large pieces of wood charcoal, nutshells or large seeds, such as those from legumes and cereals. But wild plant species are rarely represented in these assemblages, since many of them produce very small seeds (i.e. <1 mm) that can easily pass unnoticed. The use of dry-sieving alone may also result in biased archaeobotanical assemblages since the size of the meshes is rarely smaller than 0.5 mm (e.g. Melamed et al., 2008; Caracuta et al., 2014, 2015), and this may hamper the recovery of small-seeded plant species.
- 3) Another issue that archaeobotanists working on Epipaleolithic sites in southwest Asia often face is that even if samples are retrieved systematically and processed with machine-assisted flotation, low densities of plants are commonly preserved and

recovered (see Table 1 for the total numbers of plant remains found at Late Epipaleolithic or Natufian sites). Poor preservation of plant remains has often been attributed to the consumption of raw plant resources or “missing foods” (Hillman, 1989; Hillman et al., 1989b). The “missing foods” may comprise raw vegetables (leaves, flowers, shoots), underground storage organs (tubers, rhizomes, corms and bulbs), fleshy parts of fruits and nuts, and edible pollen. If these plant remains come into contact with fire they are often too fragile to withstand charring and post-depositional processes. In the particular case of underground storage organs, which are primarily composed of parenchymatic tissue, several records indicate that they tend to disintegrate during the recovery with large-scale machine-assisted water flotation techniques (Hather, 2000 p.74; Hillman et al., 1989b). When parenchymatic tissue survives the recovery process, it is often fragmented and eroded, and it either passes unnoticed during the sorting process, or is regarded as unidentified parenchyma. Preserved parenchyma remains are often too small to be identified (Colledge, 2001) and very few people are specialised in their analyses (e.g. Hather, 1988, 1993, 2000; Kubiak-Martens, 2002, 2006, 2016).

It is important to be aware of these limitations to understand the nature of the available archaeobotanical evidence for the Epipaleolithic in southwest Asia. These issues call for the urgent need to apply systematic and intense recovery programs and combine different techniques (e.g. flotation and wet-sieving) to limit biases and obtain substantial archaeobotanical assemblages with which to characterise hunter-gatherer plant use.

3. The Natufian plant-based subsistence

The Natufian period is commonly divided into two main phases: the Early Natufian (~14.6–13.2 ka cal. BP) that developed during the wet and warm Bølling-Allerød interstadial (~14.6–12.9 ka cal. BP); and the Late Natufian (~13.6–11.8 ka cal. BP), which partially overlapped with the cool and dry environmental conditions of the Younger Dryas (12.9–11.5 ka cal. BP), (Maher et al., 2011; Grosman, 2013; Henry, 2013). Below we summarise the available evidence on Natufian plant exploitation based on the analyses of the material culture and the plant macroremains (see Power et al., 2016, for a recent review on Natufian plant microremains).

3.1. Review of the Natufian material culture linked to plant exploitation

Garrod (1932, 1957) first suggested that Natufians were the earliest agriculturalists in southwest Asia, and since then, the Natufian culture has been considered by many as threshold to the origins of agriculture (Henry, 1989; Bar-Yosef and Meadow, 1995; Bar-Yosef, 1998). It has been proposed that Natufian “affluent” economic systems were based on the abundance of wild cereals, and their subsequent domestication occurred as a response to their marked reduction in their natural availability (Flannery, 1969; Henry, 1989). Besides, the exploitation of cereals during the Natufian was said to be in direct relationship with the adoption of a sedentary way of life (Henry, 1985, 1989; McCorrison and Hole, 1991; Bar-Yosef and Belfer Cohen, 1992; Smith, 1994; Bar-Yosef and Meadow, 1995). Flannery (1969) argued that some degree of sedentism must have been necessary to process, store and manage cereal fields. However, assumptions regarding the relative importance of cereal exploitation during the Natufian have been so far primarily based on “indirect” evidence for plant exploitation, particularly on the analyses of the Natufian material culture.

Since its definition by Garrod (1931) the presence of sickle

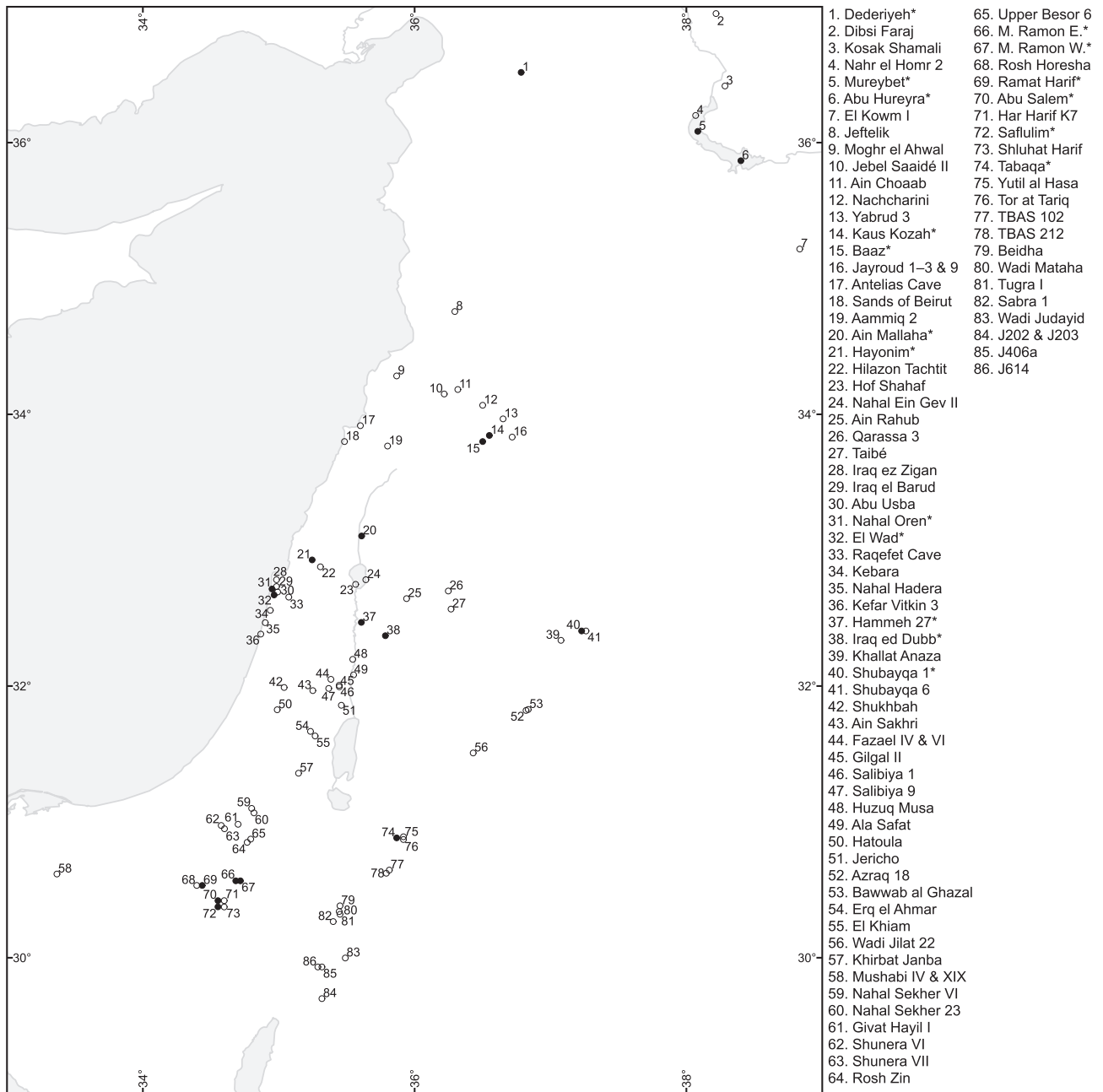


Fig. 1. Summary of Late Epipaleolithic Natufian and Harifian sites excavated and surveyed in southwest Asia. Sites with published archaeobotanical evidence for plant macroremains (e.g. wood charcoal and non-woody plant remains) have a black solid circle on the map and an asterisk in the legend. Coordinates from: MacDonald et al. (1988); Schyle (1996); Rosenberg et al. (2010); Böhner and Schyle (2006); Aladjem (2008); Garrard and Yazbeck (2013); Swinson (2016); and references therein.

blades amongst the lithic toolkit has widely been considered as one of the hallmarks of the Natufian. The characteristic gloss on sickle blades has for a long time been connected to harvesting of cereals, which was demonstrated through experiments and use-wear analysis later on (Unger-Hamilton, 1989, 1991; Anderson, 1991; Ibañez et al., 2014). However, there has been little determination to explore their use as cutting tools to harvest other siliceous plants such as reeds (e.g. Winter, 1994), large and small/medium-seeded grasses such as *Aegilops* sp. (goatgrass) and *Stipa* sp. (feathergrass), as well as Fabaceae (legumes), Cyperaceae (sedges) and Polygonaceae (knotweed family) (Anderson, 1991). This is surprising given that these taxa probably constituted common food resources during the Epipaleolithic and Neolithic, as indicated by the

archaeobotanical evidence (Weiss et al., 2004; Savard et al., 2003; 2006; Whitlam et al., 2013; 2016; Weide et al., 2017). Recent studies show that the relative frequency of sickle blades during the Late Epipaleolithic (c. 14–11.7 ka cal. BP) was mostly less than 5% (supplement Table S3 in Maeda et al., 2016). Even if they constituted specialised tools for cereal harvesting (an idea that still needs verification), the use of sickle blades was not that common during the Natufian as it was during subsequent Neolithic periods. Besides, glossed flint blades have been reported from the Upper Palaeolithic Wadi Kubaniya (Jensen et al., 1991) and Ohalo II (Snir et al., 2015a; Groman-Yaroslavski et al., 2016), which indicates that their appearance pre-dates the supposed “intensive cereal exploitation period” ascribed to the Natufian.

Table 1
 Sites with published archaeobotanical materials (non-woody plant macroremains) that are dated to or contemporary with the Natufian period. The table shows the proportional representation of different plant categories by site (indeterminate remains excluded from the counts). "Founder Poaceae" includes *T. boeotium*, *T. dicoccoides* and *Hordeum spontaneum*. "Founder Fabaceae" includes *Lens*, *Pisum*, *Vicia ervilia* and *Cicer*. Wadi Hammeh 27 (Colledge, 2013); El-Wad (Caracuta et al., 2016); Hayonim Terrace (Buxó i Capdevila et al., 1989); Hayonim Cave (Hopf and Bar-Yosef, 1987); The are no original score sheets with calculation of totals for Abu Hureyra (Colledge and Conolly, 2010), so the presence/absence of the plant categories are recorded; Mureybet (van Zeist and Bakker-Heeres, 1984/1986); Dederiyeh (Tanno et al., 2013); Iraq ed-Dubb (Colledge, 2001); Baaz (Deckers et al., 2009); Körkik Tepe (Rössner et al., 2017). Plant macroremains from Raqefet (Garrard, 1980) and Nahal Oren (Noy et al., 1973) were not included, as they did not come from secure contexts.

Site	El-Wad	Hayonim Cave	Wadi Hammeh 27	Hayonim Terrace	Dederiyeh	Abu Hureyra I	Iraq ed-Dubb	Baaz (II-III)	Körkik Tepe	Mureybet I-II
Chronology (ka cal. BP)	15–13.5	15.1–13.4	14.1–13.5	c. 13.9–13.1	13.2–12.9	13.1–12.4	13.1–11.6	13.1–12.1	12.3–12.1	c. 12.1–11.2
	counts	presence/absence	counts % frag. counts	presence/absence	counts % frag. counts	presence/absence	counts % frag. counts	counts % frag. counts	counts % frag. counts	counts % frag. counts
Founder Poaceae	39	X	7	X	185	X	64	–	37	27
Other large-seeded Poaceae	25	–	3	–	3	X	4	–	69	4
Small-seeded Poaceae	–	–	181	–	310	X	44	1	13668	70.5
Poaceae (indeterminate)	–	–	–	–	–	–	–	3	1404	15
Founder Fabaceae	12	X cf.	1	–	32	X	12	–	–	14
Other large-seeded Fabaceae	112	X	–	–	3	X	–	–	125	–
Small-seeded Fabaceae	–	–	2	–	2	X	–	16	517	258
Fabaceae (indeterminate)	–	X	10	X	52	–	13	–	175	2
Wild plants (including flax)	11	–	15	X	548	X	51	4	3161	2597
Fruits and nuts	62	X	3	–	11149	X	252	1	6	122
Total remains	261	–	222	–	12284	c. 31000	440	25	19162	3109.5
	100.0		100.0		100.0		100.0	100.0	100.0	100.0

Ground stones represent the other Natufian tools that are often linked to cereal processing. Researchers have long stressed that Natufian hand-stones, pestles and portable and bedrock mortars served for cereal and (sometimes) legume processing (Moore, 1978; Henry, 1989; Bar-Yosef, 1998; see Olszewski, 2004, 2010; Rosenberg, 2008 for hypothesis relating ground stone tools to the exploitation of nuts and acorns). Moreover, it has been argued that the abundance of pounding tools during the Natufian could be in relationship to intensified plant gathering or systematic cereal cultivation (Bar-Yosef and Belfer-Cohen, 1989; Eitam et al., 2015). Unfortunately, however, direct relationship between grinding stones and plant processing has rarely been demonstrated due to the lack of systematic use-wear analyses and microscopic identification of plant microremains such as phytoliths and starch. When these analyses have been carried out in Natufian assemblages, the results have shown that ground stones were not only used for cereal processing (Rosen, 2010; Terradas et al., 2013), but also for plants such as legumes (Dubreuil, 2004), sedges (Power et al., 2014) and small seeded grasses (Rosen, 2010; Power et al., 2016), as well as other materials such as ochre (Garrod, 1957; Weinstein-Evron and Ilani, 1994) and hide (Weinstein-Evron, 1998; Dubreuil, 2004; Dubreuil and Grosman, 2009). The artefactual record therefore does not provide unequivocal support for the idea that cereals were necessarily the Natufian staple plants.

3.2. Review of Natufian plant macroremains

The archaeobotanical evidence for the Early Natufian period is limited and comprises data from only three archaeological sites: Wadi Hammeh 27 (Colledge, 2013), el-Wad (Caracuta et al., 2016) and Hayonim Cave (Hopf and Bar-Yosef, 1987). At Wadi Hammeh 27 (Jordan), manual flotation of the sediments was carried out and a total of 3202 remains were retrieved from 14 samples, 222 of which were determinable. Within the identified remains, small-seeded Poaceae (grasses) predominated, followed by wild plants (e.g. *Malva* sp., Liliaceae) and Fabaceae (comprising both small and large-seeded) (Table 1). *Hordeum spontaneum* grains (wild barley) were also present. According to Colledge (2013), the plant-based diet of the inhabitants could have comprised the seeds of grasses and small-seeded legumes, the fruits of *Pistacia* sp. (pistachio) and also the leaves and seeds of *Malva* sp. (mallow). At Hayonim Cave (Israel), wet-sieving and flotation were carried out. Although the absolute counts of the plants have not yet been published, *Lupinus pilosus* (lupin) seeds seemed to have been very common in the assemblage, along with two *Hordeum spontaneum* grains and *Amygdalus communis* (almond) nutshells. During the recent excavations at the Early Natufian site of el-Wad in Israel, wet-sieving of soil samples resulted in the recovery of a total of 261 remains from 14 taxa. Legumes predominated in the assemblage (primarily small and medium-seeded), followed by *Hordeum spontaneum*, *Amygdalus* sp., *Crataegus* sp. (hawthorn) stones and several plants that in the literature are commonly referred to as weeds of arable crops (e.g. *Bellevalia* sp., *Cirsium* sp., *Ornithogalum* sp.). Nevertheless, the predominance of legumes in the assemblage may not necessarily indicate they were preferably exploited (see supplement Text S1). The phytolith analyses from the site showed the importance of wetland plants, including Cyperaceae and *Phragmites* sp. (reeds), along with Poaceae (grasses) (Portillo et al., 2010). The site has also yielded evidence for the wild ancestor of domesticated *Vicia faba* (faba bean, Caracuta et al., 2016).

