

Use of grass seed resources c.31 ka by modern humans at the Haua Fteah cave, northeast Libya

Huw Barton^a, Giuseppina Mutri^b, Evan Hill^c, Lucy Farr^d, Graeme Barker^d

a. School of Archaeology and Ancient History, University of Leicester, UK

b. DANTE (Diet and Ancient Technology) Laboratory, Università la Sapienza, Rome, Italy

c. School of Geography, Archaeology and Palaeoecology, Queens University Belfast, UK

d. McDonald Institute for Archaeological Research, University of Cambridge, UK

Corresponding author: Dr Huw Barton, School of Archaeology and Ancient History,
University of Leicester, Leicester, LE1 7RH, UK (hjb15@le.ac.uk)

Abstract

The recovery of a seed grinding stone from human occupation layers dating to c.31 ka in the Haua Fteah cave on the coast of the Gebel Akhdar massif in northeast Libya sheds new light on the subsistence practices of modern humans in North Africa. An integrated study of usewear and organic residue analysis confirms the use of the tool for seed grinding. Residue analysis recovered a total of 15 starch granules that could be reliably identified as belonging to wild cereals, ten of which are identified as A-type granules of *Aegilops* sp. (goat grass).

The results of this study show that modern humans had the capacity to identify large-seeded grasses as a potential food source, perhaps targeted during periods of resource stress, and were capable of adapting pounding and grinding technologies to solve the unique problems of seed processing to render an edible food from grasses. These findings further suggest that broad-spectrum diets involving the exploitation of wild cereals was emerging in the Late Stone Age in North Africa.

Introduction

This study reports the findings of a functional analysis of a Pleistocene seed grinder from the Dabban levels of the Haua Fteah cave in Libya, North Africa, and discusses the implications that an identification of seed grinding raises for our understanding of subsistence behaviours during MIS 3 in North Africa and in other regions. The analysis of usewear and starch granules recovered from a single grinding stone that dates to around 31 ka extends our knowledge of late Pleistocene food processing behaviours with the earliest definitive evidence of seed processing in the region. The results of this study join a body of evidence that supports, first, increased dietary breadth amongst modern humans during the Late Pleistocene and second, that a shift towards the use of lower ranked plant foods may have occurred earlier than generally thought (Richards et al. 2001).

The Cyrenaican Prehistory Project

The Haua Fteah is a large limestone cave facing northwards to the sea about a kilometre away, on the northern escarpment of the Gebel Akhdar or Green Mountain massif in northeast Libya, in the region of Cyrenaica (Figure 1). It was excavated in 1951, 1952 and 1955 by Charles McBurney (McBurney, 1967). He excavated a 14-m deep stepped trench that was refilled at the end of the excavation. New excavations in the Haua Fteah were undertaken as part of the Cyrenaican Prehistory Project (CPP) between 2008 and 2015 (Barker et al. 2007, 2008, 2009, 2010, 2012; Farr et al. 2014; Rabett et al. 2013). The backfill in the McBurney trench was removed and a sequence of small (mostly 2 x 1 m) trenches excavated down its southern side (Figure 2). The grinding stone discussed here was

found in Trench M, the CPP trench excavated down the middle section of the McBurney trench (the ‘Middle Trench’ in CPP nomenclature).

<insert Figure 1 about here>

<insert Figure 2 about here>

In his final report on the excavations, McBurney (1967) defined seven cultural phases of occupation based primarily on the typology and technology of the lithic material found, which have since been used as a key reference sequence for North Africa. The earliest phase (A), found in McBurney’s Deep Sounding c. 7.5-14 m below the present ground surface, was an MSA industry based on flakes and blades which he termed the ‘Pre-Aurignacian’ because he thought it resembled Pre-Aurignacian and Amudian assemblages that had been found in Southwest Asia. This was overlain in the lower part of the Middle Trench (Layers XXXV-XXV: Phase B, c. 5.5-7.5 m below the ground surface) by MSA industries that he termed ‘Levalloiso-Mousterian’ because of their affinities with similar industries in the Levant and Europe, industries which in Europe are associated with Neanderthals. There was then a marked change in the lithic assemblages (Phase C, from the upper part of Layer XXV to Layer XVI, at c. 5.5-3.75 m depth) with the appearance of a predominantly blade rather than flake technology comparable to Upper Palaeolithic industries in the Levant and Europe that McBurney termed ‘Dabban’ after the Cyrenaican cave of Hagfet ed-Dabba where he had found similar material (McBurney 1960). The Dabban lithic assemblage is characterized by blades, backed blades and chamfered tools (*Pièces à chanfrein*) formed through the removal of a tranchet flake at one extremity (McBurney 1967) and is recognised as the earliest Late Stone Age sequence in the region (Barton et al. 2007: 178). This was succeeded at 3.75-2 m

depth by a microlithic Late or Final Stone Age industry (Phase D, Layers XV-XI) termed the ‘Eastern Oranian’ or ‘Iberomaurusian’ from its similarities with assemblages in the Maghreb region of northwest Africa. Holocene occupation was found in the Upper Trench at 0-2 m depth.

The Dabban phase and the grinding stone

During the 2012 season of CPP excavations, an oval-shaped limestone grinding stone (HF12 in the CPP small find catalogue) was recovered from within the Dabban cultural sequence exposed in Trench M in context (stratigraphic unit) 11045 (Figure 3). Radiocarbon dates on the shell of the terrestrial snail, *Helix melanostoma*, age-corrected using an offset of 476 ± 48 14Cyr as determined in Hill et al. (2017) place the age of this context between 31- 31.5 ka cal. BP (Table 1) constrained within a sequential series of dates on the surrounding contexts. This falls within the middle of the Dabban sequence, that has been shown by the CPP’s multi-proxy dating programme to span between 43.5-17.1 ka (at a 95.4% confidence interval) or 40-18.1 ka (at a 68.5% confidence interval) (Douka et al. 2014: 58).

