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► To cite this version:

Clarissa Cagnato, Caroline Hamon, Aurélie Salavert, Elliott Michelle. Developing a Reference Collection for Starch Grain Analysis in Early Neolithic Western Temperate Europe. *Open Archaeology*, 2021, 7, pp.1035-1053. 10.1515/opar-2020-0186 . hal-03359764

HAL Id: hal-03359764

<https://hal.science/hal-03359764>

Submitted on 30 Sep 2021

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Research Article

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Developing a Reference Collection for Starch Grain Analysis in Early Neolithic Western Temperate Europe

<https://doi.org/10.1515/opar-2020-0186>

received October 31, 2020; accepted June 20, 2021

Abstract: While we know that cereals played an important role in the diet of Linearbandkeramik (LBK) and Blicquy/Villeneuve-Saint-Germain (BVSG) populations in the Paris Basin, many questions remain to be answered as to the real contribution of other plants. To assess this topic, the recovery of other lines of data beyond macrobotanicals is crucial: starch grains have the potential to reveal additional information regarding past plant use. However, in Western Europe, in particular, for the Neolithic period, there is a significant lag in the development of the discipline. We, therefore, present how our current reference collection (composed of nearly 100 taxa spread across 35 families) was established, the reasoning behind our plant selections, and where the material comes from. Overall, our work shows that even though not all the selected plant organs produce diagnostic starch grains, it may be possible to broaden the spectrum of plants likely consumed by Early Neolithic (and beyond) populations in the Paris Basin, in particular concerning the use of wild plants and specific plant parts, especially underground storage organs (tubers, rhizomes, roots, bulbs, etc.). We believe our research will help guide future scholars in the creation of their own starch grain reference collection and to carry out such analyses on archaeological material from this region by consulting our image database. We conclude by providing a brief summary of what the starch grain record in the Paris Basin tells us to date on ancient plant use.

Keywords: starch grain analysis, archaeology, archaeobotany, LBK, Paris Basin

1 Introduction

Plant macroremains (those visible to the naked eye) are some of the most direct evidence of the Neolithic diet, especially when they are found charred in a domestic context. Nevertheless, charred plant remains alone permit only a limited knowledge of the diversity of plants and plant parts that were consumed, as fire also damages the most fragile plant parts (Fritz & Nesbitt, 2014). This statement is applicable to the Early

Special Issue: THE EARLY NEOLITHIC OF EUROPE, edited by F. Borrell, I. Clemente, M. Cubas, J. J. Ibáñez, N. Mazzucco, A. Nieto-Espinete, M. Portillo, S. Valenzuela-Lamas, & X. Terradas

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Neolithic period in the Paris Basin where our knowledge of plant use is primarily based on the archaeobotanical record of sites ranging from the Aisne Valley in France to Hesbaye in central Belgium (Figure 1) (Bakels, 1984, 1999, 2009; Berrio, 2011; Dietsch-Sellami, 2004; Hamon, Salavert, Dietsch-Sellami, & Monchablon, 2019; Salavert, 2010, 2011). The Linearbandkeramik (LBK) culture, which originated in central Europe and expanded rapidly westwards reaching the Paris Basin around 5100 BC (Salavert, 2017), was subsequently replaced around 4900 BC by another group known as the Blicquy/Villeneuve-Saint-Germain (BVSG).

While we know that cereals played an important role in the diet of these LBK and BVSG populations (Bakels, 2014; Hamon, 2008; Salavert, 2011), many questions remain to be answered regarding the real contribution of other plants, as no single dataset can provide the entire spectrum of plants used in the past (Colledge & Conolly, 2014). For example, what other plants were processed and consumed in western LBK regions, and more specifically the Paris Basin? Did Neolithic populations consume fewer wild resources than those of the Mesolithic (or none, see Bogucki, 2000, p. 204)? What was the function of different tools such as grinding stones and ceramics? To answer these questions, the recovery of other lines of data is crucial, and this is where starch grains have the potential to reveal additional information regarding past plant use.

To create our reference collection, we began by consulting the existing macrobotanical record of our region, but as mentioned, it is limited by preservation issues. Thus, to amplify our reference collection, we turned to archaeobotanical data from neighboring countries in temperate Western Europe, notably the Netherlands, Switzerland, Germany, Denmark, and Poland for both the preceding period (Mesolithic, c. 8500–3500 BC) but also for slightly later periods, notably the Bronze Age (c. 2200 BC). We also consider ethnobotanical reviews of plants used today across Europe to provide a wider perspective of possible plant use. By doing so, we were able to consider the potential and limits of the methodology: what starch grains can we expect to find and identify in the archaeobotanical record? Which domesticated plants, recovered in