The archaeobotanical assemblage from the Late Natufian Abu Hureyra I (Euphrates area, northern Syria) is the largest recovered to date (Hillman et al., 1989a, 1997, 2001; Hillman, 1996, 2000, 2003; Colledge and Conolly, 2010). The extensive and systematic sampling of the three Late Natufian phases at the site yielded

around 31000 non-woody plant macroremains comprising more than 150 food types and 95 plant taxa (Hillman et al., 1989a; Colledge and Conolly, 2010). Early work by Gordon Hillman and colleagues highlighted the importance of wild plant food gathering at the site (Hillman et al., 1989a; Moore and Hillman, 1992), including not only the seeds of *Scirpus maritimus/tuberosus* (club-rush), *Polygonum corrigioloides* (Euphrates knot-grass), *Triticum* sp. and *Secale* sp. (wild wheat and rye), *Stipa* sp. and chenopods (*Anabasis*, *Hammada*) but probably also soft vegetative foods such as leaves, flowers, and underground storage organs (root-foods), although no direct evidence for these latter plants was found. All these indicated that the inhabitants relied on a broad spectrum of plants to fulfil their subsistence needs. Miller (1996) raised the question that some of the seeds found could have derived from the burning of gazelle dung as fuel, and therefore, could not be used to infer dietary practices. Hillman and colleagues contested this view arguing that the plant species that could have constituted food resources did not fit the period of gazelle hunting at the site, and therefore, they were unlikely to derive from dung burning (Hillman et al., 1997). In a subsequent publication, Hillman et al. (2001) explored changes in plant distribution between the three occupation phases and suggested that the sudden setting of the cold and dry Younger Dryas during phase 2 significantly reduced the wild staple plants previously exploited and could have triggered the cultivation of wild rye. The five major plant groups that decreased during phase 2 included those inhabiting *Quercus* sp. (oak) dominated park-woodlands (e.g. Rosaceae, *Pistacia* sp.), large-seeded legumes (i.e., *Lens* sp.), *Secale* sp. and *Triticum* sp., *Stipa* sp. and shrubby Chenopodiaceae. This shift coincided with an increase in small-seeded legumes (*Trigonella* sp., *Medicago* sp.) and grasses (e.g. *Hordeum bulbosum*), and stony-seeded dryland gromwells (e.g. *Arnebia* sp., *Buglossoides* sp.), most of which represent classic weeds of rainfed cultivated cereals. The evidence for rye cultivation was further supported by the presence of nine plump cultivated-type rye grains (originally referred to as domesticated-type), but it was later proved that some of them were intrusive. In a more recent publication, Colledge and Conolly (2010) made a detailed re-evaluation of the available datasets from Abu Hureyra I, and although they did not completely exclude the possibility of rye cultivation, they argued that the shifts in the plant species that originally served to suggest cultivation at the site could also be interpreted in terms of an increased dietary breadth in response to food stress induced by the harsh climatic conditions of the Younger Dryas.

At the neighbouring site of Mureybet (phase I-II), in the Euphrates area, cereal grains were not common during the Late Natufian and the Khiamian period, and were not substantially represented until phase III (Mureybetian, PPNA), which coincided with increased frequencies of potential weed species (van Zeist, 1970; van Zeist and Bakker-Heeres, 1984[1986]; Willcox, 2008). Among the plant foods exploited during the Late Natufian and the Khiamian taxa such as *Polygonum* sp. (knotgrass), *Asparagus* sp. (asparagus), *Scirpus maritimus* (sea club-rush), followed by small-seeded legumes (e.g. *Astragalus* sp.) were found. Evidence to confirm or reject crop cultivation at the site was however insufficient according to van Zeist and Bakker-Heeres (1984[1986]). Small-seeded legumes such as *Astragalus* sp. were most common in Baaz rockshelter (Deckers et al., 2009), whilst fruits and nuts such as *Pistacia* sp. and *Amygdalus* sp. predominated at two other Late Natufian sites with published archaeobotanical evidence: Iraq ed-Dubb (Colledge, 2001) and Dederiyeh (Tanno et al., 2013). Other taxa recurrently found at these latter sites included small-seeded grasses (e.g. *Stipa* sp., *Phalaris* sp.), *Ziziphora* sp. and Geraniaceae. At the broadly contemporary Epipaleolithic site of Körtek Tepe (Rössner et al., 2017), located in southeastern Anatolia and

occupied during the Younger Dryas, machine-assisted flotation of samples from a wide range of contexts resulted in the recovery of c. 20,000 remains. The assemblage showed the dominance of small-seeded grasses (c. 71% of the assemblage), especially those of the genus cf. *Eragrostis* (lovegrass). Apart from these, there were many wild plants with known ethnographic uses such as *Scirpus* sp. (club-rush), *Rumex* sp. (dock), *Polygonum* sp. and *Papaver somniferum* (opium poppy). Large-seeded grasses including *Secale* sp., *Setaria* sp. (foxtail), *Hordeum spontaneum*, *Triticum boeoticum* (wild einkorn) and *Arratherum caput-medusae/crinium* (medusahead) represented 1% of the assemblage, although they slightly increased during the Early Holocene occupation levels. Small and large-seeded legumes were present, as well as fruits and nuts such as *Amygdalus* sp., *Pistacia terebinthus* (terebinth) and *Quercus* sp. According to the authors, there was not enough evidence to suggest cereal cultivation during the Younger Dryas (Rössner et al., 2017).

Overall, what the available archaeobotanical evidence suggests is that Natufian hunter-gatherers exploited a relatively wide range of plants from different families (e.g. Cyperaceae, Poaceae, Rosaceae, Polygonaceae), including wild cereals and legumes. Inter-site differences possibly indicate availability/choice of local resources. However, this information is still patchy. The lack of archaeobotanical data poses several questions: which plants were staples during the Natufian?; what was the subsistence strategy like?; was small-scale cultivation practiced or not?; how did people adapt to the changing climatic conditions of the Bølling-Allerød and the Younger Dryas?. All these questions will only be answered with the excavation of more Natufian sites, and the systematic recovery and analyses of the plant remains.

4. Early Natufian Shubayqa 1

One of the sites that can provide important data to characterise the plant-based subsistence during the Natufian is Shubayqa 1, which is located in northeast Jordan, close to the Jabal al-Arab/Jabal Druze (32°24'N/37°13'E, Fig. 1, number 40). Shubayqa 1 was discovered and initially dug by Alison Betts in the 1990s (Betts, 1993, 1998a), but four new seasons of excavation were carried out between 2012 and 2015 by a team from the University of Copenhagen (Richter et al., 2012, 2014, 2017; Richter, 2017a,b). These new excavations have resulted in the recovery of more than 250 flotation samples dated to the Early and Late Natufian. The extraordinary preservation conditions at the site enabled the survival of thousands of plant macroremains, which provide an unprecedented opportunity to assess plant exploitation during this key time period.

Shubayqa 1 is located nowadays in a semi-arid steppic area, with average annual rainfall around 100–150 mm (Laborde and Traboulsi, 2002; Traboulsi, 2013). The Black Desert region is characterised by a mixture of landforms including extinct volcanoes, extensive lava boulder fields, wadis and mudflats (Al-Eisawi, 1996; Betts, 1998b). The rainy season commonly transforms this otherwise arid region into a much greener and vegetated landscape (start October–November, end around March). Rainwater drains from the eastern slopes of the Jabal al-Arab (Jabal al-Druze) towards the Qa' Shubayqa via a series of northwest-southeast running wadis, chiefly the Wadi Rajil. A survey of the local vegetation carried out by one of the authors (AAO) indicates the presence of an open landscape with scarce arboreal cover. The predominant plant communities that grow in the area are typical of the Saharo-Arabian region with several leading perennials of the Chenopodiaceae family (e.g. *Atriplex halimus*), *Tamarix* (tamarisk), and *Peganum hamala* (wild rue), along with glabrous perennials (e.g. *Anabasis syriaca* tp.), shrubs (*Capparis ovata* tp.), dwarf-shrubs (*Achillea fragrantissima*), and several perennial, biennial and

annual herbs (*Citrulus colocynthis*, *Onopordum alexandrinum* sp., *Malva* spp.). In addition to these, some wild grasses were recorded in the area (*Hordeum murinum* sp., *Avena longiglumis* sp., *A. wiestii* sp., *Stipa capensis*). It is interesting to stress that, despite the low average annual rainfall, dry farming of *T. aestivum* (bread wheat) and *Hordeum vulgare vulgare* (domesticated hulled barley) is carried out by local Bedouins. If the amount of rainfall precipitated in the rainy season (October–November) is adequate, they also cultivate legumes such as *Lens culinaris* (lentil) and *Cicer arietinum* (chickpea).

The Early Natufian occupation at Shubayqa 1 is dated to between 14.6 and 14.2 ka cal. BP and encompasses four distinct phases (Richter et al., 2017). A semi-subterranean, oval structure built of local basalt blocs and with a basalt flagstone floor was constructed during the earliest phase (Fig. 2A). A large fireplace (hereafter fireplace A) measuring ~1 m in diameter and a total depth of 0.4 m was inserted in the approximate centre of the building (Fig. 2B). It was almost perfectly round with a bowl-shaped base. During the first use phase, the fireplace was simply a pit dug into the ground. Subsequently, several flat basalt stones were placed around the edges of the pit, creating a stone lining. The content was characterized by an upper layer of brown wind blown sediment and a thick layer (0.2 m) of ash rich sediment replete with numerous charred plant remains, lithic artefacts and fauna. The latter included the remains of gazelle, waterfowl and hare (Richter et al., 2012, 2014). Two AMS dates place the last use of the fireplace between ~14.4 and 14.2 ka cal. BP (68.2% probability) (Richter et al., 2017).

After abandonment and infilling, a later occupation was established inside this structure, re-using the upper part of the outer wall. During this phase another fireplace was cut into the underlying fill (Fig. 2C). This second fireplace (here referred to as fireplace B) was situated c. 0.5 m above the lower fireplace, in almost the same position (Fig. 2D). The fireplace was defined by a series of large, angular basalt boulders placed in a circle. The interior measured c. 0.6 m in diameter (exterior diameter c. 1.2 m) with a total depth of c. 0.3 m. This second fireplace also had two use phases and was rebuilt at least once in the same location. Four separate fills were distinguished inside, each was rich in charred plant remains, fauna and some chipped stone artefacts. Five AMS dates place the use of the fireplace between 14.3 and 14.2 ka cal. BP (68.2% probability). The content of both hearth structures was found *in situ*, and it therefore reflects their last use episode before the abandonment of the site.

5. Materials and methods

In this work we analyse the plant macroremains found in the two fireplaces dated to the Early Natufian period (Fig. 2D). 100% of the content of the fireplaces was collected and processed to recover plant macroremains. In the case of fireplace A, sample number 90 was extremely large (flot size 1450 ml) and rich, and a quarter was selected for sorting and analyses using a riffle box. In fireplace B all the samples were sorted and analysed. This yielded a total of 463.5 l. of sediment (15 flotation samples) retrieved from different stratigraphic units within the fireplaces. The plant remains were found charred, although some mineralised seeds were also present (i.e. Boraginaceae, *Hyoscyamus* sp., *Atriplex* sp., *Malva pusilla/neglecta*, *Papaver/Roemeria*), as well as uncharred desiccated-type seeds (i.e. *Aizoon hispanicum* and *Cleome* sp.). It must be noted that the embryos inside the Boraginaceae were charred, which suggest they were ancient (van Zeist and Bakker-Heeres, 1985).

Several tubers and wood charcoal remains were observed disintegrating in water during flotation (supplementary Video S1). We therefore decided to systematically dry-sieve all the samples prior

to flotation using a 2 mm size mesh (i.e. minimum size for the identification of wood charcoal remains). After initial sieving, the residue was floated. Samples from fireplace B (youngest) were processed using bucket flotation. This method was used in the first field season because sample processing was carried out on site and there was neither running water nor facilities to build a flotation machine. The soil samples were first measured and small amounts of soil were poured into a plastic bucket previously filled with water. The bucket had 1 mm sized-mesh inside to recover the heavy residue. After stirring the soil, the water was poured into another bucket that had a 0.25 mm mesh inside, which gathered the floating plant macroremains and other light remains (e.g. small-mammal bones). The samples from fireplace A (oldest) were processed with machine-assisted flotation following methods already described in Arranz-Otaegui (2016a). Also in this case, the samples were first dry-sieved and later processed with water in order to pick the tubers and wood charcoal remains out before they were subject to disintegration in water.

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.quascirev.2018.02.011>.

Identification of the charred plant remains was made after comparison with modern specimens in the reference collection compiled by Gordon Hillman and housed at University College London (UCL). Unfortunately, genera/species-level identifications were not always possible in particular families such as Cyperaceae, Cruciferae, Poaceae and Fabaceae. Many of the taxa were represented by one or very low numbers of seeds, which hampered the assessment of intra-species morphometric variation, and thus limited the chances for a detailed identification. Future work will involve the consultation of other reference collections of Near Eastern plants, along with the systematic analyses of the specimens using Scanning Electron Microscopy (SEM, e.g. to characterise the seed coat), an approach that has been applied to achieve genera/species level identifications of plants in the Poaceae, Cruciferae and Fabaceae families (Berggren, 1981; Colledge, 1988; Butler, 1990; Fairbairn et al., 2007).

The identification of underground storage organs was carried out with the aid of an incident light microscope (Olympus BX50) using different magnifications (from 10x to 50x) and identification procedures and criteria described in Hather (1993, 2000). Some of the parenchyma remains were selected for further analyses using Scanning Electron Microscopy (SEM) and compared to modern reference materials. For SEM observation, plant remains were cleaned from soil sediments with a brush, mounted on aluminium stubs, sputter coated with ca. 1 micron of gold, and examined using a Hitachi S-3400 N scanning electron microscope. Imaging of the selected archaeobotanical remains was carried out at 10 kV and at a working distance that varied between 18 and 35 mm from the stage as needed for each individual sample depending on size and detail required for identification purposes. As convention in botanical identification, “type” represents similarity in terms of morphology and size to a particular genus/species; whilst cf. means that almost certainly the item belongs to that genus or species. The nomenclature used follows *Flora Palaestina* (Zohary, 1966, 1972; Feinbrun-Dothan, 1978, 1986), unless otherwise stated.

6. Results

In Table 2 we provide a summary of the proportional representation of different plant categories for each of the fireplaces (see supplement Table S1 for the absolute counts and ubiquity scores of each of the taxa identified). A total of 67458 non-woody plant macroremains were identified. Both fireplaces showed very similar plant composition: Cyperaceae dominated (c. 80% in each of the fireplaces comprising primarily tubers, nutlets and other plants

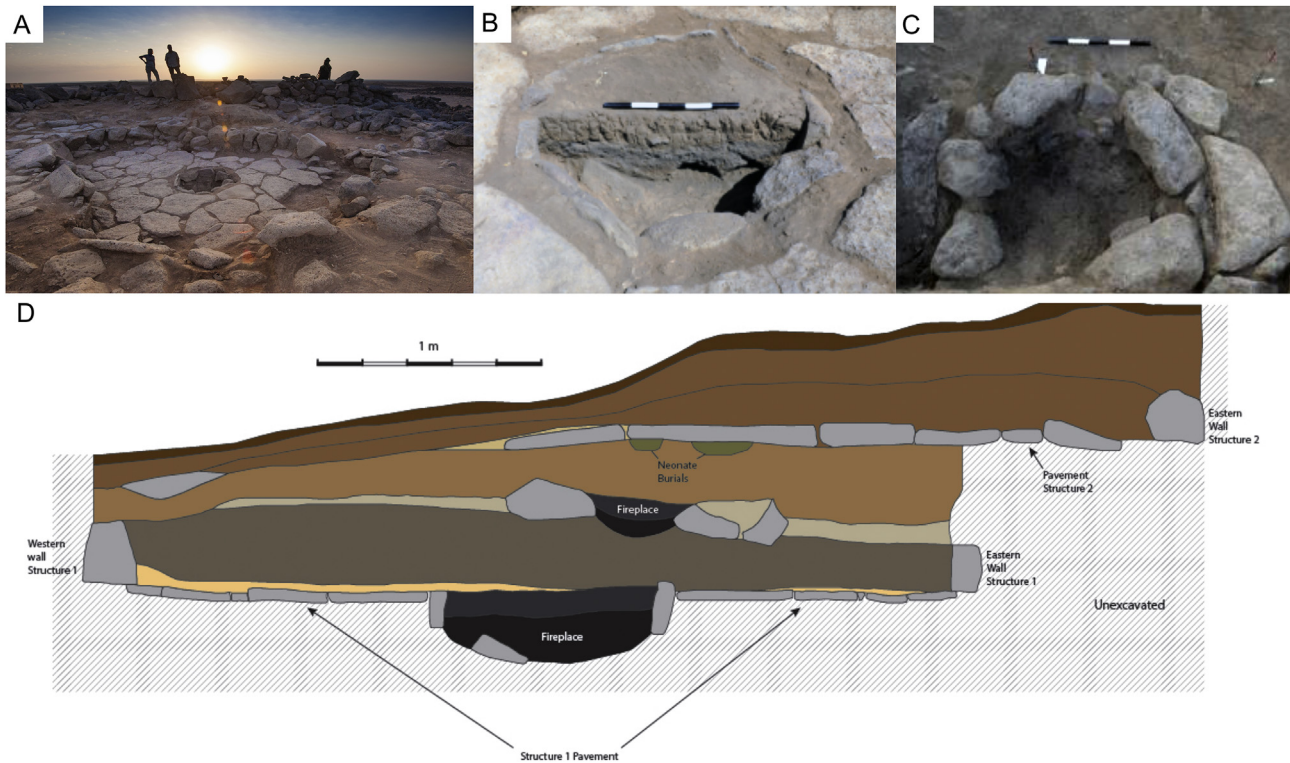


Fig. 2. A) picture of the Early Natufian hut from Shubayqa 1; B) close view of fireplace A showing intact deposits; C) detail of fireplace B after excavation; D) stratigraphic position of fireplaces A (lower) and B (upper).

Table 2
Composition of fireplace A and B based on percentage fragment counts for main plant categories.

Main plant categories	Fireplace A (3 samples)		Fireplace B (12 samples)		Fireplaces A and B	
	frag. counts	% frag. counts	frag. counts	% frag. counts	frag. counts	% frag. counts
Cyperaceae tubers	25994	79.6	27823	80.0	53817	79.8
Cyperaceae other plant parts (e.g. rhizomes, stems, stem bases)	139	0.4	181	0.5	320	0.5
Cyperaceae nutlets and seeds	258	0.8	74	0.2	332	0.5
Large-seeded Poaceae grains/chaff	98	0.3	31	0.1	129	0.2
Small-seeded Poaceae grains/chaff	128	0.4	48	0.1	176	0.3
Fabaceae (mostly small-seeded)	248	0.8	36	0.1	284	0.4
Cruciferae	5448	16.7	6262	18.0	11710	17.4
Other wild plants	350	1.1	340	1.0	690	1.0
Total	32663	100.0	34795	100.0	67458	100.0

parts), followed by Cruciferae (16.7% and 18% in fireplace A and B respectively), several wild plants (1.1% and 1% in fireplace A and B, respectively), Poaceae and Fabaceae (<1%, Table 2).