<insert Table 1 about here>

<insert Figure 3 about here>

Context 11045 is part of a sedimentary unit defined as Facies 2 by the CPP that consists of a series of thick red clay lenses and alternating gravel and silt layers, many of which appear to have accumulated in a period of increased physical weathering (Douka et al. 2014: 43; Inglis et al. 2017). Oxygen isotope records from the teeth of the main prey animal, Barbary sheep (*Ammotragus levri*), collected in the old and new excavations indicate that the Gebel Akhdar

was more arid during the last glacial than during the early/mid Holocene, with the most arid phase identified dating to c.32 ka (Reade et al. 2016). This correlates with the extended period of aridity identified in ice core data from 32 ka (GS 5.1) to 31 ka (Heinrich Event 3). Mollusc data within this part of the sediment profile indicative of warm/wet conditions may correlate with the very short climatic reversal identified in ice core records c.30.7 ka (Rasmussen et al. 2014: 20). During periods of colder, drier and/or unstable climate the Gebel Akhdar massif may have served as a refugium for humans in eastern North Africa by providing access to permanent water and a richer range of plant and animal species than the surrounding desertic regions (Reade et al. 2016: 158).

<insert Figure 4 about here>

At the time of excavation the grinding stone was identified in the field as of pink granite (Barker et al. 2012: 120) though on later examination proved to be fossiliferous limestone, probably of local origin (Figure 4). It measures 95 x 102 x 47 mm and weighs 582 grams. The artefact has been identified as an upper grinding stone that retains an active surface with evidence of smoothing and grinding with a central zone of pitting and a passive surface that has been roughly shaped by direct percussion. Initial visual observation of the tool surface indicated that the upper ground surface was used for both grinding and pounding. The smoothed surface retained small patches of visible gloss. The central area of pitting appears more likely to have been used for some form of pounding; it is not likely to have been used for bipolar reduction as there is no evidence of this technique elsewhere within the lithic assemblage and the form of the wear itself is inconsistent with that activity (see Results).

Methodology

Specimen treatment and samples preparation

After excavation, the artefact was stored in a plastic bag with its adhering soil. The grinding surface was covered by a thin layer of clay that was gently removed by rinsing the artefact under running purified water for five minutes, and further loosening sediment by hands protected by powder-free latex gloves.

Usewear and residue analysis

The usewear and residue analysis involved a combined stepped approach as recommended by Fullagar (2006: 191-195) to ensure curation of potential organic residues ahead of cleaning required for usewear analysis. Usewear observations were undertaken by GM using a Leica S8APO trinocular stereoscope and a Leica DM 4000 M compound microscope at the University of Cambridge. Initial observations identified areas of potential starch residue preservation including pits, cracks and patches of adhering matter that might contain preserved organic residues (see Barton 2007). Sample removal was carried out by placing a 20-40 microlitre drop of ultra-purified water on identified areas of the tool for one to two minutes. Material was agitated with the pipette tip; sometimes a sterilised, single-use acupuncture needle was used to help facilitate removal of material that would not go into solution, and to release material from pits and cracks on the tool surface. Samples were transferred to a 5 ml snap cap vial for later analyses. A total of 17 samples were removed in this manner and one area of the active upper surface was sonic cleaned for two minutes. The samples removed from the tool were analysed for the presence of starch granules and other organic components at the University of Leicester Residue and Starch Laboratory by HB. Microscopic analysis was conducted with a Zeiss AxioMAT up to X630 magnification. All glassware was cleaned and the working areas cleaned down before analysis to control against

potential airborne contamination (cf. Crowther et al. 2014). A single sample of 20 microlitres was transferred from the snap cap vial and the droplet left to air dry under a cover. Slides were mounted with 50/50 solution of glycerine and water.

After completion of residue sampling the entire tool was cleaned in an ultrasonic bath for 15 minutes to remove all adhering sediment. The sonicated sediment was not analysed. After ultrasonication, the central area of the active surface was further cleaned with a dilute acetic acid solution before high magnification analysis that sought to identify and characterise key usewear features. The overall methodology for the techno-functional analysis followed the principles established by Dubreuil and Savage (2014). Their protocol is designed to focus on the topography of the tool surface, the surface modification of the raw material grains, and the presence/absence of striations, polish, and other reflective surfaces.

Results

Macro-features and microwear

The surface topography of the upper active surface is complex, consisting of traces from more than one phase of tool use. The piece is slightly dished in profile, with an extensive area of pecking across more than two thirds of the upper surface. There is an area of visible smoothing and levelling around the perimeter of the piece across the top and along the left of the long axis of the tool (Figure 4a). The margins of the tool are irregular and the lower surface has been centripetally flaked (Figure 4b). The uneven distribution of smoothing across one end and one edge of the tool is not uncommon in a top stone and reflects the way pressure was applied by the user and the direction of motion relative to the body during use (Adams 2002: 102). Micro striations were associated with areas of polish and were quite

variable in form, from fine and narrow to relatively large and deep with a U-shaped profile. These wear traces were distributed in four main patches within the area of smoothing and levelling on the upper surface. Striations were multidirectional, but there was a general trend overall that was slightly oblique to the long axis of the piece, suggesting a reciprocal stroke with some hand stone rotation (Adams 2002: 102-103).

The dominant form of use polish is a glossy, reticulate form that has a slightly granular appearance (Figure 5a-b). The highest surfaces of the tool microtopography appear more highly polished than lower portions, though polish sometimes fills into the bases of striations. In places small isolated patches of particularly well-developed polish appear as ‘bright spots’ of continuous, reflective polish. In between these, in areas of lower microtopography, use polish was either slight, poorly developed, or absent. This form of polish distribution is typical of contact with hard materials, particularly from stone on stone contact (Adams 2014: 134; Fullagar et al. 2015: 11). The areas of well-developed polish occurring on slightly undulating, rather than flat, microtopography, also indicate that polishes may have formed on contact with more pliable and resilient materials such as wood or hide (Adams 2014: 135) (Figure 7b). However, the overall pattern of polish formation is also consistent with experiments of seed grinding in Australia (Fullagar et al. 2015: Figure 5).

The central and lower zones of the grinding stone are heavily pitted from a combination of percussive wear and loss of mineral inclusions during use. Some of this pitting has impacted on the smoothed surface, indicating that some of this activity occurred at a later time. Pecking grinding surfaces is a method to rejuvenate hand or nether stones, removing smoothed areas and embedded organics that create new micro-cutting projections on the tool surface (Adams

2014: 136). It is also possible that this pecking has resulted from the stone's use as an anvil either during or after its use as a grinding stone.