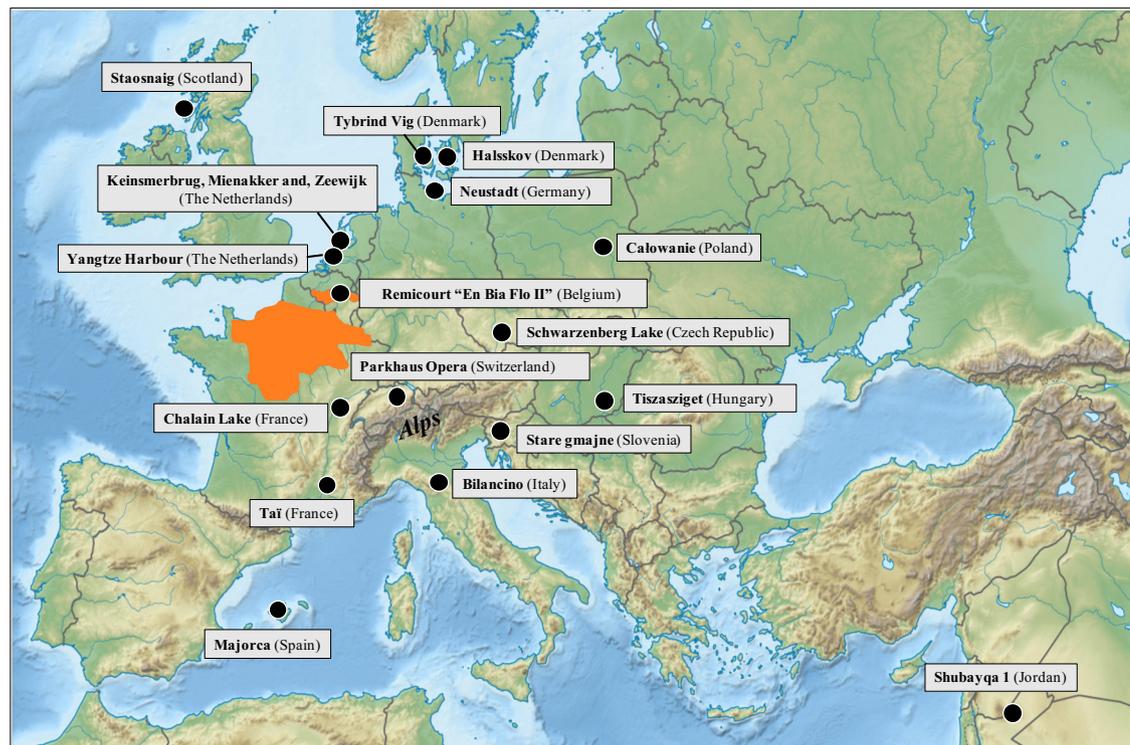


Figure 1: Map showing the geographical extent of the Paris Basin covering northern France and parts of Belgium (in orange), and sites mentioned in the text. Note: sites shown are not necessarily contemporaneous. Map modified from CC-BY-SA-3.0 by Alexrk2.

macrobotanical form, can we identify to species? Which ones are truly diagnostic? Which plants will we be unable to document through this methodology? We thus share our reference collection in the form of an image database¹ in the hope that similar analyses will multiply in the Early Neolithic contexts of temperate Europe, broadening our perception, and understanding of the exploitation of plants for this period and region.

2 Starch Grain Analysis

Starch grains are energy storage units of plants, ranging from 1 to 100 μm (1 μm = 0.001 mm) and composed of two different glucose chains, amylose and amylopectin (for an in-depth review of their complex structure see Buléon, Colonna, Planchot, & Ball, 1998). The grains are synthesized in plastids found in leaves as a result of photosynthesis and then stored in various organs in a plant; however, dense amounts of starch are often concentrated in seeds, tubers, and fruits (Haslam, 2004). Like other macro- and microbotanical remains, starch grains display a range of characteristics, which include size and shape, and are the result of their genetic makeup (Copeland & Hardy, 2018). Although morphological similarities exist between and within species, in some cases, the starch grains can be highly diagnostic to a particular plant taxon. Other important features that often allow them to be identified to taxon include the location of the hilum (the point from which the grain starts to grow), presence of lamellae (the growth rings), fissures, and the extinction cross, also known as the Maltese cross, a feature visible only when viewed under cross-polarized light (Gott, Barton, Samuel, & Torrence, 2006).