6.1. Cyperaceae

The assemblage comprised a total of 54469 Cyperaceae remains (Table 2), 98.8% of which corresponded to tubers (Fig. 3A–B, 3F–H), followed by nutlets and seeds (0.6%) (Fig. 3D–E, I–K) and other plant parts such as rhizomes, stems, stem bases, and swallowed rhizomes or developing tubers (0.6%, Fig. 3L–R).

6.1.1. Cyperaceae tubers

In Table 3 the composition of the Cyperaceae underground storage organ assemblage is detailed. Each of the fireplaces from Shubayqa 1 comprised similar number of tubers (25994 in fireplace A and 27823 in fireplace B). A total of 2411 were complete, 3642 were almost complete and showed intact rhizome detachment

scars, and the rest of the remains consisted of eroded fragments of tubers (>2 mm), which were probably broken off during recovery. It is very likely that the assemblage originally comprised many more complete tubers than those recorded after excavation. The total weight of the tuber assemblage was 880.5 gr.

The tubers varied in shape (from rounded to elongated), and size, with the smallest being 0.4 cm in diameter and the largest c. 3 cm (Fig. 3A). The cross section was in all cases circular. However, there were at least 27 tubers that exhibited signs of grinding or squashing before charring, similar to what has been documented in cereal grains (see Fig. 6L and Arranz-Otaegui et al., in preparation for the metrical and taphonomic analysis of the remains). In these cases cross sections were completely compressed. In few of the specimens marked scale leaves that grew along the length of the tuber were preserved (Fig. 3B), very similar to those present in *Cyperus rotundus* (purple nut-grass) (see Hather, 2000, Fig. 51). Rhizome detachments scars were observed both on the surface (Fig. 3B) and also detached, separated from the body of the tuber

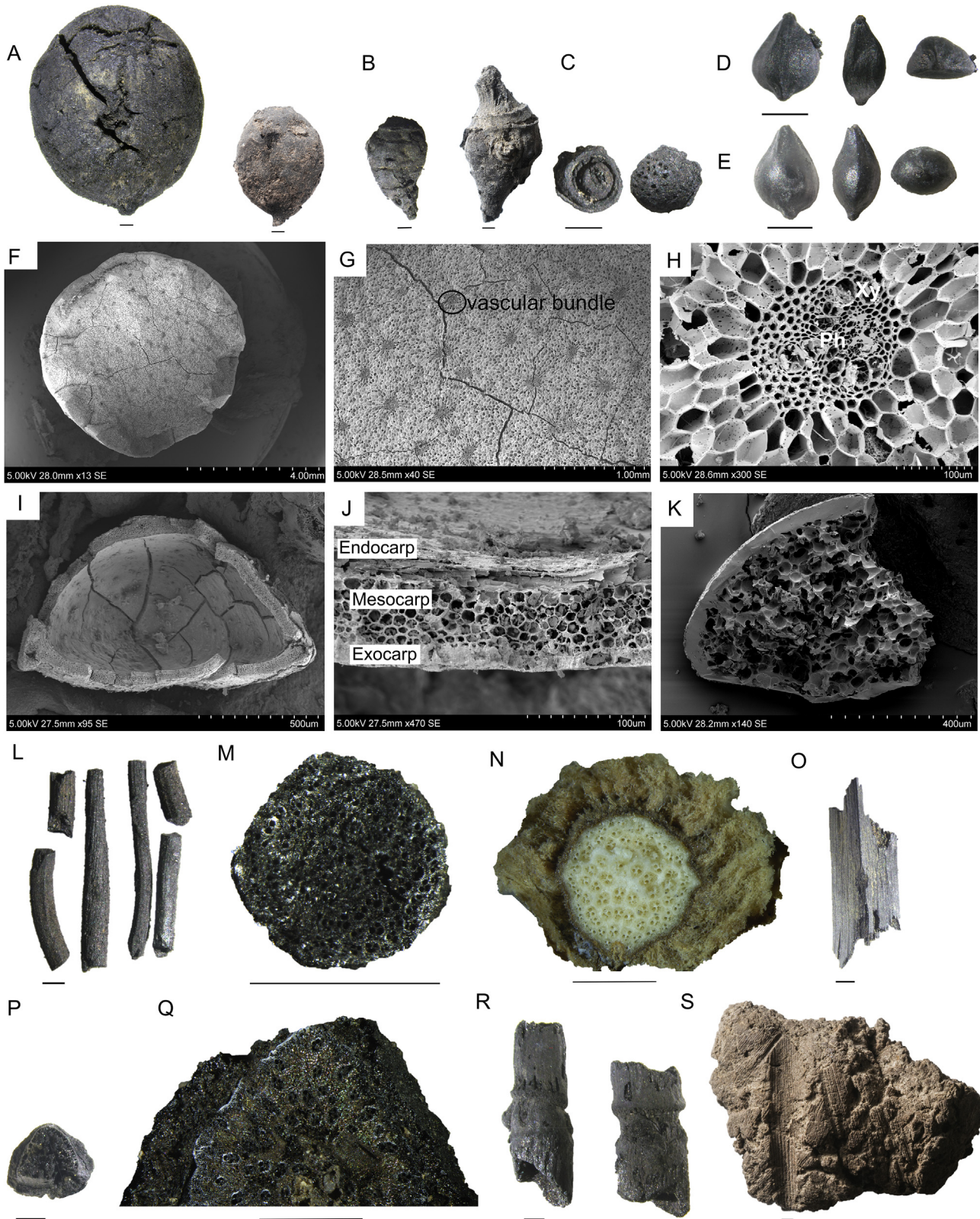


Fig. 3. The Cyperaceae assemblage from Shubayqa 1 (scale 1 mm): A) *Bolboschoenus* sp. tubers of different sizes (probably *B. glaucus*, based on nutshell identification); B) *Bolboschoenus* sp. tubers showing scale leaves and rhizome detachment scar protruding from the body of the tuber; C) a closer view of the rhizome detachment scar separated from the body of the tuber; D) *Bolboschoenus glaucus* nutlets; E) *Schoenoplectus lacustris* nutlets; F) SEM micrograph of the transverse section through the vascular tissues of *Bolboschoenus* sp. tuber; G) SEM micrograph showing random arrangement of the vascular bundles in the same specimen; H) SEM micrograph of a vascular bundle showing an arch of five to six vessels surrounding the phloem on three sides; I) SEM micrograph of the cross section of *Bolboschoenus glaucus* nutlet; J) SEM micrograph showing a detail of one of the edges characterised by a narrow exocarp, thick sclerenchymatic mesocarp and thin sclerenchymatic endocarp (Wollstonecroft et al., 2011); K) SEM micrograph of a Cyperaceae seed; L) *Bolboschoenus* rhizomes; detailed view of the cross section of an M) ancient and N) modern *Bolboschoenus* sp. rhizome showing the vascular bundles; O) *Bolboschoenus* sp. stem and N) stem bases with the characteristic triangular cross section (culm); Q) a detail of the cross section of a *Bolboschoenus* sp. stem showing the arrangement of the vascular bundles; R) *Bolboschoenus* sp. swallowed rhizomes, developing tubers; S) compacted soil residues with Cyperaceae impressions.

Table 3

Summary of the Cyperaceae underground storage organ assemblage from Shubayqa 1. (Note that all the tubers identified under the microscope so far represent *Bolboschoenus* sp.).

Plant part	Fireplace A (3 samples)				Fire place B (12 samples)				Fireplace A and B (15 samples)			
	counts	% frag. counts	ubiquity	% present	counts	% frag. counts	ubiquity	% present	counts	% frag. counts	ubiquity	% present
tuber complete	1020	3.9	3	100.0	1391	5.0	12	100.0	2411	4.5	15	100.0
tuber fragment with rhizome detachments scar	1755	6.7	5	100.0	1887	6.7	12	100.0	3642	6.7	15	100.0
tuber fragment (eroded, no scars)	23219	88.8	3	100.0	24545	87.6	12	100.0	47764	88.2	15	100.0
rhizomes	90	0.3	3	100.0	90	0.3	4	33.3	180	0.3	7	46.7
stems and stem bases	19	0.1	1	33.3	22	0.1	4	33.3	41	0.1	5	33.3
swallowed rhizome (developing tuber)	30	0.1	2	66.7	69	0.2	6	50.0	99	0.2	8	53.3
Total	26133	100.0	3	100.0	28004	100.0	12	100.0	54137	100.0	15	100.0

(Fig. 3C). The latter were particularly common in flotation samples, which indicate they are resistant to water and may, therefore, serve to identify the presence of underground storage organs in sites where parenchymatic tissue has disintegrated due to the application of water-based recovery techniques. A total of 120 tuber fragments were selected for further inspection under the incident light microscope and SEM (Fig. 3F–H). When preserved, the cortex of the tubers was characterised by a 3–4 cell thick layer of fibres and the ground tissue of the pith contained isodiametric polygonal cells (Hather, 1988). Vascular bundles were commonly ovoid and concentric, with fibre sheaths being wider in the xylem pole than in the phloem pole. Each vascular bundle had two to three metaxylem vessels surrounded by a thick sheath of fibres. The xylem formed an arch of 3–6 vessels that surrounded the phloem (Fig. 3H), which was sometimes destroyed leaving a cavity. The anatomical structure of the remains indicated they corresponded to *Bolboschoenus* sp. (club-rush) (Hather, 1988, 1993).

In southwest Asia *Bolboschoenus glaucus* and *B. maritimus* (sea club-rush, *Scirpus maritimus* L.) are the most common club-rush species (Wollstonecroft et al., 2011). The former is a thermophilous species well adapted to high summer temperatures and currently growing in several south European countries (Browning et al., 1998). The latter is a halophytic semi-aquatic plant growing in seacoasts and inland saline habitats. Based on the morphology of the nutlets (Wollstonecroft et al., 2011), *B. glaucus* is present at Shubayqa 1 (Fig. 3D), and it is the predominant species within the Cyperaceae seeds found at the site (see section 6.1.2.). It is very likely that the tubers found in the fireplaces also corresponded to this species. Yet, the presence of other species of the Cyperaceae family cannot be completely excluded given the large quantities of remains recovered.

6.1.2. Cyperaceae nutlets, rhizomes and stems

Apart from tubers, the two fireplaces produced considerable numbers of Cyperaceae nutlets and seeds (Fig. 3I–K) and other plant parts such as rhizomes (Fig. 3L–M), stems and stem bases (Fig. 3O–Q) and swallowed rhizomes or developing tubers (Fig. 3R). Amongst the nutlets, *Bolboschoenus glaucus* was dominant in terms of absolute counts (73.5%) and ubiquity values (86.7%, supplement Table S1), followed by Cyperaceae seeds (10.8% counts and present in 26.7% of the samples, Fig. 3K). *Bolboschoenus glaucus* nutlets were characterised by their obovate to elliptic outline, the cross section was sub-trigonous with smooth surfaces (Fig. 3D and I). As described by Wollstonecroft et al. (2011), the pericarp comprised a narrow exocarp (one layer of isodiametric cells), a thick sclerenchymatic mesocarp (5–6 layers of cells) and thin sclerenchymatic endocarp (Fig. 3J). Other taxa present within the nutlet assemblage comprised *Schoenoplectus* spp., *Eleocharis* sp. and possibly *Carex* sp. (*Carex* tp. and *Schoenoplectus/Carex*), but these

were comparatively rare (percentage fragments counts <11%, and present in <50% of the samples).

The rhizomes identified in the assemblage were cylindrical, 0.8–1.5 mm across, and showed faint vertical striations (Fig. 3L). In transverse section, the vascular bundles were scattered, and the xylem comprised three to six vessels that surrounded the phloem on three sides, similar to the arrangement observed in the tubers (Fig. 3M) (Hather, 1993). Fragments of stems and stem bases were triangular in cross-section with flat sides, 3–4 mm wide (Fig. 3O and P), which is a key characteristic of plants of the Cyperaceae family (see also Bamford, 2012). The central ground tissue was spongy with peripheral air cavities, sometime broken down forming irregular cavities, scattered vascular bundles (comprising three to six xylem vessels) (Fig. 3Q). Club-rush tubers are formed as a terminal swelling of the rhizomes, and some of these swallowed rhizomes or developing tubers were identified in the assemblage (Fig. 3R). These were round in cross section, 3–4 mm in diameter, showed scars left by the deterioration of adventitious roots. In addition, impressions of Cyperaceae stems were found in compacted soil residues (see Arranz-Otaegui et al. in preparation for further details, Fig. 3S). The impressions were flat or semi-circular in cross section, between 1 and 5 mm wide, and they were characterized by longitudinal and regularly spaced fine striations.

6.2. Cruciferae

Plants of the Cruciferae family were the second main plant category found in the fireplaces and comprised at least nine taxa (Fig. 4). The fruits and seeds of *Zilla spinosa* were most numerous in terms of absolute counts and ubiquity values in fireplace A (present in the three samples and summed percentage fragment counts of 98.2%, supplement Table S1, Fig. 4G and H). In fireplace B, the seeds of a different type of crucifer (type 1) were predominant in terms of absolute counts (99%) and ubiquity (present in 83.3% of the samples), and comprised a total of 6212 seeds (Fig. 4A–C). It is remarkable to note that some of these indeterminate type 1 seeds were found embedded in organic tissue, analyses of which are ongoing (Fig. 4L). Unfortunately, these seeds have not yet been positively identified to genus/species, since none of the taxa present in the reference collections consulted completely matched the archaeological remains in terms of morphology, size and seed coat surface pattern. Nevertheless, the comparative analyses carried out indicated large resemblance to *Hirschfeldia incana* M. (also known as *Sinapis incana* and *Brassica geniculata*, Fig. 4D–F), a species that commonly lives in fields and roadsides in the Mediterranean and Irano-Turanian region (Zohary, 1966). In both cases, the size of the seeds was rather small (between 0.4 and 0.7 mm in length, 0.3–0.5 mm in breadth, and 0.3–0.4 mm in thickness). In terms of shape, the seeds were elliptic with two parallel to slightly convex

sides (types 4–5 for the dorsal and ventral view and 45–46 for the lateral view, following Berggren, 1981, plate 10). The cross section was square to slightly round (type 8–9 in Berggren, 1981, plate 10). The tip of the radicle was obtuse, slightly longer than that of the cotyledon, whilst the tip of cotyledons was truncate or rounded. Radicular ridges and hilum were indistinct (the latter usually covered with remains of funiculus). The primary difference with modern descriptions of *Hirschfeldia incana* and other small-seeded crucifers such as for example *Hymenolobus procumbens* relied on the pattern of the seed coat (see Berggren, 1981, plate 104.6la). In the archaeological remains from Shubayqa 1, the seed coat was characterized by epidermal cells that were indistinctly regular (10–20 micra in diameter), with meshes angularly rounded or subquare, similar to those found for example in *Cardaria draba*

(Berggren, 1981, plate 95.4la) or *Diplotaxis tenuifolia* (Fig. 14 in Kasem et al., 2011). In the case of *Hirschfeldia incana*, the seed coat was characterized by slightly reticulate patterns that comprised small particles and 30–40 micra in diameter (see Fig. 18 in Kasem et al., 2011). Further studies are needed to compare archaeological (charred) and modern (uncharred) crucifers and to assess how the combustion process affects the overall shape of the seeds and the seed-coat pattern and in so doing provide secure criteria to identify these archaeological remains.