Flotation of sediments from the upper section of Trench M recovered a range of fruit and nut remains including charred remains of pine nuts, *Pinus* sp., pistachio nuts, *Pistacia* sp., and acorns, *Quercus* sp. (Lucarini et al. 2016: 86; Morales 2010). Direct dating provided a range of dates including 16,630-15,390 cal BP (OxA-18796) on *Pistacia* sp. and 14,840-13,910 cal BP (OxA-18744) on multiple fragments of pine nut cones. Macrobotanical remains recovered from the Grotte des Pigeons, Morocco, also revealed consumption of pine nuts and acorns between 15,000 and 13,700 cal BP (Humphrey et al. 2014) and a high incidence of dental caries showed intensive consumption of starchy foods consistent with intensive exploitation of edible acorns (Humphrey et al. 2014: 957). A fragment of a plant vessel element that is typical of *Pinus* sp. was also recovered from the pitted region of the HF12 grindstone, supporting the use of this tool as a multifunctional implement also used for nut processing.

Starch granule analysis

A reference collection of grasses was prepared specifically for this project with species known to occur within or nearby the study region. These included both wild and domesticated species sourced from collections held at the University of Leicester, University of Cambridge and from North African field collections made by Anita Radini (University of York) (Table 2).

<Table 2 about here>

A total of 44 starch granules were recovered from tool sampling, but only 15 granules could be allocated a potential taxonomic identification. The identified starches were split by size and morphology into two clear groups, denoted Type 1 and Type 2 (Table 3). These granules were in variable states of preservation, with some of the larger granules quite badly preserved, split and cracked, and some with extensive surface pits and holes, clear evidence of enzymatic degradation (e.g. Barton 2007; Barton 2009).

<Table 3 about here>

The Type 1 granules are distinctive large, flat granules ranging in size between 23.1-36 microns in maximum dimensions with a mean size of 28 microns (N=10). Two granules could be rotated, showing that they were thin and lenticular in profile. In cross-polarised light, they were weakly birefringent with a poorly defined centric cross. Where these granules were not too badly degraded, very clear lamellae could be identified (Figure 6a-d). These granules appear typical of A-type granules of several species of cereals including *Aegilops* sp., goat grass, *Hordeum* sp., barley, and *Triticum* sp., wheat (Stoddard 1999). The starch component of these cereals is strongly bimodal, with large, disc-like, A-type granules and smaller more irregularly sized and shaped B-type granules (Stoddard 1999). The biomolecular composition of A-types has been shown to be slightly different from the B-types (Zihua and Jay-lin 2007: 46-55) and to have a different microstructure (Evers 1971). While there is continuity in size between the A-type and B-type granules, Stoddard (1999: 145) recommends that the commonly used size threshold to distinguish between types is 10 microns in diameter. For several varieties of modern wheat, the mean size of the B-types is c.5 microns and A-type mean average is between 12-24 microns (Stoddard 1999: 145).

<insert Figure 6 about here>

Type 2 granules are smaller, with a mean size of 15 microns and a range of 12-19 microns (N=5) (Figure 6e-f). They are ovate in profile and where they can be rotated show that they are ovoid in three dimensions. A clear feature of these granules is a distinct groove or dish-like depression in the central region of the granule. The surface texture of these granules is smooth with a weak, centric cross in polarised light. Their overall morphology does not match any of the species of grasses in the reference collection. It is possible that these granules are actually a form of A-type granule in an earlier stage of development or B-types, which have fewer key diagnostic features. Evers (1971) provides a diagrammatic reconstruction of the growth of A-type granules showing development of an equatorial groove that is more pronounced early in the sequence than in mature A-type granules. Figure 7 shows some examples of these granules within *Aegilops speltoides*. It is also possible that these granules are from another plant entirely and may be better identified with a more comprehensive reference collection. The remaining starches were not readily identifiable and are not further discussed here.

<insert Figure 7 about here>

The size range of the Type 1 granules excludes most of the reference collection and places them at the upper end of the size range of *Aegilops* (goat grass) from the region and beyond wild varieties of wheat, though there is some overlap with outliers (Figure 8). The strongly developed lamellae are also more indicative of the *Aegilops* and *Hordeum* varieties and are

not a feature typical of the *Triticum* samples (cf. Piperno et al. 2004: Fig. A2). The large size of the Type 1 archaeological granules are beyond the maximum limits for published granule sizes of wild *Hordeum*, which is reported between 6-24 microns size with an average granule size of 17-18 microns (Piperno et al. 2004). Some published size ranges for cultivated varieties of *Hordeum vulgare* are up to 30 microns or higher (Mi Young Kang et al. 1985; Hanjun Tang et al. 2002) however it is not clear from the published data if these sizes are rare extreme outliers, as is the case with our sample, or commonly part of the upper size range. On the basis of the size of the archaeological starches and the well-developed lamellae, it is more likely that the archaeological sample lies within the size range of *Aegilops* sp., but *Hordeum* cannot be entirely ruled out as a possible candidate of some of our Type 1 starches.

<insert Figure 8 about here>

The genus *Aegilops* L. and *Hordeum* L. belongs to the tribe Triticeae that includes the major crop genera of *Triticum* (wheat), *Hordeum* (barley), and *Secale* (rye). *Aegilops* and *Hordeum* is widely distributed around the Mediterranean, across western Asia and throughout the Fertile Crescent (von Bothmer et al. 1991; Nevo 2011). *Aegilops* is considered important in wheat domestication and is thought to have contributed genetic material to einkorn (diploid), tetraploid wheats such as emmer, and the hexaploid wheats, spelt and bread wheat (Nevo 2011). The plant prefers poorer soils on rocky substrates as well as disturbed environments and grows intermingled with other grasses and shrubs (Kilian et al. 2011: 6). Spikelets range in size from 2-6 mm (Kilian et al. 2011), comparable in size to wild relatives of *Triticum* (Wilcox 2004). A total of seven species of *Aegilops* occur within the study area, all occurring

on limestone and/or sandstone bedrock, coastal areas including sand dunes, dry wadis and stony soils (Table 4).