While starch grains are susceptible to digestive enzymes (Hardy et al., 2009), they are resistant to many types of processes including grinding and drying (Cortella & Pochettino, 1994), and surprisingly, can survive processes such as cooking and carbonization (Babot, 2003; Chantran & Cagnato, 2021; Crowther, 2009; Pagán Jiménez, Guachamin-Tello, Romero-Bastidas, & Vásquez-Ponce, 2017). While starch is insoluble in cold water, it is permanently affected by extreme changes in temperature and moisture (Haslam, 2004). During cooking, gelatinization occurs, which results in the loss of native structure and morphology (Crowther, 2012). Although the long-term survival² of starch grains in the archaeological record has yet to be fully explained (see Copeland & Hardy, 2018; Mercader et al., 2018a for an excellent review on the topic), the presence of these remains makes it especially useful for understanding plants that are often under-represented in the archaeological record, including roots, tubers, corms, and rhizomes. We will use the widely employed term of underground storage organ (USO) to refer to these organs, which are poorly understood since they do not preserve well in the archaeological record, partially because of their preparation styles (Hather & Hammond, 1994; Pearsall, 2000).

Besides indicating the presence of certain plants in the past, when recovered on artifacts, their presence can indicate the function of these objects, from for example studying the function of grinding stones (Cagnato & Ponce, 2017; Hamon, Cagnato, Barbier-Emery, & Salavert, 2021; Hayes, Cnuts, Lepers, & Rots, 2017; Liu et al., 2010) to what plants were contained in vessels (Duncan, Pearsall, & Benfer, 2009; Wang et al., 2016). Finally, parts of the diet of an individual (human or animal) can be reconstructed through the study of dental calculus (Henry, Brooks, & Piperno, 2011), intestinal remains (Cagnato et al., 2021), and coprolites (Horrocks, Irwin, Jones, & Sutton, 2004). It should be noted, however, that micro-remains recovered in the dental calculus may not always reflect diet but also the ingestion of medicines and/or craft activities (Copeland & Hardy, 2018; Hardy, Buckley, & Copeland, 2018).

On a broad regional scale, notable works making use of starch grain analysis include those for Southwest Asia (Hart, 2014), Eastern North America (Messner, 2011), Central America (Piperno & Holst, 1998), the Canadian Plains (Zarrillo & Kooyman, 2006), Indonesia (Lentfer, 2009), and Sub-Saharan Africa

¹ See supplementary materials at <https://doi.org/10.1515/opar-2020-0186>.

² Some starch grains have been dated to the Middle Stone Age (Mercader, 2009).

(Mercader *et al.*, 2018b). Many studies focusing on the Neolithic, and in turn implying the beginnings of sedentary lifestyles and agriculture, have made use of the potential of starch grains. In particular, they have made it possible to establish the importance of certain resources, such as tubers, on Chinese grindstones and ceramics (Liu, Duncan, Chen, Liu, & Zhao, 2015; Liu, Kealhofer, Chen, & Ji, 2014; Wan *et al.*, 2012; Yang *et al.*, 2013, 2015, Yao *et al.*, 2016). Other work on Neolithic contexts has been carried out in North Africa (Lucarini, Radini, Barton, & Barker, 2016), Israel (Nadel, Piperno, Holst, Snir, & Weiss, 2012), South East Asia (Barker & Richards, 2013, Barker *et al.*, 2007, but on sediments), Oceania (Denham, Haberle, & Lentfer, 2004; Horrocks, Bulmer, & Gardner, 2008), and Japan (Shibutani, 2017), but also on the American continent (Dickau, Ranere, & Cooke, 2007; Inomata *et al.*, 2020; Iriarte *et al.*, 2004; Pearsall, Chandler-Ezell, & Zeidler, 2004; Piperno, Ranere, Holst, & Hansell, 2000). Beyond analyses on grinding stones and ceramics, dental calculus trapping starch grains and other microremains has made it possible to carry out analyses of the Early Neolithic in Sudan (Madella, García-Granero, Out, Ryan, & Usai, 2014; Out *et al.*, 2016) and Iraq (Scott Cummings, Yost, & Sołtysiak, 2018).

Western Europe is therefore a real gap in the development of the discipline, in particular for the Neolithic period. Few works exist in our geographical area, one example is the work by Chevalier and Bosquet (2013, 2017) who studied grinding stones from Remicourt “En Bia Flo II” in Belgium, an LBK site. Beyond our immediate area, starch grain analysis has provided insights on the Neolithic period in other parts of Europe. At Tiszasziget (Hungary), starch grains have been extracted from ceramics dating to the Late Neolithic (5000–4500 BC, Pető, Gyulai, Pópity, & Kenéz, 2013). In Northern Germany at the site of Neustadt, Saul *et al.* (2012) extracted starch grains from charred residues, also collected in ceramic vessels dating between 4600 and 3700 cal BC. The presence of tubers was identified based on the collection of parenchyma fragments from inside ceramics from Late Mesolithic and Early Neolithic sites in the Netherlands³ (Kubiak-Martens, Brinkkemper, & Oudemans, 2015; Raemaekers, Kubiak-Martens, & Oudemans, 2013), but also from Neolithic domestic sites, causewayed enclosures, and megalithic graves in Germany and Denmark (4000–1800 BC) (Klooss, Fischer, Out, & Kirleis, 2016).