6.3. Other wild plants

Among the wild plants (excluding Cruciferae, Cyperaceae, Poaceae and Fabaceae) more than 50 taxa were identified (Fig. 5,

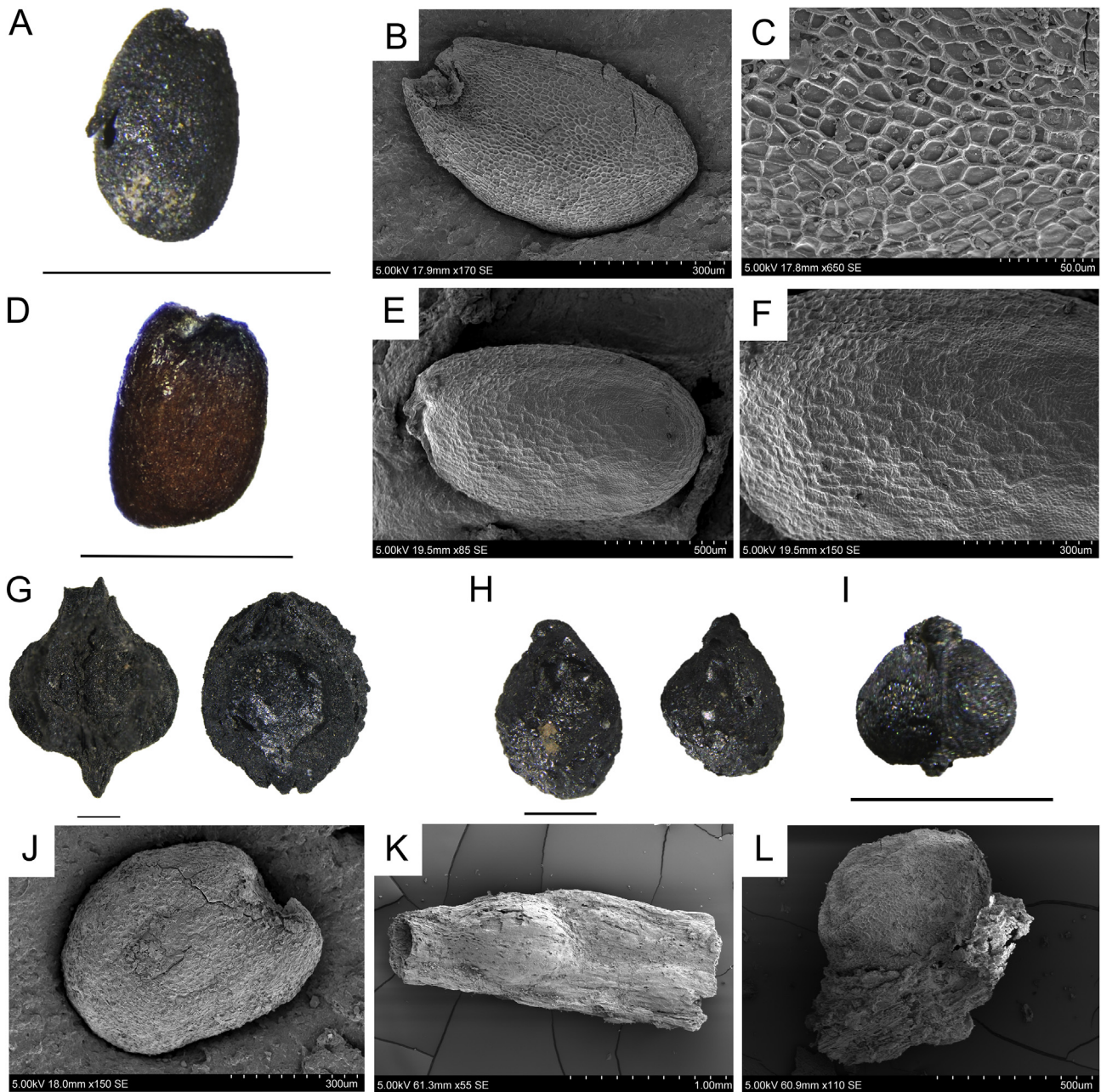


Fig. 4. The Cruciferae assemblage from Shubayqa 1 (scale 1 mm). Comparison of the indeterminate crucifer (type 1) found at Shubayqa 1 (A–C) with modern *Hirschfeldia incana* (D–F); G) fruit and H) seed of *Zilla spinosa*; I) fruit of *Lepidium* sp.; J) *Camelina* sp.; K) indeterminate Cruciferae multi-seeded dry fruit; L) indeterminate crucifer (type 1) embedded in a organic plant tissue.

supplement Table S1). In fireplace A, *Arnebia decumbens* was predominant in terms of absolute counts (26.3% counts), followed by *Hyoscyamus* sp. (16.9%) and *Vitex pseudo-negundo* (12.3%), whereas in terms of ubiquity, *Aizoon hispanicum*, *Arnebia decumbens*, *Centaurea* spp. and *Hyoscyamus* sp. were present in all the samples (100% ubiquity values). In fireplace B, *Malva pusinella/neglecta* was most abundant in terms of absolute counts (20% counts), followed by *Aizoon hispanicum* (10.3%) and *Euphorbia chamaesyce* (11.5%). In terms of ubiquity values, *Aizoon hispanicum* was most common (66.7% presence).

6.4. Poaceae

Small-seeded grasses were slightly more common than the large-seeded grasses in the archaeobotanical assemblage from Shubayqa 1 (176 and 129 remains respectively). Due to preservation issues (e.g. embryo and testa lacking, puffed seeds, seeds with protrusions etc.), and especially because many of the seeds were broken down into small fragments that did not preserve enough characteristics for identification, 77.3% of the small-seeded Poaceae were indeterminate. Excluding indeterminate remains, the most common taxa in the assemblage were *Ammochloa palaestina*/*Polypogon* type seeds, with absolute counts of 6.8% and present in 20% of the samples. The rest of the taxa were rare (<10% absolute counts and ubiquity scores).

Within the large-seeded Poaceae assemblage, *Triticum* spp. was more common than all other taxa in terms of fragment counts (45.7%). A small number were identified to species level and include *T. boeoticum/urartu* 1 g-type and 2 g-type (Fig. 6A–C), although *T. dicoccoides* might also be present (Fig. 6D). Interestingly, the taphonomic analyses of the breakage patterns of the large-seeded grasses showed the presence of wild wheat grains broken prior to charring (Fig. 6C, 46.43% of the wheat grains, 26 out of 56 grains), which are characterised by a bulging pattern on the broken edge of the grain (Valamoti, 2002; Antolín and Buxó, 2011). Apart from wheat grains, small amounts of wheat chaff were also found, including a spikelet fork and glume bases (Fig. 6E and F). The wheat spikelet fork had a characteristic wild-type scar (i.e. smooth or brittle-type), typical of morphologically wild species (Tanno and Willcox, 2012). Other large-seeded grasses such as *Hordeum spontaneum* (14.7% absolute counts) and *Avena* spp. (3.9% absolute counts) were also identified in the assemblage (Fig. 6G–K). It is interesting to note the presence of *Hordeum spontaneum* grains

with pre-charring fragmentation, indicative of grinding. Finally, there were at least 28 remains that corresponded to ground grains of indeterminate large-seeded Poaceae (Fig. 6L).

6.5. Fabaceae

The Fabaceae family was also represented in the assemblage from Shubayqa 1, but except for some *Vicia*/*Lathyrus* type seeds, the assemblage comprised small-seeded Fabaceae (length ranging from c. 0.5 mm–2 mm). The largest number of small-seeded legumes was found in fireplace A. Here, *Astragalus* spp. (Fig. 7A and B) was predominant in terms of absolute counts (59.3%). Apart from this taxon *Trigonella*/*Astragalus* (Fig. 7D) was also common (29.4% absolute counts). It must be noted that within these categories a large variety of seed shapes and sizes exist (Fig. 7A–F). Future work may allow further separation of the assemblage into sub-groups.

7. Plant exploitation in Shubayqa 1

The strikingly similar plant composition (i.e. plant taxa and fragment counts) of the two fireplaces indicates persistent patterns in terms of plant acquisition (quantities) and use over time. In Tables 4 and 5, the economic values of the species identified in the assemblage are summarised based on several ethnographic and ethnobotanical accounts (Zohary, 1966, 1972; Feinbrun-Dothan, 1978, 1986; Hillman, 1989, 2000; Ertug-Yaras, 1997; Rivera et al., 2011; and references therein). From the 29 taxa identified to species level (including those identified as tp.), 24 have a known economic value, either as food (17 species), fuel (three species), fodder (12 species), raw materials (four species) and medicines (15 species). No economic uses were found for *Spergula arvensis*, *Ammochloa palaestina*/*Polypogon*, *Stipagrostis obtusa*, *Avena longiglumis* and *Aeluropus lagopoides*. (Note that the assemblage of species with economic value will probably expand as the analyses progress).

7.1. Plant foods: the importance of wild plants and “missing foods”

Plant foods make up the bulk of the diet in many hunter-gathering, agricultural and pastoral societies across the globe and they may comprise a wide range of resources such as seeds, tubers, fruits, nuts, leaves, stems, and flowers among others. In the last few years, archaeobotanical studies have started to show direct evidence for the use and consumption of plants other than cereals and

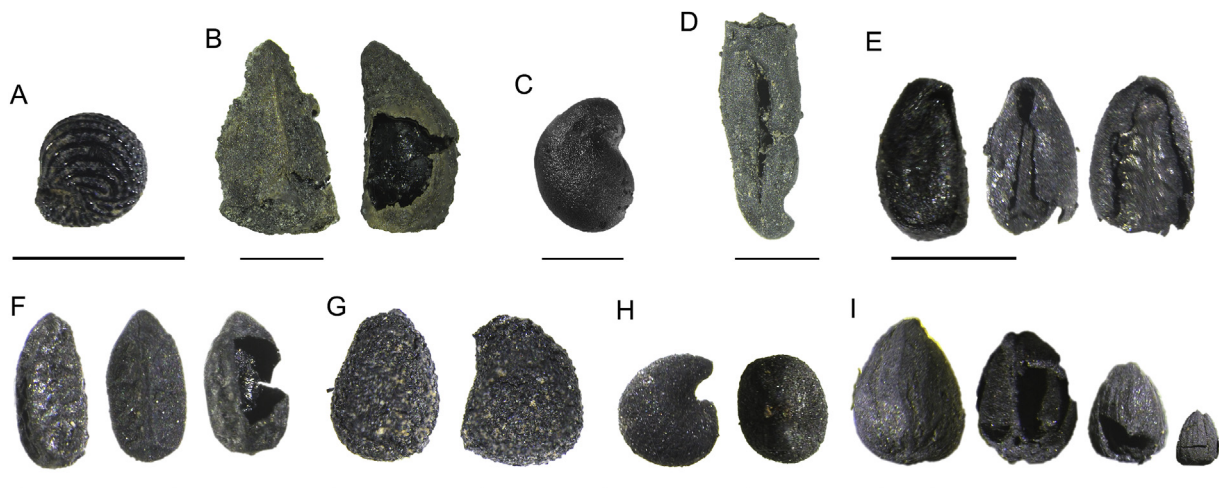


Fig. 5. Main wild plant taxa from Shubayqa 1 (scale 1 mm). A) *Aizoon hispanicum*; B) *Arnebia decumbens*; C) *Capparis spinosa*; D) *Centaurea* spp.; E) fruit and F) seed of *Euphorbia chamaesyce*; G) *Hyoscyamus* sp.; H) *Malva pusinella/neglecta*; I) *Vitex pseudo-negundo* fruits with different sizes.

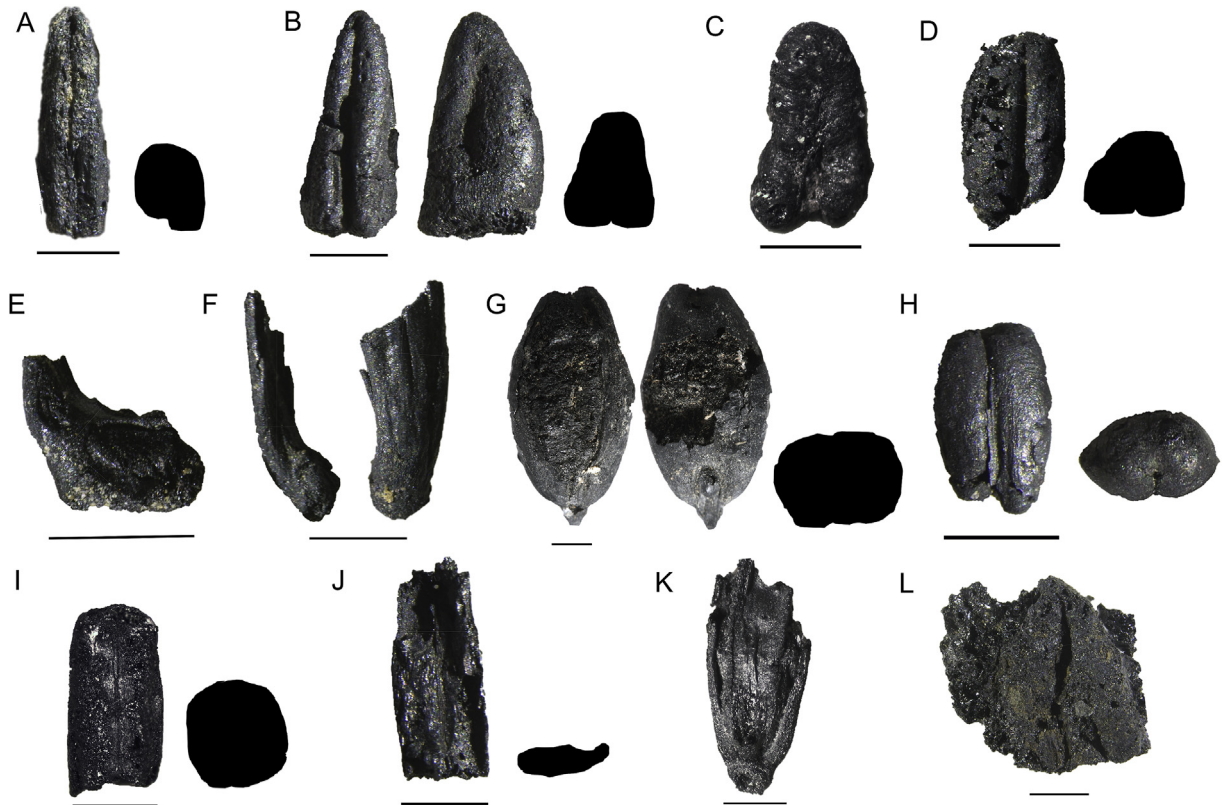


Fig. 6. Poaceae grain and chaff remains from Shubayqa 1 (scale 1 mm). A) apical end of *T. boeoticum/urartu* (2 g-tp.) in ventral view and cross section; B) ventral and lateral view and cross section of *T. boeoticum/urartu* (1-2 g-tp.); C) cross section of *T. boeoticum* (1 g-tp.) with pre-charring fragmentation pattern; D) medial part of *T. boeoticum* (2 g-tp.) showing pre-charring fragmentation pattern in cross section; E) *Triticum* sp. spikelet fork with wild-type rachis scar; F) *Triticum* sp. glume base; G) *Hordeum spontaneum* in ventral, dorsal and cross section; H) *Hordeum spontaneum* showing pre-charring fragmentation pattern in cross section; I) *Stipa* sp. in ventral and cross section; J) *Bromus* sp. in ventral view and cross section; K) *Avena longiglumis* tp. spikelet fork; L) ground large-seeded Poaceae grain (probably wheat).

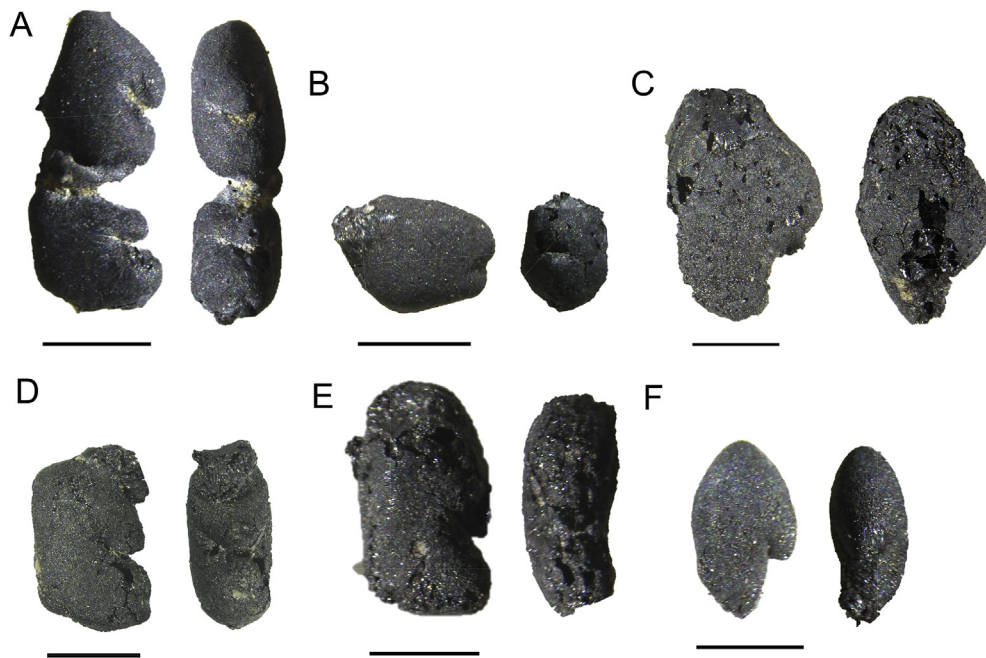


Fig. 7. Fabaceae from Shubayqa 1 (scale 1 mm). A) *Astragalus* sp.; B) *Astragalus* sp.; C) *Melilotus* sp.; D) *Trigonella/Astragalus* sp.; E) *Trigonella* sp.; F) *Trigonella* sp.

Table 4

Species identified in Shubayqa 1 and their potential uses as food (as recorded in Zohary, 1966, 1972; Feinbrun-Dothan, 1978, 1986; Hillman, 1989, 2000; Ertug-Yaras, 1997; Rivera et al., 2011 and references therein). There were 12 species for which no consumption records were found. *Bolboschoenus glaucus* is not present in the *Flora of Palaestina*, but the presence of *Scirpus maritimus* or *Bolboschoenus maritimus* is mentioned. (Note that some of these species were identified as “type” in Shubayqa 1).