<insert Table 4 about here>

Seeds of *Aegilops* have been recovered from charred plant assemblages in Epipalaeolithic and early Neolithic sites in Southwest Asia (Savard et al. 2015). At the site of M'Lefaat in Iraq, the abundance of *Aegilops* grain indicated that it was an important food resource for hunter-gatherers along with other wild grasses from at least the 10th millennium BP (Savard et al. 2003: 102). *Aegilops* spp. is also present in assemblages of PPNA and later sites, though it is often relegated to the status of a 'weed' or interpreted as animal fodder (e.g. Emberling and McDonald 2001; Martinoli and Nesbitt 2003; McCorrison 1992). Its presence in the waterlogged assemblage from Ohallo II, Israel, indicates that wild grasses like *Aegilops* were an important component of variable, broad spectrum diets of mobile and sedentary communities in Southwest Asia already by the Late Pleistocene.

Discussion

The integrated application of usewear and organic residue analysis was crucial in the determination of tool function and provides further evidence that the development of seed grinding by Late Pleistocene hunter-gatherers was widespread geographically (Table 5). In Italy a sandstone grindstone from Bilancino has well-abraded surfaces, asymmetric deep wear and a pestle grinder shows evidence of diffuse and direct thrusting percussion and residue analysis recovered starch granules from possibly Gramineae grass seeds and *Typha* spp., cattail roots (Revedin et al. 2010). The majority of starch granules recovered from the surface

of a pestle-grinder of fine sandstone in the Grotta Paglicci in southern Italy were from Poaceae, including *Avena* spp., wild oat (Lippi et al. 2015: 2079). Usewear on the surface of a groundstone from Hut 1 at Ohallo II, a lower stone slab with a plano-convex cross section, is consistent with the processing of non-greasy vegetables such as cereals (Dubreuil and Nadel 2015) and organic residues recovered from the ground surface included relatively high numbers of Poaceae starch grains including types (particularly A-type granule morphotypes) consistent with *Aegilops* spp., *Hordeum* spp., and *Triticum* spp. (Piperno et al. 2004). The high quantity of preserved cereal remains on the hut floor indicates that the consumption of wild grasses was at times a major part of the diet (Weiss et al. 2008). In eastern Europe, starch granules extracted from residues on grinding stones from Kostienki 16 (Russia) and Pavlov VI (Czech Republic) dating to 28-30 ka include wild bunch grasses, *Brachypodium* (Reverdin et al. 2010). In China, starches on grindstones indicate the processing of the Panicoideae and Pooideae grass families c.23 ka (Li Liu et al. 2011, 2014).

<insert Table 5 about here>

In Australia, several of 25 fragmentary grinding stones including mullers, millstones, and pounders recovered from the open site of Cuddie Springs, New South Wales, dating to around 27 ka, showed morphological characteristics typical of modern seed grinders that were well smoothed, with a thinning depression in the centre and polish consistent with wet milling of seeds (Fullagar and Field 1997: 304-305; Fullagar et al. 2008: 159-172). A similar number of groundstone fragments dating to c. 25-14 ka from Lake Mungo, both upper and lower fragments made from fine-grained well-cemented sandstone, also have morphologies consistent with seed grinding activities; confirmed by usewear analysis (Fullagar et al. 2015:

9-11). Macro plant remains in Australia are rare, but flotation work at Carpenters Gap 1 recovered charred seeds and stems of grasses from deposits dating to c. 40-16 ka, with a concentration of seed remains during the Last Glacial Maximum c. 20-16 ka (McConnell & O'Connor 1997). Identified species included Poaceae grasses (*Panicum* sp., *Plectrachne* sp.), shrubs (Chenopodiaceae) and sedges (Cyperaceae), all known to have been used by recent and present-day Aboriginal groups in desert areas (McConnell & O'Connor 1997).

How were the seeds consumed?

One of the questions that arises from this widespread evidence of 'seed grinding' is what was the final product? How were the seeds consumed? Several studies have suggested that the aim was to produce a dried flour that could be stored and transported, and/or cooked as dough (Biancamaria Aranguren et al. 2007: 853; Revedin et al. 2010: 18819; Lippi et al. 2015: 10279; Piperno et al. 2004: 671). Analysis of the large and small-seeded grasses from Ohallo II shows that people were harvesting ripe cereals and other grasses, dehusking, drying and cracking hulled seeds (Weiss et al. 2004). Recent analysis of the botanical material from Hut 1, Floor III, dating to c.23 ka, suggests that the occupants were possibly even making the equivalent of 'burgul' (Snir et al. 2015: 63). Mariotti Lippi et al. (2015: 12079) have argued that a dried flour would need to be rehydrated and cooked to render the starch component digestible, or that the raw plant food cannot supply sufficient calories (Revedin et al. 2015: 18819). The production of a dried flour, though, is not a necessary outcome of seed processing, nor is it necessary to cook it to render the product digestible. Cooking starchy plant foods, including seeds, does increase the nutritional content by increasing the glycemic index and the quantity of available dietary energy (Piperno et al. 2004: 671), though this does not prevent them from being ingested raw (Table 6) or simply 'parched' by heating (e.g. Fry 1980: 331).

Australian Aborigines of the Western Desert were known to grind fresh seeds into a wet paste that could either be consumed raw in paste form or cooked (sometimes only partially, with a baked exterior and raw interior) (O’Connell et al. 1983: 89-90). Scott Cane (1987: 401) describes a typical process of seed collection and preparation of the final product:

“The collection of grass seed is relatively easy, and it is possible to collect roughly 1 kg of seed in about half an hour. Most grass seeds are stripped straight from the grass in a wooden dish by running/rubbing the heads of seeds through a loosely clenched fist. Some of the grasses (particularly *Fimbristylis oxystachya* and *Panicum australiense*) could also be collected from the ground or from the surface of ants’ nests...Once collected, the outer husks of most seeds have to be removed. This is done by rubbing handfuls of seeds between the heel of one hand and the palm of the other...When the women are ready to start grinding they set the grinding slab into the ground and place a wooden dish under the lip of the slab. A small quantity of seeds is placed on the grinding slab and steady trickle of water is dribbled onto them to facilitate grinding and to help the flow of seeds down the grinding groove and onto the wooden dish. Seed grinding is the most arduous part of the preparation process and takes about 50% of the total time required to make seed cakes...When the seeds are ground, the paste is either eaten raw or several small dampers are baked in a campfire. In the latter case, the raw paste is placed in a shallow depression dug into the hot ashes.”

The ethnographic data from Australia show that it is perfectly feasible to consume freshly ground seed paste without cooking, though cooking does significantly increase the nutritional content (Table 6). If seed cakes were being prepared in this fashion by Late Pleistocene hunter-gatherers, we might expect to find charred remains within hearth deposits, though great care would need to be taken to recover such delicate material.