We sought to address this gap by beginning a preliminary starch grain study on a range of Early Neolithic tools and ceramics from across the Paris Basin⁴ (Hamon *et al.*, 2021). To carry out a successful study, however, a solid reference collection is necessary. Unlike other parts of the world, where detailed plant lists and in some cases images of starch grains have been produced, this does not exist for Western Europe. In this paper, we present the characteristics of the reference collection we assembled (how and why the plants were included), to facilitate future analyses in this area in other Early Neolithic contexts in Western Temperate Europe.

3 Materials and Methods

3.1 Selecting Species for the Reference Collection

In this section, we consider how our current reference collection was established, the reasoning behind our plant selections, and where the material comes from.

We began by considering the lists of species identified in the macrobotanical record in archaeological assemblages of the Early Neolithic from northwestern Temperate Europe (Bakels, 1984, 1999; Berrio, 2011; Dietsch, 1997; Jadin & Heim, 2003; Salavert, 2011; Saqalli *et al.*, 2014). These data indicate the presence of a range of both domesticated and pulses, as well as wild/weedy plants including Poaceae (*i.e.*, wild cereals). A large majority of these plants were available in the reference collection (“carpothèque”) of the UMR 7209

³ Sites of Keinsmerbrug, Mienakker and Zeewijk.

⁴ A study funded by a DIM MAP 2018 (Ile de France) postdoctoral fellowship and a ANR Homes grant (ANR-18-CE27-0011).

at the Muséum National d'Histoire Naturelle (MNHN) in Paris, France. We thus included hulled wheat (*Triticum monococcum*, *T. turgidum dicoccon*) as these are the most important crops for the LBK. Naked barley (*Hordeum vulgare* subsp. *nudum* L.) and hulled barley (*Hordeum vulgare* subsp. *vulgare* L.), recovered in minor quantities in archaeobotanical assemblages, are also included. Two oat species (*Avena sativa* L., *A. strigosa* Schreb.) were also selected. Domesticated oats are clearly attested in Europe starting in the Bronze Age (Zohary, Hopf, & Weiss, 2012), while wild oat (e.g., *A. strigosa*) is documented in Late Neolithic contexts in France (Marinval, 1988 in Fairweather & Ralston, 1993). Domesticated pulses included peas (*Pisum sativum* L.) and lentils (*Lens culinaris* Medik.), the most frequent species, as well as vetches (*Vicia sativa* L./*V. ervilia* (L.) Willd.), and grass pea (*Lathyrus sativus*/L. *cicera*). Plants used for their oil, fibers, or for their psychoactive properties include flax (*Linum usitatissimum* L.) and opium poppy (*Papaver somniferum* L.).

Fruits are widespread recovered in the archaeobotanical record of the Neolithic period, whether in LBK contexts in the Paris Basin (Berrio, 2011; Salavert, 2011) or at sites in western-Central Europe spanning between 4400 and 2400 cal BC (Colledge & Conolly, 2014). While it is known that ripened fruits in general tend to be relatively poor in starch grains (with for example the exception of tropical fruits such as the banana or avocado), we still tested some fruits (*Crataegus monogyna* Jacq., *Prunus spinosa* L., *Malus sylvestris* (L.) Mill., *Sambucus* sp.). The presence of hazelnuts (*Corylus avellana* L.) and acorns⁵ from deciduous oak (*Quercus* sp.) are reported from LBK sites in our region of interest and were therefore included (Berrio, 2011). We also included the starch-rich fruits of water caltrop (*Trapa natans* L.), which have been reported from Mesolithic sites in the Netherlands and at Schwarzenberg Lake in the Czech Republic (Divišová & Šída, 2015), and from Neolithic sites (3500–3000 cal. BC) in Slovenia (Tolar, Jacomet, Velušček, & Čufar, 2011).