Species	Plant part	Use as food
<i>Schoenoplectus mucronatus</i>	tuber	Consumed in the Caucasus
<i>Lepidium latifolium</i>	seed	Bruised and eaten by Persians
	leaves	Consumed as potherb or salad in southwest Asia. Tender leaves and stems consumed in the Caucasus. Plant with valuable essential oils.
<i>Diploaxis harra</i>	flowers	Eaten fresh by Bedouins
<i>Carrichtera annua</i>	leaves and stems	Eaten fresh by Bedouins
<i>Phragmites australis</i>	young shoot	Chewed like sugar cane in Iraq
	tender leaves and stems	Consumed in the Caucasus, they contain vitamins of group A and C
	underground storage organs	Source of starch
<i>Euphorbia chamaesyce</i>	not specified	Consumed roasted, or boiled into soup
<i>Bolboschoenus glaucus</i> (<i>Scirpus maritimus</i>)	young tubers	Eaten as snack by children, source of starch
	nutlets	Eaten raw or pounded to mush, roasted and ground to flour
<i>Zilla spinosa</i>	leaves	Boiled and eaten by in Egypt and Arabia
<i>Malva neglecta</i>	leaves, stems and flowers	Added to salad and pastries or cooked as a meal. Young shoots and leaves consumed in Jordan. Tender leaves and stems consumed in the Caucasus. <i>Malva</i> spp. used as potherb or salad in the Near East
	not specified	Plant used in Assyrian cuisine in the Tur Abdin area
	not specified	The plant contains vitamins of the group A
<i>Malva pusilla</i>	not specified	Leaves may be cut and cooked as a potherb. Used in the Assyrian cuisine in the Tur Abdin area, Persians very fond of the cooked leaves. The leaves are collected, cooked and eaten as a vegetable in Iraq. Consumed boiled, fried or in soups un
<i>Malva parviflora</i>	leaves, stems and aerial part	Bedouins.
	seeds	Eaten by Bedouins
	flowers and leaves	Consumed as green in Turkey. Flowers used to dye tea
<i>Papaver syriacum</i>	seeds	Contain 40–50% of edible oil
	young stems	Consumed fried and boiled
	seed	Suitable as food, Bedouin tribes in the Negev, Jordan and Sinai deserts eat the seeds (including bran) as pita bread
<i>Hordeum spontaneum</i>	seed	The seeds consumed in the Caucasus. The leaves contain vitamin C
<i>Tribulus terrestris</i>	seeds and leaves	<i>A. fatua</i> contains vitamin C and it is consumed by Christian hermits in Tur Abdin area. <i>A. sterilis</i> is edible, Bedouins prepare bread and porridge for diabetic people
<i>Avena fatua/sterilis</i>	not specified	The plant contains vitamin C
<i>Poa bulbosa</i>	not specified	Flavour dishes in the Caucasus, it has small amounts of vitamin C
<i>Zygophyllum fabago</i>	not specified	

legumes during the Palaeolithic/Epipaleolithic (Hillman et al., 1989a; Weiss et al., 2004; Martinoli and Jacomet, 2004) and the Pre-Pottery Neolithic A and B (Willcox, 2002; Savard et al., 2006; Fairbairn et al., 2007; Weide et al., 2017), the time when early plant food production activities, cereal domestication and agriculture developed.

However, taphonomic issues have largely biased our perception of prehistoric plant-based diets. There has been an emphasis on the importance of grain/seed consumption of domesticated cereals and legumes and to a lesser extent wild plants, as these are recurrently found in archaeological sites. and The exploitation of resources such as roots, flowers, stems and leaves, commonly referred to as “missing foods” due to their low archaeological visibility, has been underestimated. The results from Shubayqa 1 help us shed light on some of the little investigated plant-foods consumed during the Natufian period.

7.1.1. Cyperaceae

Hillman (1989; Hillman et al., 1989a, 1989b) suggested that Cyperaceae tubers and rhizomes could have constituted staple plants for Epipaleolithic hunter-gatherers, but solid evidence for this practice has not been found until now. The repetitive presence of club-rush tubers in two fireplaces from Shubayqa 1 demonstrates that not only the seeds of wild plants, but also the underground storage organs were an integral part of the Natufian plant-based subsistence. The continuous occurrence of *Bolboschoenus* sp. tubers in two fireplaces that corresponded to two different occupation phases shows that this plant species was recurrently dug out from the mud, brought to site, and charred in the fireplaces. The presence of charred tubers, nutlets and stems indicates that the harvesting strategies of the inhabitants relied on the collection and

transportation of whole *Bolboschoenus* sp. plants. It is likely that this taxon was used for several purposes, depending on the part of the plant selected (see Tables 4 and 5).

Ethnographic and ethno-historical accounts provide evidence for the consumption of *Bolboschoenus* spp. tubers in different countries worldwide (Hillman et al., 1989b; Wollstonecroft, 2007, 2009; Rivera et al., 2011). They are regarded as energy-rich plant foods and contain around 20% of carbohydrates, including fibre and starch, 1.4% protein, 0.2% lipids and 0.8% of minerals (Kirk and Sawyer, 1991; Wollstonecroft, 2009). Besides, energy (kcal/h) and carbohydrate/h return-rates are comparable to staple plants such as cereals (Wollstonecroft, 2009). It is therefore very likely that this plant constituted an important source of food particularly during spring-time, when the tubers are most succulent (Hillman et al., 1989b; Wollstonecroft et al., 2011, Arranz-Otaegui personal observation). The bulk of the records indicate that these tubers are commonly dried before being ground into flour to make bread or gruel, mush or cakes (Hillman et al., 1989b and references therein). Furthermore, some species such as *Scirpus kysoor* or *Scirpus paludosus* can be sliced and eaten raw (Tanaka, 1976 as cited in Hillman et al., 1989b). Modern experimental studies indicate that gruel and bread are the most easily chewed and swallowed foods made out of the tubers and those with the most pleasant flavour (Wollstonecroft, 2009). Archaeobotanical research into the analysis of cooked foodstuffs at the PPNB site of Çatalhöyük has recently identified the use of *Bolboschoenus glaucus* tubers as food by ca. 9.1 ka cal. BP (González Carretero et al., 2017). The presence of squashed tubers in the fireplaces from Shubayqa 1 suggests that grinding activities took place at the site (see Arranz-Otaegui et al., in preparation for more details). The large assemblage of grinding and pounding tools recovered in both the Early and Late Natufian

Table 5
Species identified in Shubayqa 1 and their potential economic uses as fuel, fodder, raw materials and medicine (as recorded in Zohary, 1966, 1972; Feinbrun-Dothan, 1978, 1986; Hillman, 1989, 2000; Ertug-Yaras, 1997; Rivera et al., 2011; and references therein). There were eight species for which no economic uses were identified. *Schoenoplectus litoralis* is referred to as *Scirpus litoralis* in the *Flora of Palaestina*. *Bolboschoenus glaucus* is not present in the *Flora of Palaestina*, but the presence of *Scirpus maritimus* or *Bolboschoenus maritimus* is mentioned. (Note that some of these species were identified as “type” in Shubayqa 1; medicinal uses of the plant species identified are not discussed in this work).

Species	Plant part	Fuel	Fodder	Raw materials	Medicine
<i>Schoenoplectus litoralis</i>	not specified				x
<i>Vitex pseudo-negundo</i>	stem	x		Broom making	
<i>Lepidium latifolium</i>	seed				x
	leaves				x
<i>Polypogon monspeliensis</i>	not specified		Grazed by animals in Iraq but not of a great fodder value (long-awned forms can be dangerous for sheep and goat)		
<i>Phragmites australis</i>	not specified stems	Tinder	Grazed by animals. In Iraq, young plants grazed by water buffalo, cattle and even horse	Used to make hunting tools in Turkey. Also to build fences, manufacture baskets, shelters, rooftops and kites To make musical instruments. Ropes are made of finely split reeds pounded into cords that are twisted around each other. Construction of huts and fences For weaving sitting mats in Wadi Gaza, Gaza Strip and Palestine	x
	leaves				
<i>Bolboschoenus glaucus</i> (<i>Scirpus maritimus</i>)	stem	Dry stems as tinder		People fill cushions with the stem. Also used for weaving mats and baskets in Turkey. Dry stems to build roofs and as insulation under the floors	Used to produce smoke as an insect repellent in Turkey
	tuber			In Turkey, they collect mud with tubers in spring to manufacture mud-bricks for garden walls	x
<i>Aizoon hispanicum</i>	not specified				x
<i>Arnebia decumbens</i>	root			It makes a violet dye	
<i>Zilla spinosa</i>	not specified				x
<i>Diploaxis harra</i>	not specified		Grazed by animals in Iraq		x
<i>Carrichtera annua</i>	not specified		Camels and other animals graze freely on it		
<i>Malva neglecta</i>	whole plant		x		x
<i>Malva parviflora</i>	not specified		Grazed by livestock in Kuwait, Gaza Strip, and Palestine		x
<i>Papaver syriacum</i>	flowers, leaves and petals				x
<i>Hordeum spontaneum</i>	seed		When tender a forage of little value		x
<i>T. boeoticum/urartu</i>	not specified		Grazed by animals		
<i>Tribulus terrestris</i>	aerial parts, fruits, leaves		Eaten by sheep in its young stages (obnoxious in fruit as the sharp spines may stick into their feet). In Kuwait camels graze on it occasionally		x
<i>Papaver hybridum</i>	not specified		Grazed by animals		x
<i>Avena fatua/sterilis</i>	not specified		<i>A. fatua</i> fodder grass in the Caucasus. <i>A. sterilis</i> fodder in Turkey		x
<i>Poa bulbosa</i>	aerial part		Used as fodder in Turkey and Iraq. Poor feeding grass owing to its wiry fibrous nature		
<i>Zygophyllum fabago</i>	not specified				x (referred to as poisonous in Iraq)

phases were very probably used to process them (Richter et al., 2012, 2014; Pedersen et al., 2016).

The identification of more than 50000 *Bolboschoenus* sp. tubers in Shubayqa 1 is an exceptional find. Whilst the presence of Cyperaceae nutlets is common in archaeological sites in the region (see summary in Wollstonecroft et al., 2011; Rivera et al., 2011), tubers have been recorded on very few occasions. Hillman (1989; Hillman et al., 1989b) found a fragment of *Scirpus maritimus* tuber along with seven whole and several fragments of *Cyperus rotundus* (purple nut-grass) rhizome tubers at Wadi Kubaniya, a Late Palaeolithic site located close to Aswan, in Egypt. He argued that the exploitation of this kind of root-foods would have been common during the Epipaleolithic, in particular during the Late Natufian at Abu Hureyra (Hillman et al., 1989a). *Bolboschoenus* sp. tubers were reported in the 1960s at the Neolithic site of Çatalhöyük (Helbæk, 1964; Butler, 1995; see also Fairbairn et al., 2002). In Europe, charred Cyperaceae tubers were recorded at several Epipaleolithic/Mesolithic sites (Perry, 1999, 2002; Kubiak-Martens et al., 2015; see a summary in Kubiak-Martens, 2016) and Neolithic sites in the Netherlands (Kubiak-Martens, 2006), although their presence in European prehistoric sites is overall rare.

One of the reasons why underground storage organs are rarely recorded in archaeological sites has to do with the recovery techniques used. Hather (2000, p. 74) pointed out that water should not be used to recover parenchymatic tissue, since a high input of remains and the rapid flushing through of water can easily destroy identifiable fragments of parenchyma. Hillman et al. (1989b) also highlighted that at Wadi Kubaniya *Cyperus rotundus* and *Scirpus maritimus* tubers disintegrated as soon as they entered in contact with water, and they decided to carry out systematic sieving of the sediments to overcome this problem. The instant disintegration of tubers (and some wood charcoal remains) was also noticed at Shubayqa 1, which led to the decision to dry-sieve all the samples before they were processed with the flotation technique (see supplement video 1). It is therefore likely that the disintegration of the parenchymatic tissue has occurred at sites where water flotation had been used to recover plant macroremains. This and other recently reported evidence (Arranz-Otaegui, 2016a) highlights the need to adjust or develop new protocols for the recovery of plant macroremains (such as the systematic dry-sieving of the samples prior to flotation) and avoid the destruction of extremely fragile plant remains such as parenchyma.

Apart from *Bolboschoenus* sp. tubers, the assemblage from Shubayqa 1 also yielded a substantial number of nutlets. The nutlets of *B. maritimus* (sea club-rush) have been recorded at sites dated to from the Epipaleolithic to the Hellenistic period in southwest Asia (see summary in Rivera et al., 2011). Ethnobotanical evidence shows that they are edible especially if roasted, since they explode similar to popcorn (Hillman et al., 1989b). Once roasted the nutlets can also be ground to flour and used to bake cakes (Hillman et al., 1989b). Direct evidence for the consumption of *Bolboschoenus* nutlets is limited to rare finds, such as the human faeces with embedded seeds from the Palaeolithic site of Wadi Kubanya (Egypt, Hillman et al., 1989b). The presence of large proportions of nutlets belonging to *Bolboschoenus glaucus* and other species of the Cyperaceae family in the fireplaces from Shubayqa 1 suggests they were probably harvested along with the whole plant. However additional evidence is needed to confirm they were actually used as food or were introduced through dung burning, as suggested in later Neolithic sites (Filipovic, 2014, p. 61).

7.1.2. Other edible wild plants

Crucifers were second in terms of absolute counts in the fireplaces from Shubayqa 1. However, there were very few taxa that could have been exploited as food (Table 4). These included the

seeds of *Lepidium latifolium*, which was bruised and eaten by Persians and consumed as potherb or in salads across Southwest Asia; and the green leaves and the flowers of *Zilla spinosa*, which are eaten in countries such as Egypt and Saudi Arabia (Hedrick, 1919 as cited by Rivera et al., 2011). Within the several genera identified in the assemblage, there are species such as *Camelina microcarpa* with high oil contents (25–34% Grossheim, 1952 as cited by Rivera et al., 2011), as well as remarkably well-known spices such as *Lepidium sativum* and *Sinapis arvensis*. Nevertheless, the “modes of arrival” of the Cruciferae in Shubayqa 1 were diverse (see section 7.2).

The role of small-seeded grasses in the subsistence activities of Epipaleolithic and Neolithic communities in southwest Asia is still poorly understood due to the scarceness of the archaeobotanical data. The available evidence suggests that small-seeded grasses were an important source of food since the Palaeolithic period well before the emergence of plant-food production (Weiss et al., 2004). At the Upper-Palaeolithic/Early Epipaleolithic site of Ohalo II, species such as *Alopecurus utriculatus/arundinaceus*, *Bromus pseudo-brachytachys/tigridis*, *Hordeum glaucum*, *Hordeum murinum/hystrix*, *Puccinellia cf. convoluta* were referred to as staple plants (Weiss et al., 2004). At the Early Pre-Pottery Neolithic site of Sheikh e-Abad in Iran, the grains of *Stipa* sp. and other small-seeded grasses were found with clear signs of grinding before carbonization (Whitlam et al., 2016). Several phytolith analyses in Natufian sites highlight the large numbers of small-seeded grasses over cereals, and their likely contribution to Natufian diets (Rosen, 2010; Power et al., 2016). At Shubayqa 1, small-seeded grasses were also more common than large-seeded taxa, but no direct evidence has yet been found for their exploitation. Instead, the results show the exploitation of morphologically wild one and two-grained einkorn (i.e. either *T. boeoticum* or *T. urartu*) and barley *Hordeum spontaneum*. The presence of *T. boeoticum/urartu* and *Hordeum spontaneum* grains ground before charring indicates these species were consumed at the site. Similar evidence of grain processing has been recorded at Pre-Pottery Neolithic sites such as Jerf el Ahmar (Willcox, 2002), el-Hemmeh (White and Makarewicz, 2012) and Tell Qarassa North (Arranz-Otaegui et al., 2016b). For the Epipaleolithic, cereal grains with pre-charring fragmentation patterns have only been documented so far at the Early-Epipaleolithic site of Ohalo II (Snir et al., 2015b). Here, broken grains of *H. spontaneum*, *Avena barbata/sterilis*, and *Piptatherum holciforme* (millet grass) were found on the Floor III with the typical bulging pattern that indicates grinding of grains before charring. Systematic taphonomic analyses on grain fragmentation patterns in other sites will no doubt reveal that this activity was more common than the archaeobotanical evidence indicates to date.

Finally, there were other edible species at Shubayqa 1, such as *Avena fauta/sterilis*, *Tribulus terrestris* and *Papaver rhoeas*, which have edible seeds that can be consumed in the form of bread or oil (Table 4). Other plant-food resources would have been seasonal, available during spring-time, before the plants matured and become fibrous, such as the palatable leaves, stems and flowers of *Phragmites australis*, *Diploptaxis harra*, *Carrichtera annua*, *Malva neglecta* and *Malva parviflora*. These are nowadays used for potherbs and salads (Table 4).

7.2. Remains of fuel and raw materials

The archaeobotanical assemblage recovered from the fireplaces in Shubayqa 1 also included some plant species that derive from the burning of fuel and their use for raw materials. Preliminary analyses of the wood charcoal remains from the fireplaces indicates the burning of *Zilla spinosa*, Chenopodiaceae, *Zygophyllum fabago*, *Bal-lota* sp., *Vitex pseudo-negundo* and *Atriplex* sp. wood. The collection and subsequent burning of these species could explain why not

only the wood, but also their fruits and seeds were found in the fireplaces. In particular, this hypothesis possibly explains the large concentrations of *Zilla spinosa* remains found in the assemblage.

The presence of charred Cyperaceae stems could derive from the use of *Bolboschoenus glaucus* stems as tinder (Table 5). However, the amorphous mud clumps with Cyperaceae stem impressions found at the site suggests that *Bolboschoenus* stems could have also used as raw material. Ethnobotanical accounts show that the stems of Cyperaceae (sedges) have a diverse economic use in several countries worldwide (Simpson and Inglis, 2001). Despite this, the archaeological evidence for the use of Cyperaceae stems in southwest Asia is still patchy. Whilst the presence of basket, roofing, mats and textiles have been reported in several Epipaleolithic and Neolithic sites (see summary in Ryan, 2011; Boyd, 2017), there is still little information about the species from which they derive since identifications to genus or species level is limited to few case studies (e.g. Schick, 1988; Shimony and Jucha, 1988; Rosen, 2005; Ryan, 2011).