<insert Table 6 about here>

Studies of the caloric content of grass seeds show that they are nutritious foods and comparable in raw energetic terms with many other plant food sources (Cane 1987), but it is the costs associated with handling and processing to render better access to nutrients - time and energy spent dehusking (removing the glume) and in particular grinding that decrease their overall energetic returns and move these resources to the margins of hunter-gatherer diets. Aboriginal hunter-gatherers in the Western Deserts of Australia spend more than half of the total labour involved in the preparation of edible seed past and/or cooked damper on the task of grinding; labour that is usually measured in hours (Cane 1987; O'Connell et al. 1983: 92). While the particular growth habit of plants will directly influence post-encounter returns, values for ripe tree and grass seeds from Australian desert regions, after hand processing, are estimated to range between 500 and 750 kcal/h (O'Connell et al. 1983: 92), comparable to the 111-680 kcal/h for hand processing seeds reported by Simms (1987: 44) for North American grasses (see also Jones and Madsen 1989). To put that in comparison with some other plant resources recovered from the Haua Fteah such as acorns (*Quercus* sp.), post-encounter return rates for gathering ripe acorns have been calculated at around 1488 kcal/h if picked from trees, and nearly 3000 kcal/h if gathered from the ground (Simms 1987: 126). Other high return plant foods include roots and tubers that typically range from around 1000 to 6000 kcal/h (Denham and Barton 2006: 260; O'Connell et al. 1987: 85; Piperno 2006) and it is no surprise that hunting has always featured so strongly in evolutionary narratives of modern humans in the Pleistocene given the very high calorific returns from medium and large animals (Hawkes & O'Connell 1992). However, MIS 3 was characterised by increasing aridity and periods of rapid climate change on centennial and even decadal scales (Barham and Mitchell 2008: 263) that may have placed additional pressures on animal populations. In drier less productive environments such as those of Cyrenaica, during periods of increasing

unpredictability of key resources such as *Ammotragus* sp., ubiquitous but otherwise low-ranked grass seeds may have helped groups cope in these locations.

Conclusions

The results of this study demonstrate that Late Stone Age hunter-gatherers at the Haua Fteah cave in northeast Libya c. 31 ka were using grinding stone technology to process wild goat grasses, *Aegilops* sp, evidence that a broad-spectrum diet involving wild cereals was emerging in the Late Pleistocene in North Africa. The resulting food product is unknown, but could have included raw seed paste or some form of cooked paste, like a seed cake. While evidence of cooking has not been demonstrated at this site, cooking is shown to significantly increase the caloric yield of ground seeds. Evidence of wild seed use and, in particular, seed grinding is now known from sites in Near East, Europe, China and Australia from at least 32 ka (e.g. Fullagar et al. 2015; Lippi et al. 2015; Liu et al. 2014; Piperno et al. 2004). It appears that the use of grass seeds and seed grinding was widespread amongst modern human groups in the Late Pleistocene and may perhaps be considered as part of the behavioural repertoire of all modern humans deployed with increasing frequency from at least 32 ka, that is, towards the MIS 3/2 boundary. Preserved macroremains of charred roots and tubers from Late Stone Age sites in South Africa indicate that roots and tubers may have been an important source, if not the most important source, of carbohydrates during the Late Pleistocene. However, on the evidence of a growing number of sites, now including the Haua Fteah, grass seeds also appear to have been an increasingly significant portion of the dietary repertoire of foragers in many regions of the world at this time, perhaps primarily as an important fallback food or supplemental source of carbohydrates. For many hunter-gatherer groups faced with the challenges of living in MIS 3 and MIS 2, seed use and seed grinding, despite the significant

labour costs involved in the latter, are likely to have represented an important adaptive subsistence strategy to solve a variety of short-term problems in times of resource stress.

Acknowledgements

GB would like to acknowledge in particular the support of the Libyan Department of Antiquities in the development of the new fieldwork at the Haua Fteah, and the financial support of the European Research Council (Advanced Investigator Grant 230421: TRANS-NAP project: Cultural Transformations and Environmental Transitions in North African Prehistory), the Society for Libyan Studies, the Leakey Foundation, and the Natural Environment Research Council (NERC Radiocarbon Facility). Author roles: H. Barton was responsible for the residue analysis and led the writing of the paper; G. Mutri was responsible for the technological and usewear analysis of the grinding stone; E. Hill was responsible for the shell analysis and shell dating; L. Farr was responsible for the stratigraphic interpretations; and G. Barker was the project director. All authors contributed to the writing of the paper.

References

- Adams, J. 2002. *Ground Stone Analysis: A Technological Approach*. Salt Lake City: The University of Utah Press.
- Adams, J., 2014. Ground stone use-wear analysis: a review of terminology and experimental methods. *Journal of Archaeological Science* 48: 129-138.
- Aranguren B, Becattini R, Mariotti Lippi M, Revedin A. 2007. Grinding flour in Upper Palaeolithic Europe (25000 years BP) *Antiquity* 81:845–855.

- Barker, G., Antoniadou, A., Armitage, S., Brooks, I., Candy, I., Connell, K., Douka, K., Drake, N., Farr, L., Hill, E., Hunt, C., Inglis, R., Jones, S., Lane, C., Lucarini, G., Meneely, J., Morales, J., Mutri, G., Prendergast, A., Rabett, R., Reade, H., Reynolds, T., Russell, N., Simpson, D., Smith, B., Stimpson, C., Twati, M., & White, K., 2010. The Cyrenaican Prehistory Project 2010: the fourth season of investigations of the Haua Fteah cave and its landscape, and further results from the 2007–2000 fieldwork. *Libyan Studies* 41: 63–88.
- Barker, G., Antoniadou, A., Barton, H., Brooks, I., Candy, I., Drake, N., Farr, L., Hunt, C., Ibrahim, A.A., Inglis, R., Jones, S., Morales, J., Morley, I., Mutri, G., Rabett, R., Reynolds, T., Simpson, D., Twati, M., & White, K., 2009. The Cyrenaican Prehistory Project 2009: the third season of investigations of the Haua Fteah cave and its landscape, and further results from the 2007–2008 fieldwork. *Libyan Studies* 40: 1–41.
- Barker, G., Basell, L., Brooks, I., Burn, L., Cartwright, C., Cole, F., Davison, J., Farr, L., Hamilton, R., Hunt, C., Inglis, R., Jacobs, Z., Leitch, V., Morales, J., Morley, I., Morley, M., Pawley, S., Pryor, A., Rabett, R., Reynolds, T., Roberts, R., Simpson, D., Stimpson, C., Touati, M., & der Veen, M., 2008. The Cyrenaican Prehistory Project 2008: the second season of investigations of the Haua Fteah cave and its landscape, and further results from the initial 2007 fieldwork. *Libyan Studies* 39: 175–222.
- Barker, G., Bennett, P., Farr, L., Hill, E., Hunt, C., Lucarini, G., Morales, J., Mutri, G., Prendergast, A., Pryor, A., Rabett, R., Reynolds, T., & Twati, M., 2012. The Cyrenaican Prehistory Project 2012: the fifth season of investigations of the Haua Fteah cave. *Libyan Studies* 43: 115–136.
- Barker, G., Hunt, C., & Reynolds, T., 2007. The Haua Fteah, Cyrenaica (northeast Libya): renewed investigations of the cave and its landscape, 2007. *Libyan Studies* 38: 93–114.