Wild/weedy plants were also considered. For the most part, these were collected at the MNHN and completed with seeds from the collection at the Archaeobotany lab of ArScAn (UMR 7041, Arch. Env) in Nanterre, France. Seeds found commonly in Early Neolithic Paris Basin contexts include goosefoot (*Chenopodium album* L.) various species of a dock (*Rumex* ssp.), nipplewort (*Lapsana communis* L.), cleaver (*Gallium* ssp.), knotgrass (*Polygonum* ssp.), bromes (*Bromus* ssp.), green foxtail millets (*S. viridis* (L.) P. Beauv., *S. verticillata* (L.) P. Beauv.), black bindweed (*Fallopia convolvulus* (L.) Á. Löve), vetches (*Vicia hirsuta* (L.) Gray/*V. tetrasperma* (L.) Schreb.), hemp-nettle (*Galeopsis* sp.), and orache (*Atriplex* ssp.) (Bakels, 1999; Berrio, 2011; Dietsch, 1996; Salavert, 2011). The wild carrot (*Daucus carota* L.), in seed form, has been recovered from the region, albeit in small quantities (Berrio, 2011; Dietsch, 1996). It is unclear which part(s) would have been consumed, but roots (raw) and young stewed leaves are today consumed in some parts of Spain (Tardío, Pardo-de-Santayana, & Morales, 2006). We were able to test both the wild carrot's root and seed. The common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), a completely edible plant – in particular the young stems and rhizomes – was also included in our collection as it has been reported from Neolithic sites in central Europe (Colledge & Conolly, 2014) but also from Mesolithic contexts (Kubiak-Martens, 1999). Also, in the Poaceae family, and found in small quantities in the Paris Basin archaeobotanical record, are cockspur grass (*Echinochloa crus-galli* (L.) Beauv.) and annual meadow grass (*Poa annua* L.), which we included (Bakels, 1999; Berrio, 2011). Hairy crab-grass (*Digitaria sanguinalis* (L.) Scop.) does not seem to be mentioned in the archaeobotanical record of the Paris Basin, yet the seeds can be ground into flour (Simkova & Polesny, 2015), and it was present along the Mediterranean for potential use by the Neolithic populations between the early sixth millennium to the late third millennium BC (Delhon, Binder, Verdin, & Mazuy, 2020).

We have also considered plants that are reported to have only appeared or become important in the region both earlier and later. For example, the earliest gold of pleasure (*Camelina sativa* (L.) Crantz) has been reported in Switzerland around 4000 BC, becoming more common only between 1800 and 1200 BC in south-eastern and central Europe (Zohary et al., 2012, cited by Larsson, 2013). Although there is some limited evidence of *Camelina* in France in the Middle Neolithic, it is argued that cultivation in Western

⁵ The acorns (*Q. ilex*) used in this study are not native to the Paris Basin, but are from the Mediterranean region instead.

France likely began in the Late Bronze Age (Toulemonde, 2010). The same can be said about the sweet chestnut (*Castanea sativa* Mill.), whose introduction to southern France dates to probably the Roman period (Buonincontri, Saracino, & Di Pasquale, 2015).

One of the major problems in trying to establish the actual spectrum of plant use is to a certain extent due to the lack of USOs, recovered in macrobotanical form, in part due to the way they are consumed or prepared (fresh or boiled), making it unlikely that they will end up carbonized (Scheel-Ybert, 2001). While exceptions exist regarding the presence and probable use of USOs for the entire Neolithic period from contexts across Northern, Central, and Western Europe, there is a real gap of information on the presence of USOs at Early Neolithic sites in the Paris Basin. The little data that we have beyond the Paris Basin come in the form of tubers of lesser celandine (*Ficaria verna* Huds.), which have been widely reported from Early Neolithic (4000–3400 BC) contexts in northern Germany and Denmark (Klooss *et al.*, 2016), while wild garlic (*Allium ursinum* L.) is reported as having been consumed by the Neolithic populations living near the Chalain Lake in the Jura, France (Dommelier, Bentrard, Paicheler, Pétrequin, & Bouchet, 1998 citing Pétrequin & Pétrequin, 1988). Turnip⁶ (*Brassica rapa* var. *rapa*) has been reported from waterlogged contexts (4400–2400 cal BC) in Central Europe (Colledge & Conolly, 2014) and in seed form from Stare gmajne (Slovenia) dated between 3500 and 3000 cal BC (Tolar *et al.*, 2011). Other remains include a Liliaceae bulb from Early Neolithic (5240–4990 cal BC) contexts at the site of Taï near the Mediterranean (Bouby, Durand, Rousselet, & Manen, 2019), and tuber oat-grass bulbs (*Arrhenatherum elatius* subsp. *bulbosum*) from Late Neolithic Germany (3500–2800 cal BC) (Kirleis, Kloof, Kroll, & Müller, 2012). In fact, more information concerning the use of USOs comes from European Mesolithic sites in Poland, the Netherlands, and Scotland⁷ (see full references in Kubiak-Martens, 2016), where Scanning Electron Microscope (SEM) techniques have made it possible to identify parenchyma. Archaeological research at these hunter-gatherer sites has yielded a rich collection of starchy foods in the form of knotgrass rhizomes (*Polygonum* sp.), tubers of arrowhead (*Sagittaria* cf. *sagittifolia*), and horsetail (*Equisetum* sp.). Moreover, a potential sedge family (Cyperaceae) corm/stem base along with *Schoenoplectus lacustris* (L.) Palla was also recovered. In Neolithic contexts, a few mentions are made for the recovery of *Scirpus*, *Carex*, *Cyperus*, and *Bolboschoenus* (Kirleis *et al.*, 2012), although not all species will necessarily be related to food consumption (e.g., *Scirpus lacustris*, Dietsch, 1996). *Bolboschoenus maritimus* (syn. *Scirpus bolboschoenus*) charred tubers were recovered from Late Neolithic contexts in the Netherlands (Kubiak-Martens *et al.*, 2015); the stem bases, nutlets (achenes) and tubers can all be consumed (Kubiak-Martens, 1999). It was interpreted that tubers of a related taxon (*Bolboschoenus glaucus*) were used to produce flat bread-like products at Shubayqa 1, a Natufian hunter-gatherer site in northeastern Jordan (Arranz-Otaegui, Carretero, Ramsey, Fuller, & Richter, 2018).