Apart from the possible use of plants as fuel and building materials in Shubayqa 1, ethnobotanical records indicate the presence of least 12 species that are commonly grazed by animals (Table 5). Several studies show that the seeds and chaff remains of cereals and other wild plants survive animal digestion and are preserved after dung has been charred (Miller, 1984; Valamoti and Charles, 2005; Valamoti, 2013; Wallace and Charles, 2013). In particular, small seeds and plants that have hard coating, such as those attested at Shubayqa 1, seem to be most commonly preserved (Anderson and Ertug-Yaras, 1998 and references therein). Whilst the use of animal dung during the Natufian was suggested in the past (see Miller, 1996), the lack of finds of animal pellets or dung spherulites in Natufian sites has hampered its positive identification. Further analyses of the fireplace contents will no doubt provide insights to differentiate the plant species that were consciously used by the inhabitants (e.g. as food) from those that entered the assemblage by chance (e.g. fuel burning).

8. Assessing the role of the “founder crops” before the emergence of agriculture

Archaeobotanical evidence indicates that a group of eight species including *T. boeoticum* (wild einkorn), *T. dicocoides* (wild emmer), *Hordeum spontaneum* (wild barley), *Lens orientalis* (wild lentil), *Pisum humile* (wild pea), *Cicer reticulatum* (wild chickpea), *Vicia ervilia* (wild bitter vetch) and *Linum bienne* (wild flax) were domesticated ~10 ka cal. BP, and become the “founder crops” of the Neolithic agriculture (Weiss and Zohary, 2011). These eight crops, which later spread to Europe, have long received the most attention amongst archaeologists and archaeobotanists working in southwest Asia. However, the extent to which they contributed to Epipaleolithic economies has so far only been evaluated through indirect evidence (see section 3). We here assess the potential economic role of the Neolithic “founder crops” before the emergence of agriculture in southwest Asia, in particular from the Late Epipaleolithic to the Early Pre-Pottery Neolithic B (EPPNB).

The scatter plot in Fig. 8 shows the percentage of “founder crops” at 35 sites dated to between 15 and 9.7 ka cal. BP and is based on the analyses of a total of 333409 non-woody plant macroremains. The dataset includes secure identifications of the “founder crops” (i.e. wild and domesticated einkorn, emmer, barley, lentil, pea, chickpea, bitter vetch and flax) and other wild plants per site, and excludes indeterminate remains from the total counts (see supplement Text S1 and Table S2 for the rationale on data selection and interpretation, and supplement Table S3 for the raw data used in the figure). The results show a correlation between the proportional representation of “founder crops” and the chronology of the

sites (Pearson’s $r = -0.425$, $p = 0.009$). This means there is a significant increase in the exploitation of the so-called “founder crops” over time. However, the t -test indicates significant differences in terms of plant composition between the Late Epipaleolithic and the Pre-Pottery Neolithic ($t = -3.307$, $p = 0.002$).

Natufian plant assemblages are characterised by large proportions of edible plants that would probably constituted the staple plants of the period, and included several species of the Cyperaceae, Polygonaceae and Cruciferae families, as well as small and large-seeded (non-founder) Poaceae and Fabaceae (Table 1, section 3.2). The wild ancestors of the “founder crops” made up <20% of the assemblages, c. 8% on average, and in three out of the five Natufian sites they represented <5% of the assemblage (see supplement Table S3). This evidence indicates that in the period immediately preceding the development of plant food production in southwest Asia a wide range of plant resources were consumed. Although it has long been stated that cereals were an important component of the Natufian hunter-gatherer subsistence, the available archaeobotanical evidence suggests otherwise (see Table 1). Cereal exploitation did not become extended practice until the EPPNB and MPPNB (see supplement Table S4 in Maeda et al., 2016 for the proportional representation of cereal grains at Epipaleolithic and Neolithic sites in SWA). Besides, several phytolith analyses carry out at key Natufian sites such as Eynan, Hilazon Tachtit (Rosen, 2004, 2007, 2010), el-Wad (Portillo et al., 2010) and Raqefet Cave (Power et al., 2014, 2016) indicate that small-seeded wild grasses were equally or more commonly exploited than wild wheat and barley, and they could have played a more important economic role during this time (Rosen, 2004, 2010; Power et al., 2014).

The low overall presence of the wild ancestors of the “founder crops” continues at sites dated to the Late Epipaleolithic/Pre-Pottery Neolithic, around 12.1–10.7 ka cal. BP (14.2% on average, Fig. 8, Supplement Table S3). The first clear shift in plant subsistence is attested during the Pre-Pottery Neolithic A (PPNA, 11.7–10.7 ka cal. BP), when the wild ancestors of the “founder crops” increase in proportion, and represent c. 30% of the assemblages on average. Sites dated to around 11.3–10.4 ka cal. BP and located in the southern Levant and the Euphrates area (e.g. Jerf el Ahmar, Mureybet III, el-Hemmeh) show the largest dependence on selected number of species such as *T. boeoticum*, *Hordeum spontaneum* and *Lens* sp. At these sites the wild ancestors of the “founder crops” represent >50% of the assemblage (supplement Table S3). However, in other broadly contemporary sites such as Iraq ed-Dubb, Demirköy, Chogha Golan (X-XI) and Pınarbaşı (A Early) the overall values of the wild ancestors of the “founder crops” are similar to those attested during the precedent Epipaleolithic period (i.e. <14% of the assemblage). This diversity in plant exploitation strategies is also observed during the subsequent EPPNB (10.7–9.7 ka cal. BP, including the start of the MPPNB). Although there is an overall increase in the exploitation of the “founder crops”, which constitute 41.7% of the assemblages on average, the cereal and legume species that eventually form the Neolithic agricultural crop-package are not represented in all the EPPNB sites (see Table S3). In Mureybet IV, Chogha Golan (VI-IX) and Pınarbaşı (A late and D) very low proportions of “founder crops” are still attested (<15%), suggesting reliance on the exploitation of other types of plant resources.

If we consider that the numbers of plant macroremains found in archaeological sites represent to some extent the intensity with which plant species were exploited in the past (at least in sites where there are no limiting factors derived from sampling, sample processing and overall preservation, see Supplement Text S1), we must conclude that the wild ancestors of the Neolithic “founder crops” were not an essential part of the plant-based subsistence during the Late Epipaleolithic and most part of the PPNA. A notable

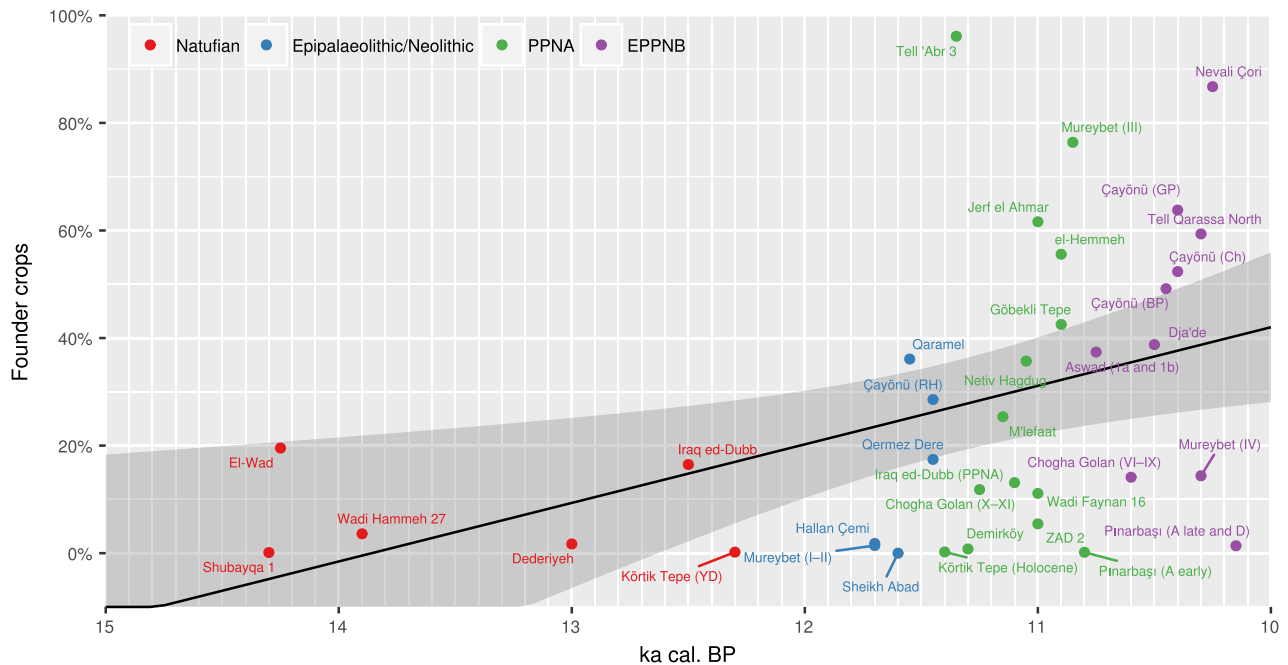


Fig. 8. Scatter plot of the percentage of “founder crops” by median date, at sites dated to between 15 and 9.7 ka cal. BP. The results show a significant correlation between the proportional representation of “founder crops” and the chronology of the sites (Pearson’s $r = -0.425$, $p = 0.009$). A linear model fitted to the data is represented by the black solid line, with the 95% confidence interval indicated by the grey envelope. Note that in Dederiyeh and ZAD 2 the wild ancestors of the “founder crops” might be under-represented due to large concentrations of *Pistacia*. We here include the original data, but see Supplement Table S3 for values excluding *Pistacia*. In Tell Abr’ 3 plant remains were retrieved from a concentration of stored grains found in a burnt communal building. In el-Wad, the wild ancestors of the “founder crops” might be over-represented due to the size of the mesh used during recovery (see supplement Text S1).

increase is only observed during the EPPNB, although Neolithic “founder crops” did not become completely established until the late PPN. The available evidence indicates that the consumption of plants other than the “founder crops” was very common during the PPNA and EPPNB. This is further supported by the growing evidence for the exploitation and possible cultivation of plant species that do not traditionally belong to Neolithic agricultural crop-package such as *Avena sterilis* (Weiss et al., 2004), *Vicia peregrina* (Melamed et al., 2008) and *Vicia faba* (Caracuta et al., 2015). Early Pre-Pottery Neolithic plant exploitation was therefore diverse in terms of the plant species selected (probably conditioned by regional availability of plant resources) and the type of subsistence strategies adopted. Pre-domestication cultivation practices were not common in all the sites, and if present, they may have comprised plant species that did not necessarily evolved into domestication. The results highlight the need to separate the “founder crops” of the Neolithic agricultural period, from the preceding “founder plants” of the foraging and early farming subsistence. Future studies should therefore be aimed at defining the group of plant species that represented the “pre-agricultural staple plants”.

9. Conclusions

The content of two fireplace structures from Shubayqa 1 has yielded the largest non-woody plant assemblage for the Natufian period to date. Both fireplaces comprised similar numbers and plant taxa, an interesting feature that suggests repetitive patterns in the use of plant resources during two occupation phases. The presence of such a large number of tubers is exceptional and demonstrates that root-foods were of great economic importance, and played a substantial role in the economy of the Early Natufian

hunter-gather groups that inhabited Jordan’s Black Desert. Our finds therefore add a new dimension to explore the role of starch-rich vegetative plant parts as potential staples during the Late Pleistocene. The application of recovery techniques such as dry-sieving prior to flotation coupled with more intense training of archaeobotanists on the recognition and identification of underground storage organs will no doubt contribute to increase the visibility of this “missing food”, and in so doing produce reliable data to evaluate their past exploitation.

The economic importance that cereals have acquired in the modern world has strongly affected the types of questions we ask to the archaeological record, and it has also influenced the interpretations we carry out. As pointed by Wright (1991) pre-historians have considered wild cereals as an exceptionally appealing source of food, based on their large seed size, the presence of high densities and storability (see Henry et al., 1981; Bar-Yosef and Kislev, 1989). However, the archaeobotanical evidence shows that despite their potential, Natufian groups did not exploit the wild ancestors of domesticated cereals and legumes in similar ways or to the same extent as Neolithic populations did. Therefore, early claims for Natufian economic systems based on the exploitation of the wild ancestors of domesticated “founder crops” need to be reconsidered.

Our results have also some implications for the understanding of the origins of sedentism, which has often been linked to the exploitation of cereals and to a lesser extent nuts and legumes (Henry, 1989, 1991; Bar-Yosef and Belfer-Cohen, 1989). The available data seems to suggest that Natufian sedentary patterns emerged well before cereal and legume exploitation become common practice. Therefore, the consumption of such resources was not a necessary pre-condition for the development of the sedentary way of life.

Overall, we argue that there has been a tendency to interpret Natufian plant assemblages in terms of the importance of the plant species that are nowadays economically relevant for us. This has led to a significant underestimation of the economic role that (non-founder) wild plants played in the past. As recently emphasized, there has been an unjustified tendency to fit different elements of the Natufian culture into the Neolithic narrative related to the shift to sedentism and plant food production (Boyd, 2017). This has inevitably biased our perception of the pre-agricultural plant-based subsistence.

The cereal-based subsistence of the Natufian groups is deeply rooted in the literature due to the lack of large and well-preserved archaeobotanical assemblages and the systematic and over-reliance on secondary sources of evidence. We hope that future development of identification criteria for the recognition of wild (non-founder) plant exploitation in archaeological sites (through use-wear, microscopic and macroscopic plant remains etc.) will provide more balanced insights into the plant-based subsistence activities carried by the last hunter-gatherers in southwest Asia.

Acknowledgments

This project has been funded by the Independent Research Fund Denmark (Sapere Aude Starting Grant Number DFF – 4001-00068 and Postdoctoral Grant Number 11-116136 awarded to T. Richter), H.P. Hjerl Mindefondet for Dansk Palæstinaforskning and the Danish Institute in Damascus. We wish to thank the Department of Antiquities of Jordan for allowing the excavation and exportation of the materials, and the Danish Institute Damascus for co-funding the excavation seasons at Shubayqa 1. We thank Alexis Pantos (Glasgow School of Art) for recording the supplement video, Prof. Ehud Weiss (Bar-Ilan University), Prof. Dorian Fuller (University College London), Dr. Michele Wollstonecroft (University College London) and Terry C. Spurgeon (Simon Fraser University) for their help on the identification of some of the plant remains from Shubayqa 1, and last but not least, we thank the anonymous reviewers for their useful comments and suggestions.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quascirev.2018.02.011>.