- Barham, L., & Mitchell, P. 2008. *The First Africans: African archaeology from the earliest toolmakers to most recent foragers*. Cambridge: Cambridge University Press.
- Barton H. 2007. Starch residues on museum artefacts: implications for determining tool use. *Journal of Archaeological Science* 34: 1752-1762.
- Barton, H. 2009. Starch granule taphonomy: the results of a two year field experiment.. In M. Haslam, G. Robertson, A. Crowther, L. Kirkwood, & S. Nugent (Eds) *Archaeological Science Under a Microscope: Studies in Residue and Ancient DNA Analysis in Honour of Tom Loy*, pp. 129-140. Brisbane: University of Queensland Press.
- Barton, R.N.E., Bouzouggar, A., Bronk-Ramsey, C., Collcutt, S., Higham, T.F.G., Humphrey, L.T., Parfitt, S.A., Rhodes, E.J., Schwenninger, J.-L., Stringer, C., Turner, E., & Ward, S., 2007. Abrupt climatic change and chronology of the Upper Palaeolithic in northern and eastern Morocco. In: Mellars, P., Boyle, K., Bar-Yosef, O., & Stringer, C. (eds.) *Rethinking the Human Revolution*, pp.177-186. Cambridge: McDonald Institute for Archaeological Research.
- Bronk Ramesy, C. 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51: 337-360.
- Cane, S. 1987. Australian Aboriginal subsistence in the Western Desert. *Human Ecology* 15: 391-434.
- Crowther, A., Haslam, M., Oakden, N., Walde, D., & Mercader, J. 2014. Documenting contamination in ancient starch laboratories. *Journal of Archaeological Science* 49: 90-104.
- Denham, T., & Barton, H. 2006. The emergence of agriculture in New Guinea. In Kennet, D.J., & Winterhalder, B. (eds.) *Behavioural Ecology and the Transition to Agriculture*, pp. 237-264. Berkeley, University of California Press.

- Douka, K., Jacobs, Z., Lane, C., Grun, R., Farr, L., Hunt, C., Inglis, R., Reynolds, T., Albert, P., Aubert, M., Cullen, V., Hill, E., Kinsley, L., Roberts, R.G., Tomlinson, E.L., Wulf, S., Barker, G. 2014. The chronostratigraphy of the Haua Fteah cave (Cyrenaica, northeast Libya). *Journal of Human Evolution* 66: 39-63.
- Dubreuil, L., & Nadel, D. 2015. The development of plant food processing in the Levant: insights from use-wear analysis of Early Epipalaeolithic ground stone tools. *Philosophical Transactions B* 370: 1-11.
- Dubruel, L., & Savage, D. 2014. Ground stones: a synthesis of the use-wear approach. *Journal of Archaeological Science* 48: 139-153.
- Emberling, G., & McDonald, H. 2001. Excavations at Tell Brak 2000: Preliminary Report. *Iraq* 63: 21-54.
- Evers, A.D. 1971. Scanning electron microscopy of wheat starch. *Die Stärke* 23: 157-162.
- Farr, L., & Jones, S., 2014. Spatial and temporal variation in North African and Southwest Asian palaeoenvironmental and archaeological records during Marine Isotope Stage 4. In: Boyle, K., Rabett, R., & Hunt, C.O. (eds.) *Living in the Landscape: Essays in Honour of Graeme Barker*, pp. 59-81. Cambridge: McDonald Institute for Archaeological Research.
- Fry, G.F. 1980. Pleistocene diet and parasites in the desert west of North America. In: Browman, D.L. (ed.) *Early Native Americans: Prehistoric Demography, Economy, and Technology*, pp. 325-340. The Hague: Mouton.
- Fullagar, R., & Field, J. 1997. Pleistocene seed-grinding implements from the Australian arid zone. *Antiquity* 71: 300-307.
- Fullagar, R., Field, J., & Kealhofer, L. 2008. Grinding stones and seeds of change: starch and phytoliths as evidence of plant food processing. In: Rowan, Y.M., & Ebling, J.R. (eds.)

- New Approaches to Old Stones: Recent Studies of Ground Stone Artefacts*, pp. 159-172.
London: Routledge.
- Fullagar, R., Hayes, E., Stephenson, B., Field, J., Matheson, C., Stern, N., & Fitzsimmons, K.
2015. Evidence for Pleistocene seed grinding at Lake Mungo, south-eastern Australia.
Archaeology in Oceania 50: 3-19.
- Hawkes, K., & O'Connell, J.F. 1992. On optimal foraging models and subsistence transitions.
Current Anthropology 33: 63-66.
- Hanjun Tang, Katsumi Watanabe, Toshio Mitsunga. 2002. Structure and functionality of
large, medium and small granule starches in normal and waxy barley endosperms.
Carbohydrate Polymers 49: 217-224.
- Henry, A.G., Brooks, A.S., Piperno, D.R. 2014. Plant foods and the dietary ecology of
Neanderthals and early modern humans. *Journal of Human Evolution* 69: 44-54.
- Hill, E., Reimer, P., Hunt, C., Prendergast, A., & Barker, G. (2017). Radiocarbon Ecology of
the Land Snail *Helix Melanostoma* in Northeastern Libya. *Radiocarbon*, 59(5), 1521-
1542. doi:10.1017/RDC.2017.49
- Humphrey, L., De Groote, I., Morales, J., Barton, N., Collcutt, S., Bronk Ramsey, C., &
Bouzouggar, A. 2014. Earliest evidence for caries and exploitation of starchy plant
foods in Pleistocene hunter-gatherers from Morocco. *Proceedings of the National
Academy of Sciences, USA* 111: 954-959.
- Jones, K., Madsen, D. 1989. Calculating the cost of resource transportation: A Great Basin
example. *Current Anthropology* 30: 529-533.
- Kilian, B., Mamman, K., Millet, E., Sharma, R., Graner, A., Salamini, F., Hammer, K., &
Özkan H. 2011. Aegilops. In: Kole, C. (ed.) *Wild Crop Relatives: Genomics and
Breeding Resources: Cereals*, pp. 1-76. Berlin: Springer-Verlag.