Late Mesolithic datasets (c. fifth mill. BC), reported from Tybrind Vig and Halsskov, both lacustrine areas in Denmark, testify to the presence of sea beet (*Beta vulgaris* ssp. *maritima*), whose roots are rich in starch and sugar, and pignut (*Conopodium majus* (Gouan) Loret.) tubers (Kubiak-Martens, 1999, 2002); we were unfortunately unable to get a hold of these latter two plants. Seeds of waterlilies (*Nuphar* and *Nymphaea*) have been reported from Mesolithic and Neolithic contexts, indicating that they were probably consumed (see Bouby, Dietsch-Sellami, Martin, Marinval, & Wiethold, 2018; Dietsch, 1996; Kirleis *et al.*, 2012;⁸ Kubiak-Martens, 2002, 2016, pp. 128–129; Raemaekers *et al.*, 2013). However, it is known that waterlily rhizomes are also edible, and their consumption is widely attested in the ethnographic record (Kubiak-Martens, 2016). The Mesolithic archaeobotanical record is also a good source of information on other plants besides USOs. For example, a charred caryopsis of floating sweetgrass (*Glyceria fluitans* (L.) R. Br.) was recovered at Tybrind Vig (Kubiak-Martens, 1999). Ethnobotanical studies in the Czech Republic indicate that these seeds can be ground into flour (Simkova & Polesny, 2015). We were unable to get a hold of this species but tested a relative-*G. maxima*-instead. Cattail reeds (*Typha* sp.) have a long history of use, as far back as the Upper Palaeolithic, where hunter-gatherers at the Bilancino site in Italy prepared flour from the

⁶ Unclear if seed or bulb.

⁷ For example, Całowanie (Poland), Yangtze Harbour (The Netherlands), and Staosnaig (Scotland) (see Figure 1).

⁸ Also recovered charred storage tissue of waterlily (p. 235).

starchy rhizomes (Aranguren, Becattini, Lippi, & Revedin, 2007). They are also reported in Mesolithic contexts from northern Netherlands and Poland (Kubiak-Martens, 1999; Perry, 1999). Two species are noted as likely being present at the time, *T. angustifolia* and *T. latifolia*, and we were able to include the latter in our reference collection.

The presence of a rare celery (*Apium graveolens* L.) schizocarp⁹ from Parkhaus Opera, a Neolithic site on the shore of Lake Zurich, Switzerland (3176–3153 BC), indicates that this plant may have been used as a bread condiment (Heiss et al., 2017). We, therefore, included this plant, along with wild celery (*Apium graveolens* var. *graveolens*) in our reference collection. Other members of the Apiaceae family, although not reported in the literature to date, were considered: bulbous chervil (*Chaerophyllum bulbosum* L.) and celeriac (*Apium graveolens* var. *rapaceum*), both of which were purchased from local markets in France.

Raemaekers et al. (2013) cogently noted that species recovered in seed form from Early Neolithic sites in the Netherlands produce edible stems or fleshy shoots. These include glasswort (*Salicornia europaea* L.), sea aster (*Aster tripolium* L.), stinging nettle (*Urtica dioica* L.), greater burdock (*Arctium lappa* L.), and chickweed (*Stellaria media* (L.) Vill.), to mention but a few. Remains of *Arctium minor* and stinging nettle are reported from central European Neolithic sites, dated between 4400 and 2400 cal BC (Colledge & Conolly, 2014), although it is unclear which parts of the plants were recovered. The authors do note that for *Arctium minor*, the entire plant is edible, while the stinging nettle is usually used for its leaves and oil. We were unable to find any archaeobotanical evidence of sea aster or of glasswort. However, the leaves of the former are well known for their edibility, while the young stems of the latter are consumed. Seeds of chickweed are reported from the Paris Basin in small quantities, but not necessarily from the Early Neolithic (see Bakels, 1999).

The recovery of ferns is rare in the archaeobotanical record, yet some examples do exist and document their use as food or medicines (see for example Fiorin et al., 2018 who studied dental calculus from people in Medieval Majorca). In the case of bracken fern (*Pteridium aquilinum* (L.) Kuhn), this plant has been widely used around the world, especially for its rhizomes and young fronds (Divišová & Šída, 2015). Mesolithic period charred parenchyma studied by Kubiak-Martens (2008) was shown to belong to bracken and likely male fern (*Dryopteris filix-mas* (L.) Schott). Bracken fern was also recovered from Late Bronze (905–869 BC) settlements in the French Alps (Bouby & Billaud, 2005).