References

- Aladjem, E., 2008. Khirbat Janba. *Hadashot Arkheologiyot* 120. http://www.hadashot-eshi.org.il/report_detail_eng.aspx?id=936.
- Albert, R.M., Bar-Yosef, O., Meignen, L., Weiner, S., 2003. Quantitative phytolith study of hearths from the Natufian and Middle Paleolithic levels of Hayonim cave (Galilee, Israel). *J. Archaeol. Sci.* 30, 461–480.
- Al-Eisawi, D., 1996. *Vegetation of Jordan*. Unesco Cairo Office, Regional Office for Sciences and Technology for the Arab States.
- Anderson, P.C., 1991. Harvesting of wild cereals during the Natufian as seen from experimental cultivation and harvest of wild Einkorn wheat and microwear analysis of stone tools. In: Bar-Yosef, O., Valla, F.R. (Eds.), *The Natufian Culture in the Levant*. International Monographs in Prehistory: Archaeology Series, Michigan, pp. 521–556.
- Anderson, S., Ertug-Yaras, F., 1998. Fuel fodder and faeces: an ethnographic and botanical study of dung fuel use in central Anatolia. *Environ. Archaeol.* 1, 99–109.
- Antolín, F., Buxó, R., 2011. Proposal for the systematic description and taphonomic study of carbonized cereal grain assemblages: a case study of an early Neolithic funerary context in the cave of Can Sadurni (Begues, Barcelona province, Spain). *Veg. Hist. Archaeobot.* 20, 53–66.
- Arranz-Otaegui, A., 2016a. Evaluating the impact of water flotation and the state of the wood in archaeological wood charcoal remains: implications for the reconstruction of past vegetation and identification of firewood gathering strategies at Tell Qarassa North (South Syria). *Quatern. Int.* 457, 60–73. <https://doi.org/10.1016/j.quaint.2016.06.030>.
- Arranz-Otaegui, A., Colledge, S., Ibanez, J.J., Zapata, L., 2016b. Crop husbandry activities and wild plant gathering, use and consumption at the EPPNB Tell Qarassa North (south Syria). *Veg. Hist. Archaeobot.* 25 (6), 629–645.
- Bamford, M.K., 2012. Fossil sedges, macroplants, and roots from Olduvay Gorge, Tanzania. *J. Hum. Evol.* 63, 351–363.
- Bar-Yosef, O., 1998. The Natufian culture in the Levant: threshold to the origins of agriculture. *Evol. Anthropol.* 6, 159–177.
- Bar-Yosef, O., Kislev, M., 1989. Early farming communities in the Jordan Valley. In: Harris, D.R., Hillman, G.C. (Eds.), *Foraging and Farming: the Evolution of Plant Domestication*. Hyman, London, pp. 632–642.
- Bar-Yosef, O., Belfer-Cohen, A., 1989. The origins of sedentism and farming communities in the Levant. *J. World Prehist.* 3, 447–498.
- Bar-Yosef, O., Belfer-Cohen, A., 1992. From foraging to farming in the Mediterranean Levant. In: Gebauer, A.B., Price, T.D. (Eds.), *Transitions to Agriculture in Prehistory*. Prehistory Press, Madison, pp. 21–48.
- Bar-Yosef, O., Meadow, R.H., 1995. The origins of agriculture in the Near East. In: Price, T.D., Gebauer, A.B. (Eds.), *Last Hunters, First Farmers: New Perspectives on the Prehistoric Transition to Agriculture*. School of American Research Press, Santa Fe, pp. 39–94.
- Betts, A.V.G., 1993. Wadi al-'Ajib/Shubaiqa Survey 1993. Unpublished Report. Department of Antiquities of Jordan, Amman.
- Betts, A.V.G., 1998a. The Harra and the Hamad. *Excavations and Surveys in Eastern Jordan*, vol. 1. Sheffield Academic Press, Sheffield.
- Betts, A.V.G., 1998b. Holocene Cultural Ecology and Environments of the North-Eastern Badia. In: Henry, D. (Ed.), *The Prehistoric Archaeology of Jordan*. British Archaeological Reports International Series 705, Oxford, pp. 149–161.
- Berggren, G., 1981. Atlas of Seeds and Small Fruits of Northwest European Plant Species, with Morphological Descriptions. Part 3. Salicaceae-cruciferae. Swedish Natural Science Research Council, Stockholm.
- Böhner, U., Schyle, D., 2006. Radiocarbon CONTEXT Database, 10.1594/GFZ.CONTEXT.Ed1. <http://context-database.uni-koeln.de/>.
- Boyd, B., 2017. Ecologies of fiber-work: animal technologies and invisible craft practices in prehistoric Southwest Asia. *Quatern. Int.* <https://doi.org/10.1016/j.quaint.2017.06.050>.
- Browning, J., Gordon-Gray, K.D., Smith, S.G., van Staden, J., 1998. *Bolboschoenus glaucus* (Cyperaceae), with emphasis upon Africa. *Nordic. J. Bot.* 18, 475–482.
- Butler, A., 1990. Legumes in Antiquity: a Micromorphological Investigation of Seeds of the Viciaeae. PhD thesis. University College London.
- Butler, A., 1995. The plant remains. In: Hodder, I., Çatalhöyük Research Trust (Eds.), *Çatalhöyük 1995 Archive Report*. <http://catal.arch.cam.ac.uk/Archive-rep95>.
- Buxó i Capdevila, R., Plisson, H., Valla, F.R., 1989. Notes préliminaires sur les feuilles en cours sur la terrasse d'Hayonim. *Paléorient* 15 (1), 245–257.
- Caracuta, V., Weiss, E., van den Brink, E.C.M., Liran, R., Vardi, J., Barzilay, O., 2014. From natural environment to human landscape: new archaeobotanical data from the Neolithic site of Nahal Zippori 3, Lower Galilee. *Neo-lithics* 1 (14), 33–41.
- Caracuta, V., Barzilay, O., Khalaily, H., Milevski, I., Paz, Y., Vardi, J., Regev, L., Boaretto, E., 2015. The onset of faba bean farming in the Southern Levant. *Sci. Rep.* 5, 14370.
- Caracuta, V., Weinstein-Evron, M., Kaufmann, D., Yeshurun, R., Silvent, J., Boaretto, E., 2016. 14,000-year-old seeds indicate the Levantine origin of the lost progenitor of faba bean. *Sci. Rep.* 6, 37399.
- Colledge, S.M., 1988. SEM Studies of the cell patterns of the pericarp layers of some wild wheats and ryes. methods and problems. In: Olsen, S.L. (Ed.), *Scanning Electron Microscopy in Archaeology*. British Archaeological Reports International Series 452, Oxford, pp. 225–236.
- Colledge, S., 2001. Plant Exploitation on Epipalaeolithic and Early Neolithic Sites in the Levant. *British Archaeological Reports International Series* 986, Oxford.
- Colledge, S., 2013. Plant remains and archaeobotanical analysis. In: Edwards, P.C., Brill, N.V. (Eds.), *Wadi Hammeh 27, an Early Natufian Settlement at Pella in Jordan*. Brill, Leiden, Netherlands, pp. 353–366.
- Colledge, S., Conolly, J., 2010. Reassessing the evidence for the cultivation of wild crops during the younger Dryas at Tell Abu Hureyra, Syria. *Environ. Archaeol.* 15 (2), 124–138.
- Deckers, K., Riehl, S., Jenkins, E., Rosen, A., Dodonov, A., Simakova, A.N., Conard, N.J., 2009. Vegetation development and human occupation in the Damascus region of southwestern Syria from the Late Pleistocene to Holocene. *Veg. Hist. Archaeobot.* 18, 329–340.
- Dubreuil, L., 2004. Long-term trends in Natufian subsistence: a use-wear analysis of ground-stone tools. *J. Archaeol. Sci.* 31 (11), 1613–1629.
- Dubreuil, L., Grosman, L., 2009. Ochre and hide-working at a Natufian burial place. *Antiquity* 83 (322), 935–954.
- Eitam, D., Kislev, M., Karty, A., Bar-Yosef, O., 2015. Experimental Barley flour production in 12,500-year-old rock-cut Mortars in southwestern Asia. *PLoS One* 10 (7), e0133306. <https://doi.org/10.1371/journal.pone.0133306>.
- Ertug-Yaras, F., 1997. *An Ethnoarchaeological Study of Subsistence and Plant Gathering in Central Anatolia*. PhD thesis. Washington University.
- Fairbairn, A., Asouti, E., Near, J., Martinoli, D., 2002. Macro-botanical evidence for plant use at Neolithic Çatalhöyük south-central Anatolia, Turkey. *Veg. Hist. Archaeobot.* 11 (1–2), 41–54.
- Fairbairn, A., Martinoli, D., Butler, A., Hillman, G., 2007. Wild plant seed storage at Neolithic Çatalhöyük East, Turkey. *Veg. Hist. Archaeobot.* 16, 467–479.
- Feinbrun-Dothan, N., 1978. *Flora Palaestina*, vol. III. Israel Academy of Sciences and Humanities, Jerusalem.
- Feinbrun-Dothan, N., 1986. *Flora Palaestina*, vol. IV. Israel Academy of Sciences and Humanities, Jerusalem.
- Filipovic, D., 2014. Early Farming in Central Anatolia: an archaeobotanical Study of

- Crop Husbandry, Animal Diet and Land Use at Neolithic Çatalhöyük. British Archaeological Reports International Series 2667, Oxford.
- Flannery, K.V., 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko, P.J., Dimbleby, G.W. (Eds.), *The Domestication and Exploitation of Plants and Animals*. Duckworth, London, pp. 73–100.
- Garrard, A.N., 1980. Man-animal-plant Relationships during the Upper Pleistocene and Early Holocene. PhD thesis. University of Cambridge.
- Garrard, A., Yazbeck, C., 2013. The Natufian of Moghr el-Ahwal in the Qadisha Valley, Northern Lebanon. In: Bar-Yosef, O., Valla, F. (Eds.), *Natufian Foragers in the Levant*. Terminal Pleistocene Social Changes in Western Asia. International Monographs in Prehistory, Ann Arbor, Michigan, pp. 17–27.
- Garrod, D.A.E., 1931. Excavations in the caves of the Wady-el-Mughara, 1929–1930. *Bull. Am. Sch. Prehist. Res.* 7, 5–11.
- Garrod, D.A.E., 1932. A new Mesolithic industry: the Natufian of Palestine. *J. R. Anthropol. Inst.* 62, 257–270.
- Garrod, D.A.E., 1957. The Natufian culture: the life and economy of a Mesolithic people in the Near East. *P. Brit. Acad.* 43, 211–227.
- González Carretero, L., Wollstonecroft, M., Fuller, D.Q., 2017. A methodological approach to the study of archaeological cereal meals: a case study at Çatalhöyük East (Turkey). *Veg. Hist. Archaeobot.* 26, 415–432.
- Groman-Yaroslavski, I., Rosenberg, D., Yeshurun, R., Kaufman, D., Weinstein-Evron, M., 2016. The function of early Natufian grooved basalt artefacts from el-Wad Terrace, Mount Carmel, Israel: preliminary results of a use-wear analyses. *J. Lithic Stud.* 3 (3) <https://doi.org/10.2218/jls.v3i1.1508>.
- Grosman, L., 2013. The Natufian chronological scheme - new insights and their implications. In: Bar-Yosef, O., Valla, F.R. (Eds.), *Natufian Foragers in the Levant*. Terminal Pleistocene Social Changes in Western Asia. International Monographs in Prehistory, Ann Arbor, Michigan, pp. 622–637.
- Grossheim, A.D., 1952. *Rastitelnie Bogatsva Kaukasa*. Moskovskoe Obshestvo Ispitatelej Prirodi, Moskva. Moskva.
- Hather, J.G., 1988. The Morphological and Anatomical Interpretation and Identification of Charred Vegetative Parenchymatous Plant Remains. PhD thesis. London University.
- Hather, J.G., 1993. *An Archaeobotanical Guide to Root and Tuber Identification*, vol. 1. Oxbow Monograph 28, Oxford, Europe and South West Asia.
- Hather, J.G., 2000. *Archaeological Parenchyma*. Archetype Publications, London.
- Helbaek, H., 1964. First impressions of the Çatalhöyük plant husbandry. *Anatol. Stud.* 14, 121–123.
- Henry, D.O., 1985. Preagricultural sedentism: the Natufian example. In: Price, T.C., Brown, J.A. (Eds.), *Prehistoric Hunter-Gatherers: the Emergence of Complex Societies*. Academic Press, New York, pp. 365–384.
- Henry, D.O., 1989. From Foraging to Agriculture: the Levant at the End of the Ice Age. University of Pennsylvania Press, Philadelphia.
- Henry, D.O., 1991. Foraging, sedentism, and adaptive vigor in the Natufian: rethinking the linkages. In: Clark, G.A. (Ed.), *Perspectives on the Past Theoretical Biases in Mediterranean Hunter-gatherer Research*. University of Pennsylvania Press, Philadelphia, pp. 353–370.
- Henry, D.O., 2013. The Natufian and the Younger Dryas. In: Bar-Yosef, O., Valla, F.R. (Eds.), *Natufian Foragers in the Levant*. Terminal Pleistocene Social Changes in Western Asia. International Monographs in Prehistory, Ann Arbor, Michigan, pp. 584–610.
- Henry, D.O., Leroi-Gourhan, A., Davis, S., 1981. The excavation of Hayonim Terrace: an examination of terminal Pleistocene climatic and adaptive changes. *J. Archaeol. Sci.* 8, 33–58.
- Hillman, G.C., 1989. Late Palaeolithic plant foods from Wadi Kubbania in Upper Egypt: dietary diversity, infant weaning, and seasonality in a riverine environment. In: Harris, D.R., Hillman, G.C. (Eds.), *Foraging and Farming: the Evolution of Plant Exploitation*. Unwin Hyman, One World Archaeology 13, London, pp. 207–239.
- Hillman, G.C., 1996. Late Pleistocene changes in wild plant-foods available to hunter-gatherers of the northern Fertile Crescent: possible preludes to cereal cultivation. In: Harris, D.R. (Ed.), *The Origins and Spread of Agriculture and Pastoralism in Eurasia*. Smithsonian Institution Press, Washington, DC, pp. 159–203.
- Hillman, G.C., 2000. The economy of the two settlements at Abu Hureyra. In: Moore, A.M.T., Hillman, G.C., Legge, A.J. (Eds.), *Village on the Euphrates: from Foraging to Farming at Abu Hureyra*. Oxford University Press, Oxford, pp. 327–398.
- Hillman, G.C., 2003. Investigating the start of cultivation in western Eurasia: studies of plant remains from Abu Hureyra on the Euphrates. In: Ammerman, A.J., Biagi, P. (Eds.), *The Widening Harvest: the Neolithic Transition in Europe: Looking Back, Looking Forward*. Archaeological Institute of America, Boston, MA, pp. 75–97.
- Hillman, G.C., Colledge, S.M., Harris, D.R., 1989a. Plant-food economy during the Epipalaeolithic period at Tell Abu Hureyra, Syria: dietary diversity, seasonality, and modes of exploitation. In: Harris, D.R., Hillman, G.C. (Eds.), *Foraging and Farming: the Evolution of Plant Exploitation*. Unwin Hyman, One World Archaeology 13, London, pp. 240–268.
- Hillman, G.C., Madeyska, E., Hather, J., 1989b. Wild plant foods and diet at Late Palaeolithic Wadi Kubbania: the evidence from charred remains. In: Wendorf, F., Schild, R., Close, A.E. (Eds.), *The Prehistory of Wadi Kubbania*. Stratigraphy, Paleoecology, and Environment, vol. 2. Southern Methodist University Press, Dallas, TX, pp. 162–242.
- Hillman, G.C., Legge, A.J., Rowley-Conwy, P., 1997. On the charred seeds from Epipalaeolithic Abu Hureyra: food or fuel? *Curr. Anthropol.* 38, 651–655.
- Hillman, G.C., Hedges, R., Moore, A., Colledge, S., Pettitt, P., 2001. New evidence of lateglacial cereal cultivation at Abu Hureyra on the Euphrates. *Holocene* 11, 383–393.
- Hole, F., Flannery, K., Neely, J., 1969. *Prehistory and Human Ecology of the Deh Luran Plain: an Early Village Sequence from Khuzistan*. University of Michigan Museum of Anthropology, Ann Arbor.
- Hopf, M., 1983. Appendix B: Jericho plant remains. In: Kenyon, K.M., Holland, T.A. (Eds.), *Excavations at Jericho, The Pottery Phases of the Tell and Other Finds*, vol. 5. British School of Archaeology in Jerusalem, London, pp. 576–621.
- Hopf, M., Bar-Yosef, O., 1987. Plant remains from Hayonim cave, Western Galilee. *Paléorient* 13, 117–120.
- Ibañez, J.J., Gonzalez-Urquijo, J., Gibaja, J.F., 2014. Discriminating wild vs. domestic cereal harvesting micropolish through laser confocal microscopy. *J. Archaeol. Sci.* 48 (1), 96–103.
- Jensen, H.J., Schild, R., Wendorf, F., Close, A.E., 1991. Understanding the late palaeolithic tools with lustrous edges from the Lower Nile Valley. *Antiquity* 65 (246), 122–128.
- Kasem, W.T., Ghareeb, A., Marwa, E., 2011. Seed morphology and seed coat sculpturing of 32 taxa of family Brassicaceae. *J. Americal Sci.* 7 (2), 166–178.
- Kirk, R.S., Sawyer, R., 1991. *Pearson's Composition and Analysis of Foods*. Longman, Essex.
- Kubiak-Martens, L., 2002. New evidence for the use of root foods in pre-agrarian subsistence recovered from the late Mesolithic site at Halsskov, Denmark. *Veg. Hist. Archaeobot.* 11, 23–31.
- Kubiak-Martens, L., 2006. Roots, tubers and processed plant food in the local diet. In: Louwe Kooijmans, L.P., Jongste, P.F.B. (Eds.), *Schipluiden, a Neolithic Settlement on the Dutch North Sea Coast c. 3500 Cal BC*. *Analecta Praehistorica Leidensia* 37/38. Leiden University, pp. 339–352.
- Kubiak-Martens, L., 2016. Scanning electron microscopy and starchy food in Mesolithic Europe: the importance of roots and tubers in Mesolithic diet. In: Hardy, K., Kubiak-Martens, L. (Eds.), *Wild Harvest, Plants in the Hominin and Pre-agrarian Human Worlds*. Oxbow Books, Oxford, pp. 113–133.
- Kubiak-Martens, L., Verbruggen, F., Kooistra, L.I., 2015. Archaeobotany: landscape reconstruction and plant food subsistence economy on a meso and microscale. In: Moree, J.M., Sier, M.M. (Eds.), *Interdisciplinary Archaeological Research Programme Maasvlakte 2, Rotterdam, Part 1, Twenty Metres Deep! the Mesolithic Period at the Yangtze Harbour Site- Rotterdam Maasvlakte, the Netherlands*. Early Holocene Landscape Development and Habitation. BOOR-rapporten 566, Rotterdam, pp. 223–286.
- Laborde, J.P., Traboulsi, M., 2002. Cartographie automatique des précipitations: application aux précipitations moyennes annuelles du Moyen-Orient. *Publ. de l'Assoc. Inter. de Climatologie* 14, 296–303.
- MacDonald, B., Clark, G.A., Neeley, M., 1988. Southern Ghors and Northeast 'Araba archaeological survey 1985 and 1986, Jordan: a preliminary report. *Bulletin of the American School of Oriental Research* 272, 23–45. <https://doi.org/10.2307/1356784>.
- Maeda, O., Lucas, L., Silva, F., Tanno, K.-I., Fuller, D.Q., 2016. Narrowing the harvest: increasing sickle investment and the rise of domesticated cereal agriculture in the Fertile Crescent. *Quat. Sci. Rev.* 145, 226–237.
- Maher, L., Banning, E.B., Chazan, M., 2011. Oasis or Mirage? assessing the role of abrupt climate change in the prehistory of the Southern Levant. *Camb. Archaeol. J.* 21 (1), 1–29.
- Martinoli, D., Jacomet, S., 2004. Identifying endocarp remains and exploring their use at Epipalaeolithic Öküzini in southwest Anatolia, Turkey. *Veg. Hist. Archaeobot.* 14, 45–54.
- McCorriston, J., Hole, F., 1991. The ecology of seasonal stress and the origins of agriculture in the Near East. *Am. Anthropol.* 93, 46–94.
- Melamed, Y., Plietzmann, U., Kislev, M.E., 2008. *Vicia peregrina*: an edible early Neolithic legume. *Veg. Hist. Archaeobot.* 17 (1), S29–S34.
- Miller, N.F., 1984. The interpretation of some carbonized cereal remains as remnants of dung cake fuel. *Bull. Sumer. Agric.* 1, 45–47.
- Miller, N.F., 1996. Seed eaters of the ancient near east, human or herbivore? *Curr. Anthropol.* 37, 521–528.
- Moore, A.M.T., 1978. *The Neolithic of the Levant*. PhD thesis. University of Oxford.
- Moore, A.M.T., Hillman, G.C., 1992. The pleistocene to Holocene transition and human economy in southwest Asia: the impact of the younger Dryas. *Am. Antiq.* 57 (3), 482–494.
- Noy, T., Legge, A.J., Higgs, E.S., 1973. Recent excavations at Nahal Eron, Israel. *P. Prehist. Soc.* 39, 75–99.
- Olszewski, D.I., 2004. Plant food subsistence issues and scientific inquiry in the early Natufian. In: Delage, C. (Ed.), *The Last Hunter-gatherer Societies in the Near East*. British Archaeological Reports International Series 1320, Oxford, pp. 189–209.
- Olszewski, D.I., 2010. On the margins: early Natufian in the Wadi al-Hasa region, Jordan. *Eurasian Prehist.* 7 (1), 85–97.
- Pedersen, P., Richter, T., Arranz-Otaegui, A., 2016. Preliminary analysis of the ground stone from Shubayqa 1, Jordan. *J. Lithic Stud.* 3 (3). <https://doi.org/10.2218/jls.v3i3.1647>.
- Perry, D., 1999. Vegetative tissues from Mesolithic sites in the northern Netherlands. *Curr. Anthropol.* 40, 231–237.
- Perry, D., 2002. Preliminary results of an archaeobotanical analysis of Mesolithic sites in the Veenkoloniën, Province of Groningen, The Netherlands. In: Mason, S.L., Hather, J.G. (Eds.), *Hunter-gatherer Archaeobotany. Perspectives from the Northern Temperate Zone*. Routledge, London, pp. 108–116.
- Portillo, M., Rosen, A.M., Weinstein-Evron, M., 2010. Natufian plant uses at el-Wad