- Li Liu, Wei Ge, Bestel, S., Jones, D., Jinming Shi, Yanhua Song, Xingcan Chen. 2011. Plant exploitation of the last foragers and Shizitan in the Middle Yellow River Valley China: evidence from grinding stones. *Journal of Archaeological Science* 38: 3524-3532.
- Li Liu, Bestel, S., Jinming Shi, Yanhua Song, Xingcan Chen. 2013. Paleolithic human exploitation of plant foods during the last glacial maximum in North China. *Proceedings of the National Academy of Sciences USA* 110:5380–5385.
- Lucarini, G., Radini, A., Barton, H., Barker, G. 2016. The exploitation of wild plants in Neolithic North Africa. Use-wear and residue analysis on non-knapped stone tools from the Haua Fteah cave, Cyrenaica, Libya. *Quaternary International* 410: 77-92.
- Mariotti Lippi, M., Foggi, B., Aranguren, B., Ronchitelli, A., & Revedin, A. 2015. Multistep (Multi-step??) food plant processing at Grotta Paglicci (Southern Italy) around 32,600 cal. B.P. *Proceedings of the National Academy of Sciences USA* 112: 12075-12080.
- Martinolo, D., & Nesbitt, M. 2003. Plant stores at Pottery Neolithic Höyücek, Southwest Turkey. *Anatolian Studies* 53: 17-32.
- McBurney, C.B.M. 1960. *The Stone Age of Northern Africa*. London: Penguin Books.
- McBurney, C.B.M. 1967. *The Haua Fteah in Cyrenaica and the Stone Age of the South-East Mediterranean*. Cambridge: Cambridge University Press.
- McConnell, K., & O'Connor, S. 1997. 40,000 year record of food plants in the Southern Kimberly Ranges, Western Australia. *Australian Archaeology* 45: 20-31.
- McCorriston, J. 1992. Article title. *Journal of Field Archaeology* 19: 315-333.
- Mercader, J. 2009. Mozambican grass seed consumption during the Middle Stone Age. *Science*, 326: 1680–1683.

- Mi Young Kang, Yoshimi Sugimoto, Ichiro Kato, Sadao Sakamoto, Hidetsugu Fuwa. 1985. Some properties of large and small starch granules of Barley (*Hordeum vulgare* L.) endosperm. *Agricultural and Biological Chemistry* 49: 1291-1297.
- Morales, J. 2010. The macrobotanical remains. Pp. 76-78 in: Barker, G. *et al.*, The Cyrenaican Prehistory Project 2010: the fourth season of investigations of the Haua Fteah cave and its landscape, and further results from the 2007–2000 fieldwork. *Libyan Studies* 41: 63–88.
- Nevo, E. 2011. *Triticum*. In: Kole, C. (ed.) *Wild Crop Relatives: Genomics and Breeding Resources: Cereals*, pp. 407-456. Berlin: Springer-Verlag.
- O’Connell, J.F., Latz, P.F., & Barnett, P. 1983. Traditional and modern plant use among the Alyawarra of Central Australia. *Economic Botany* 37: 10-109.
- Piperno, Weiss, E., Holst, I., & Nadel, D. 2004. Processing of wild cereal grains in the Upper Palaeolithic revealed by starch grain analysis. *Nature* 430: 670-673.
- Piperno, D. R. 2006. The origins of plant cultivation and domestication in the Neotropics. In: Kennett, D.J., & Winterhalder, B. (eds.) *Behavioural Ecology and the Transition to Agriculture*, pp. 137-166. Berkeley: University of California Press.
- Rabett, R., Farr, L., Hill, E., Hunt, C., Lane, R., Moseley, H., Stimpson, C., & Barker, G., 2013. The Cyrenaican Prehistory Project 2012: the sixth season of excavations in the Haua Fteah cave. *Libyan Studies* 44: 113–125.
- Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanovic, I., Dalhl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W.Z., Lowe, J., Pedro, J.B., Popp, T., Seierstad, I. K., Steffensen, J.P., Svensson, A.M., Vallelonga, P., Vinther, B.M., Walker, M.J.C., Wheatley, J.J., Winstrup, M. 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial

- period based on three synchronised Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quaternary Science Reviews* 106: 14-28.
- Reade, H., O'Connell, T., Barker, G., & Stevens, R.E. 2016. Pleistocene and Holocene palaeoclimates in the Gebel Akhdar (Libya) estimated using herbivore tooth enamel oxygen isotope compositions. *Quaternary International* 404: 150-162.
- Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Staff, R. A., Turney, C. S. M., & van der Plicht, J. 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0-50,000 Years cal BP. *Radiocarbon*, 55(4).
- Revedin, A., Aranguren, B., Becattini, R., Longo, L., Marconi, E., Mariotti Lippi, M., Skakun, N., Sinitsyn, A., Spiridonova, E., & Svoboda, J. 2010. Thirty thousand-year-old evidence of plant food processing. *Proceedings of the National Academy of Sciences of the United States of America* 107: 18815-18819.
- Richards, M., Pettitt, P., Stiner, M., & Trinkhaus, E. 2001. Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. *Proceedings of the National Academy of Sciences of the United States of America* 98: 6528-6532.
- Savarad, M., Nesbitt, M., & Gale, R. 2003. Archaeobotanical evidence for early Neolithic diet and subsistence at M'lefaat (Iraq). *Paléorient* 29: 93-106.
- Savard, M., Nesbitt, M., & Jones, M. K. 2015. The role of wild grasses in subsistence and sedentism: new evidence from the northern Fertile Crescent. *World Archaeology* 38: 179-196.
- Simms, S.R. 1987. Behavioural ecology and hunter-gatherer foraging: an example from the Great Basin. Oxford: British Archaeological Reports, International Series 381.
- Snir, A., Nadel, D., & Weiss, E. 2015. Plant-food preparation on two consecutive floors at Upper Palaeolithic Ohalo II, Israel. *Journal of Archaeological Science* 53: 61-71.