As there is a lack of data on USOs in the archaeobotanical record, we turned to ethnobotanical reviews that mentioned roots, tubers, and corms as being consumed to expand our reference collection. These studies for example mentioned the use of consuming raw rampion bellflower (*Campanula rapunculus* L.) roots,¹⁰ as well as their shoots and leaves (Mattalia, Quave, & Pieroni, 2013; Simkova & Polesny, 2015). Other USOs consumed include rhizomes of Lords-and-Ladies (*Arum maculatum* L.), used as a flour or boiled, and tubers of bulbous chervil, which are noted as being used in boiled dishes (Simkova & Polesny, 2015). The rhizomes of common comfrey (*Symphytum officinale* L.) are also noted as being eaten. The consumption of the tubers of the tuberous pea (*Lathyrus tuberosus* L.) seems to be common in parts of Italy, France, and the Netherlands, but more rarely in Spain (Mattalia et al., 2013; Tardío et al., 2006). We also included the tubers of great pignut (*Bunium bulbocastanum* L.) as these are reported as being consumed in the Western Italian Alps (Mattalia et al., 2013). The bitter roots of the great yellow gentian (*Gentiana lutea* L.) are used to prepare a digestive liquor (Abbet et al., 2014). Dandelion (*Taraxacum officinale* (L.) Weber ex F.H. Wigg) leaves and flowers are used in multiple ways (Abbet et al., 2014), and so are the roots, which can be consumed either raw or cooked. Horseradish (*Armoracia rusticana* G.Gaertn., B.Mey. & Scherb.) is another plant that could have been gathered for its roots (Saul et al., 2012), even though to date no archaeobotanical remains have been recovered suggesting its use in ancient times. Parsnip (*Pastinaca sativa* L.) is a commonly consumed root but not well-known in the archaeological record: according to Zohary et al. (2012) it has been recovered from Roman sites in Europe.

⁹ A type of dry fruit that when ripe, splits into single-seeded parts known as mericarps.

¹⁰ Also reported in Bronze Age contexts (905–869 BC, see Bouby & Billaud, 2005).

Table 1: Plant taxa included in our reference collection with provenience information and whether starch grains are present