- terrace (Mount Carmel, Israel): the phytolith evidence. *Eurasian Prehist.* 7 (1), 99–112.
- Power, R.C., Rosen, A., Nadel, D., 2014. The economic and ritual utilization of plants at the Raqefet Cave Natufian site: the evidence from phytoliths. *J. Anthropol. Archaeol.* 33, 49–65.
- Power, R.C., Rosen, A.M., Nadel, D., 2016. Phytolith evidence of the use of plants as food by late Natufians at Raqefet cave. In: Hardy, K., Kubiak-Martens, L. (Eds.), *Wild Harvest: Plants in the Hominin and Pre-agrarian Human Worlds*. Oxbow Books, Oxford, pp. 191–203.
- Richter, T., 2017a. The late epipalaeolithic and early neolithic in the Jordanian Badia: recent fieldwork around the Qa' Shubayqa. *Near E. Archaeol.* 80 (2), 30–37.
- Richter, T., 2017b. Natufian and early Neolithic in the Black Desert. In: Enzel, I.Y., Bar-Yosef, O. (Eds.), *Quaternary Environments, Climate Change and Humans in the Levant*. Cambridge University Press, Cambridge, pp. 715–722.
- Richter, T., Bode, L., House, M., Iversen, R., Arranz-Otaegui, A., Saehle, I., Thaarup, G., Tvede, M.L., Yeomans, L., 2012. Excavations at the late epipalaeolithic site of Shubayqa 1: preliminary report on the first season. *Neo-lithics* 2 (12), 3–14.
- Richter, T., Arranz, A., House, M., Yeomans, L., 2014. The second season of excavations at Shubayqa 1. *Neo-lithics* 1 (14), 10–17.
- Richter, T., Arranz-Otaegui, A., Yeomans, L., Boaretto, E., 2017. High resolution AMS dates from Shubayqa 1, northeast Jordan, reveal complex origins of late epipalaeolithic natufian in the Levant. *Sci. Rep.* 7, 17025.
- Rosen, A.M., 2004. Phytolith evidence for plant use at Mallaha/Eynan. *J. Israel Prehist. Soc.* 34, 189–201.
- Rosen, A.M., 2005. Phytolith indicators of plant and land use at Çatalhöyük. In: Hodder, I. (Ed.), *Inhabiting Çatalhöyük, Reports from the 1995–99 Seasons*. McDonald Institute for Archaeological Research Cambridge and British Institute at Ankara, London, pp. 203–212.
- Rosen, A.M., 2007. Phytolith remains from final natufian contexts at Mallaha/Eynan. *J. Israel Prehist. Soc.* 37, 340–355.
- Rosen, A., 2010. Natufian plant exploitation: managing risk and stability in an environment of change. *Eurasian Prehist.* 7 (1), 113–127.
- Rosen, A., 2011. Change and stability in an uncertain environment: foraging strategies in the Levant from the early natufian through the beginning of the pre-pottery neolithic B. In: Miller, N.F., Moore, K.M., Ryan, K. (Eds.), *Sustainable Lifeways: Cultural Persistence in an Ever-changing Environment*. The University of Pennsylvania Press, Philadelphia, PA, pp. 128–149.
- Rosen, A., 2012. Shifting household economics of plant use from the early to late natufian periods of the southern Levant. In: Parker, B.J., Foster, C. (Eds.), *New Perspectives on Household Archaeology*. Eisenbrauns, pp. 165–182.
- Rosen, A., 2013. Natufian foragers and the 'Monocot Revolution': a phytolith perspective. In: Bar-Yosef, O., Valla, F.R. (Eds.), *The Natufian Culture in the Levant II*. University of Michigan Press, Ann Arbor, Michigan, pp. 638–648.
- Rosenberg, D., 2008. The possible use of acorns in past economies of the southern Levant: a staple food or a negligible food source? *Levant* 40 (2), 167–175.
- Rosenberg, D., Yeshurun, R., Groman-Yaroslavski, I., Winter, H., Zertal, A., Brown-Goodman, R., Nadel, D., 2010. Huzuq Musa – a preliminary report on the test excavation at a final epipalaeolithic/PPNA Site in the Jordan Valley. *Paléorient* 36 (2), 189–204.
- Rössner, C., Deckers, K., Benz, M., Özkaya, V., Riehl, S., 2017. Subsistence strategies and vegetation development at Aceramic Neolithic Körtik Tepe, southeastern Anatolia, Turkey. *Veget. Hist. Archaeobot.* <https://doi.org/10.1007/s00334-017-0641-z>.
- Rivera, D., Matilla, G., Obón, C., Alcaraz, F., 2011. Plants and Humans in the Near East and the Caucasus. *Ancient Traditional Uses of Plants as Food, and Medicine. An Ethnobotanical Diachronic Review*. Servicio de publicaciones Universidad de Murcia, Murcia.
- Ryan, P., 2011. Plants as material culture in the near eastern neolithic: perspectives from the silica skeleton artifactual remains at Çatalhöyük. *J. Anthropol. Archaeol.* 30, 292–305.
- Savard, M., Nesbitt, M., Gale, R., 2003. Archaeobotanical evidence for early Neolithic diet and subsistence at M'lefaat (Iraq). *Paléorient* 29 (1), 93–106.
- Savard, M., Nesbitt, M., Jones, M.K., 2006. The role of wild grasses in subsistence and sedentism: new evidence from the northern Fertile Crescent. *World Archaeol.* 38, 179–196.
- Schick, T., 1988. Nahal hemar cave: cordage, basketry and fabrics. In: Bar-Yosef, O., Alon, D. (Eds.), *Nahal Hemar Cave. Atiqot* 18, Jerusalem, pp. 31–43.
- Schyle, D., 1996. Das frühe Epipaläolithikum der Levante. *Tübinger Atlas des Vorderen Orients (TAVO)* 85. Reichert Verlag, Wiesbaden.
- Shimony, C., Jucha, R., 1988. Nahal hemar cave: the fibres and yarn measurements. In: Bar-Yosef, O., Alon, D. (Eds.), *Nahal Hemar Cave. Atiqot* 18, Jerusalem, p. 44.
- Simpson, D.A., Inglis, C.A., 2001. Cyperaceae of economic, ethnobotanical and horticultural importance: a checklist. *Kew Bull.* 56, 257–360.
- Smith, B.D., 1994. *The Emergence of Agriculture*. W. H. Freeman, New York.
- Snir, A., Nadel, D., Groman-Yaroslavski, I., Melamed, Y., Sternberg, M., Bar-Yosef, O., Weiss, E., 2015a. The origin of cultivation and proto-weeds, long before neolithic farming. *PLoS One* 10 (7), e0131422. <https://doi.org/10.1371/journal.pone.0131422>.
- Snir, A., Nadel, D., Weiss, E., 2015b. Plant-food preparation on two consecutive floors at the Upper Paleolithic Ohalo II. *Israel. J. Archaeol. Sci.* 53, 61–71.
- Swinson, K., 2016. Testing the Expectations of the Broad Spectrum Revolution: a Meta-analysis of Fauna from the PPNA and Natufian of the Southern Levant. Unpublished MSc Dissertation. Institute of Archaeology, University College London.
- Tanaka, J., 1976. Subsistence ecology of central Kalahari San. In: Lee, R.B., DeVore, I. (Eds.), *Kalahari hunter-gatherers. Studies of the Kung San and the neighbors*. Harvard University Press, Mass, Cambridge, pp. 98–119.
- Tanno, K., Willcox, G., 2012. Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Veg. Hist. Archaeobot.* 21, 107–115.
- Tanno, K., Willcox, G., Muhesen, S., Nishiaki, Y., Kanjo, Y., Akazawa, T., 2013. Preliminary results from analyses of charred plant remains from a burnt natufian building at dederiyeh cave in Northwest Syria. In: Bar-Yosef, O., Valla, F.R. (Eds.), *The Natufian Culture of the Levant II. International Monographs in Prehistory, Ann Arbor, Michigan*, pp. 83–87.
- Terradas, X., Ibañez, J.J., Braemer, F., Hardy, K., Iriarte, E., Madella, M., Ortega, D., Radini, A., Teira, L., 2013. Natufian bedrock mortars at Qarassa 3: preliminary results from an interdisciplinary methodology. In: Borrell, F., Ibañez, J.J., Molist, M. (Eds.), *Stone Tools in Transition: from Hunter-gatherers to Farming Societies in the Near East*. 7th Conference on PPN Chipped and Ground Stone Industries of the Fertile Crescent. Servei de Publicacions, Universitat Autònoma de Barcelona, Bellaterra, pp. 449–464.
- Traboulsi, M., 2013. Les précipitations dans les marges arides du Proche-Orient: l'exemple du bassin versant du Yarmouk. *Hannon, revue de géographie libanaise* 26, 7–39.
- Unger-Hamilton, R., 1989. The Epi-Palaeolithic of southern Levant and the origins of cultivation. *Curr. Anthropol.* 31, 88–103.
- Unger-Hamilton, R., 1991. Natufian plant husbandry in the Southern Levant and comparison with that of the Neolithic periods: the lithic perspective. In: Bar-Yosef, O., Valla, F.R. (Eds.), *The Natufian Culture in the Levant. International Monographs in Prehistory, Ann Arbor, Michigan*, pp. 483–520.
- Valamoti, S.M., 2002. Food remains from bronze age archondiko and mesimeriani tomba in northern Greece? *Veg. Hist. Archaeobot.* 11, 17–22.
- Valamoti, S.M., Charles, M., 2005. Distinguishing food from fodder through the study of charred plant remains: an experimental approach to dung-derived chaff. *Veg. Hist. Archaeobot.* 14, 528–533.
- Valamoti, S.M., 2013. Towards a distinction between digested and undigested glume bases in the archaeobotanical record from Neolithic northern Greece: a preliminary experimental investigation. *Environ. Archaeol.* 18 (1), 31–42.
- van Zeist, W., 1970. The oriental institute excavations at Mureybet, Syria: preliminary report on the 1965 campaign Part III: the palaeobotany. *J. Near E. Stud.* 29 (3), 167–176.
- van Zeist, W., Bakker-Heeres, J.H., 1984[1986]. Archaeobotanical studies in the Levant 3. Late-Palaeolithic Mureybet. *Palaeohistoria* 26, 171–199.
- van Zeist, W., Bakker-Heeres, J.H., 1985. Archaeobotanical studies in the Levant 1. Neolithic sites in the Damascus Basin: Aswad, Ghorafe, Ramad. *Palaeohistoria* 24, 165–256.
- Wallace, M., Charles, M., 2013. What goes in does not always come out: the impact of the ruminant digestive system of sheep on plant material, and its importance for the interpretation of dung-derived archaeobotanical assemblages. *Environ. Archaeol.* 18 (1), 18–30.
- Weide, A., Riehl, S., Zeide, M., Conard, N.J., 2017. Reconstructing subsistence practices: taphonomic constraints and the interpretation of wild plant remains aceramic Neolithic Chogha Golan, Iran. *Veg. Hist. Archaeobot.* 1–18. <https://doi.org/10.1007/s00334-017-0607-1>.
- Weinstein-Evron, M., 1998. Early Natufian el-Wad revisited. *ERAUL* 77. University of Liège Press, Liège.
- Weinstein-Evron, M., Ilani, S., 1994. Provenance of ochre in the Natufian layers of el Wad cave, Mt. Carmel, Israel. *J. Archaeol. Sci.* 21, 461–467.
- Weiss, E., Kislev, M.E., Simchoni, O., Nadel, D., 2004. Small-grained wild grasses as staple food at the 23,000 year old site of Ohalo II. *Israel. Econ. Bot.* 58, S125–S134.
- Weiss, E., Zohary, D., 2011. The neolithic southwest Asian founder crops: their biology and archaeobotany. *Curr. Anthropol.* 52 (S4), S237–S254.
- Whitlam, J., Ilkhani, H., Bogaard, A., Charles, M., 2013. The plant macrofossil evidence from Sheikh-e Abad: first impressions. In: Matthews, R., Matthews, W., Mohammadifard, Y. (Eds.), *The Earliest Neolithic of Iran: 2008 Excavations at Sheikh-e Abad and Jani*. Oxbow Books and British Institute for Persian Studies, Oxford, pp. 175–184.
- Whitlam, J., Bogaard, A., Charles, M., 2016. The origins of agriculture in the eastern Fertile Crescent: new archaeobotanical evidence from recently excavated Neolithic sites in Iran and Iraq. In: Paper Presented at the 17th Conference of the International Work Group for Paleoethnobotany, July 4–9. Muséum National d'Histoire Naturelle, Paris.
- White, C.E., Makarewicz, C.A., 2012. Harvesting practices and early Neolithic barley cultivation at el-Hemmeh, Jordan. *Veg. Hist. Archaeobot.* 21, 85–94.
- Winter, H., 1994. Reed harvesting experiment. In: Lechevallier, M., Ronen, A. (Eds.), *Le gisement de Hatoula en Judée occidentale, Israël: Rapport des fouilles, 1980–1988*. Editions Fatou, Quetigny Cedex, France, pp. 271–275.
- Willcox, G., 2002. Charred plant remains from a 10th millennium B.P. kitchen at Jerf el Ahmar (Syria). *Veg. Hist. Archaeobot.* 11, 55–60.
- Willcox, G., 2008. Nouvelles données archéobotaniques de Mureybet et la néolithisation du moyen Euphrate. In: Ibañez, J.J. (Ed.), *Le site néolithique de Tell Mureybet (Syrie du Nord), en hommage à Jacques Cauvin*. British Archaeological Reports International Series 1843(1), Oxford, pp. 103–114.
- Wollstonecroft, M., 2007. Post-harvest Intensification in Late Pleistocene Southwest Asia: Plant Food Processing as a Critical Variable in Epipalaeolithic Subsistence and Subsistence Change. PhD thesis. University College London.
- Wollstonecroft, M., 2009. Harvesting experiments on the clonal macrophyte sea club-rush (*Bolboschoenus maritimus* (L.) Palla): an approach to identifying

- variables that may have influenced hunter-gatherer resource selection in Late Pleistocene Southwest Asia. In: Fairbairn, A.S., Weiss, E. (Eds.), *From Foragers to Farmers: Papers in Honour of Gordon C. Hillman*. Oxbow Monographs, Oxford, pp. 127–139.
- Wollstonecroft, M., Hroudová, Z., Hillman, G.C., Fuller, D.Q., 2011. *Bolboschoenus glaucus* (Lam.) S.G. Smith, a new species in the flora of the ancient Near East. *Veg. Hist. Archaeobot.* 20, 459–470.
- Wright, K., 1991. The Origins and development of ground stone assemblages in late pleistocene Southwest Asia. *Paleorient* 17 (1), 19–45.
- Yeomans, L.M., Richter, T., 2016. Exploitation of a seasonally abundant resource: bird hunting during the late natufian at Shubayqa 1. *Int. J. Osteoarchaeol.* <https://doi.org/10.1002/oa.2533>.
- Yeomans, L., Martin, L., Richter, T., 2017. Environment, seasonality and hunting strategies as influences on Natufian food procurement: the faunal remains from Shubayqa 1. *Levant* 49 (2), 85–104.
- Zohary, M., 1966. *Flora Palaestina*, vol. I. Israel Academy of Sciences and Humanities, Jerusalem.
- Zohary, M., 1972. *Flora Palaestina*, vol. II. Israel Academy of Sciences and Humanities, Jerusalem.