- Stoddard, F.L. 1999. Survey of starch particle-size distribution in wheat and related species. *Cereal Chemistry* 76: 145-149.
- Van Peer, P., Fullagar, R., Stokes, S., Bailey, R.M., Moeyersons, J., Steenhoudt, F., Geerts, A., Vanderbeken, T., De Dapper, M., Geus, F. 2003. The Early to Middle Stone Age transition and the emergence of modern human behaviour at site 8-B-11, Sai Island, Sudan. *Journal of Human Evolution* 45: 187-193.
- von Bothmer, R., Jacobson, R., Baden, C., Jørgensen, R.B., Linde-Laursen, J. 1991. An ecogeographical study of the genus *Hordeum*. Systematic and Ecogeographic Studies on Crop Genepools 7. International Board for Plant Genetic Resources, Rome.
- Weiss, E., Kislev, M., Simchoni, O., & Nadel, D. 2004. Small-grained wild grasses as staple food at the 23,000-year-old site of Ohalo II, Israel. *Economic Botany* 58: S125-S134.
- Wilcox, G. 2004. Measuring grain size and identifying Near Eastern cereal domestication: evidence from the Euphrates valley. *Journal of Archaeological Science* 31: 145-150.
- Zihua, A., & Jay-lin, J. 2007. Characterisation and modeling of the A- and B- granule starches of wheat, triticale, and barley. *Carbohydrate Polymers* 67: 46-55.

Table Captions

Table 1. Sequence of ^{14}C dates from Trench M Lithofacies where the grinding stone was recovered. The stratigraphic section of the CPP excavation slot, Trench M Grinding Stone HF12 is located mid-way down the section in context 11045. Radiocarbon dates were calibrated and corrected using Oxcal 4.3 (Bronk Ramsey 2009) using the INTCAL13 Calibration curve (Reimer et al. 2013) and the age offset of 476 ± 48 for *H. melanostoma* determined in Hill et al. (2017).

Table 2. Starch grain size of modern reference grasses analysed for this study.

Table 3. Type 1 (A-type) and Type 2 starch granules recovered from residue sampling.

Table 4. Species of *Aegilops* (goat grass) and *Hordeum* (barley) that currently occur in the study region.

Table 5. Grass residues recovered from Neanderthal and AMH dental calculus and groundstone tools.

Table 6. Nutritional analysis of raw seeds and cooked seed cakes, Western Desert, Australia.

Figure Captions

Figure 1: Location map of sites mentioned in the text.

Figure 2: View of the cave and CPP excavation. a) View looking toward Haua Fteah cave entrance. b) Main excavation trench reopened by the CPP. Figure in foreground is standing in front of CPP excavation slot, trench M.

Figure 3: Stratigraphic section of CPP excavation slot, trench M. Grinding stone HF12, is located mid-way down section in context 11045 (Drawing L. Farr).

Figure 4: Grinding stone HF12: a) view of upper surface with area of smoothing – top right of image and areas of rough pecking – centre and bottom left of image. b) view of lower surface with evidence of flaking around the perimeter towards the centre of the piece.

Figure 5: Typical usewear features on the smoothed upper surface of the grinding stone. a) use-polish and striations. b) well-developed, high-gloss ‘bright spot’ that follows surface contours indicating processing of a yielding or soft material. Scale bars are 100 microns.

Figure 6: a-f) Typical type 1 starch granules recovered from HF12. These are all identified as A-type, lenticular starch granules from cereal grasses. Based on their morphometric characteristics these granules best fit with *Aegilops* spp. These A-types have very well defined lamellae (*l*) that is typical of the genus (see Figure 8). The granules are all heavily degraded, most with clear evidence of enzymatic attack in the form of pits (*p*) (visible in a, d and e-f – two views of the same granule), heavy cracking and granule disaggregation. Some granules also appear partially hollowed out. All scale bars 20 microns.

Figure 7: Examples of some of the cereal grass reference material recorded in this study. a) wild einkorn, *Triticum monococcum*. b) Spelt wheat, *Triticum speta*. c) Bread wheat, *Triticum aestivo-compactum*. Arrow indicates B-type smaller granules and larger, lenticular A-type labelled. d) Wild emmer, *Triticum turgidum*. e) Six-rowed barley, *Hordeum vulgare*. f). Oat, *Avena sativa*. Typical compound-type granule of the species: many granules formed within an amyloplast. All scale bars 20 microns.

Figure 8: Examples of some of the *Aegilops* species reference material recorded in this studies. Plates a- c) show species that are known to occur in the study region today. a) *Aegilops bicornis*. b) *Aegilops biuncialis*. c) *Aegilops kotschy*, (f) indicates internal fissures of the granule. d) *Aegilops speltoides*, (ea) shows equatorial groove, typical of lenticular cereal A-types when granule is viewed in side view, rather than top or bottom down as is the

typical orientation of these images. e) *Aegilops tawuschii*. f) *Aegilops geniculata-neglecta*. All scale bars 20 microns.

Figure 9: Box plot of all starches recorded for this study. From left to right: Type 1 and 2 (red) indicate the archaeological categories identified in this study. Type 1 are the category identified as A-types and shown by examples in Figure 8. The outliers in the cereal grasses which includes, *Aegilops*, *Triticum* and *Hordeum*, are all A-type morphotypes. Type 2 include starches not readily identified in this study, but some of which fit morphotypes consistent with B-type cereal starches; *Aegilops* species includes seven samples, the three far left (green) are known to occur in the study region today, the other four samples (buff) occur nearby or outside the study area either in the Near East or Mediterranean region. *Triticum* species (wheats) are shown in two groups, as wild types (buff) or as domesticates (orange). The remaining samples are excluded from consideration in this study due to their morphotypes and overall size. Common names are listed in Table 1.