Binomial name	Common name	Family	Source	Plant part tested	Starch present
Cereals					
<i>Avena sativa</i> L.	Oats	Poaceae	MNHN UMR 7209	Seed	Y
<i>Avena strigosa</i> Schreb.	Bristle oats	Poaceae	MNHN UMR 7209	Seed	Y
<i>Hordeum vulgare</i> subsp. nudum L.	Cultivated naked barley	Poaceae	Caroline Hamon	Seed	Y
<i>Hordeum vulgare</i> subsp. vulgare L.	Cultivated hulled barley	Poaceae	MNHN UMR 7209	Seed	Y
<i>Triticum aestivum</i> L.	Bread wheat	Poaceae	MNHN UMR 7209	Seed	Y
<i>Triticum durum</i> Desf.	Macaroni wheat	Poaceae	MNHN UMR 7209	Seed	Y
<i>Triticum turgidum</i> Desf.	Durum wheat	Poaceae	MNHN UMR 7209	Seed	Y
<i>Triticum monococcum</i> L.	Einkorn	Poaceae	MNHN UMR 7209	Seed	Y
<i>Triticum</i> cf. <i>timopheevi</i>	New glume wheat	Poaceae	MSH Mondes	Seed	Y
<i>Triticum dicoccon</i> Schrank.	Cultivated emmer	Poaceae	MNHN UMR 7209	Seed	Y
Pulses					
<i>Lathyrus sativus</i> L.	Grass pea	Fabaceae	MNHN UMR 7209	Seed	Y
<i>Lens culinaris</i> Medik.	Lentil	Fabaceae	MNHN UMR 7209	Seed	Y
<i>Pisum sativum</i> L.	Pea	Fabaceae	MNHN UMR 7209	Seed	Y
<i>Vicia ervilia</i> (L.) Willd.	Bitter vetch	Fabaceae	MNHN UMR 7209	Seed	Y
<i>Vicia sativa</i> L.	Common vetch	Fabaceae	MSH Mondes	Seed	Y
Oily/Fiber Plants					
<i>Linum usitatissimum</i> L.	Flax	Linaceae	MNHN UMR 7209	Seed	Y
<i>Papaver somniferum</i> L.	Opium poppy	Papaveraceae	MNHN UMR 7209	Seed	N
<i>Pinus</i> sp.	Pine kernel/nut	Pinaceae	Market	Seed	Y
Wild Plants					
<i>Aesculus hippocastanum</i> L.	Horse chestnut	Sapindaceae	Laura Longo	Fruit	Y
<i>Aethusa cynapium</i> subsp. <i>cynapium</i>	Fool's parsley	Apiaceae	MSH Mondes	Seed	N
<i>Allium ursinum</i> L.	Wild garlic	Amaryllidaceae	Charlène Bouchaud	USO	N
<i>Armoracia rusticana</i>	Horseradish	Brassicaceae	Nursery	USO	Y
<i>Aster tripolium</i> (Jacq.) Dobrocz	Sea aster	Asteraceae	MNHN UMR 7209	Seed	N
<i>Apium graveolens</i> L.	Celery	Apiaceae	Market	Stem	N
<i>Apium graveolens</i> var. <i>graveolens</i>	Wild celery	Apiaceae	MSH Mondes	Seed	N
<i>Apium graveolens</i> var. <i>rapaceum</i>	Celeriac	Apiaceae	Market	USO	N
<i>Atriplex hortensis</i> L.	Garden orache	Amaranthaceae	MSH Mondes	Seed	N
<i>Beta vulgaris</i> ssp. <i>maritima</i>	Sea beet	Amaranthaceae	MSH Mondes	Seed	Y
<i>Bolboschoenus maritimus</i> (L.) Palla	Sea club-rush	Cyperaceae	MSH Mondes	Seed	Y
<i>Brassica rapa</i> var. <i>rapa</i>	Turnip	Brassicaceae	Market	Seed	Y
<i>Bromus secalinus</i> L.	Rye brome	Poaceae	MSH Mondes	Seed	Y
<i>Bromus sterilis</i> L.	Barren brome	Poaceae	MSH Mondes	Seed	Y
<i>Bromus tectorum</i> L.	Drooping brome	Poaceae	MSH Mondes	Seed	Y
<i>Bunium bulbocastanum</i> L.	Great pignut	Apiaceae	Nursery	USO	Y
<i>Camelina sativa</i> (L.) Crantz	Gold of pleasure	Brassicaceae	Francoise Toulemonde	Seed	N
<i>Campanula rapunculus</i> L.	Rampion bellflower	Campanulaceae	Nursery	USO	N
<i>Capparis spinosa</i> subsp. <i>rupestris</i>		Capparaceae	MSH Mondes	Seed	N
<i>Carex hirta</i> L.	Sedge	Cyperaceae	MSH Mondes	Seed	Y
<i>Castanea sativa</i> Mill.	Chestnut	Fagaceae	Market	Fruit	Y
<i>Chaerophyllum bulbosum</i> L.	Bulbous chervil	Apiaceae	Market	USO	Y
<i>Chenopodium album</i> L.	Goosefoot	Amaranthaceae	MSH Mondes	Seed	Y
<i>Corylus avellana</i> L.	Hazelnut	Betulaceae	Market	Fruit	N

(Continued)

Table 1: Continued

Binomial name	Common name	Family	Source	Plant part tested	Starch present
<i>Crataegus monogyna</i> Jacq.	Common hawthorn	Rosaceae	MNHN UMR 7209	Fruit	N
<i>Cyclamen</i> sp.	Cyclamen	Primulaceae	Laura Longo	USO	Y
<i>Cyperus esculentus</i> L.	Yellow nutsedge	Cyperaceae	MSH Mondes	USO	Y
<i>Cyperus rotundus</i> L.	Purple nutsedge	Cyperaceae	Laura Longo	USO	Y
<i>Daucus carota</i> L.	Wild carrot	Apiaceae	Aurélie Salavert	USO	N
<i>Daucus carota</i> L.	Wild carrot	Apiaceae	Aurélie Salavert	Seed	N
<i>Digitaria sanguinalis</i> (L.) Scop.	Hairy crab-grass	Poaceae	MSH Mondes	Seed	Y
<i>Echinochloa crus-galli</i> (L.) Beauv.	Cockspur grass	Poaceae	MNHN UMR 7209	Seed	Y
<i>Elymus caninus</i> L.	Bearded wheatgrass	Poaceae	MSH Mondes	Seed	Y
<i>Equisetum</i> spp.	Horsetail	Equisetaceae	Nursery	Stem	Y
<i>Erythronium dens-canis</i> L.	Dogs' tooth-violet	Liliaceae	Nursery	USO	Y
<i>Fagus sylvatica</i> L.	Common beech	Fagaceae	MSH Mondes	Seed	Y
<i>Fallopia convolvulus</i> (L.) Á.Löve	Black-bindweed	Polygonaceae	MSH Mondes	Seed	Y
<i>Festuca arundinacea</i> Schreb.	Tall fescue	Poaceae	MSH Mondes	Seed	Y
<i>Ficaria verna</i> Huds.	Lesser celandine	Ranunculaceae	Nursery	USO	Y
<i>Galeopsis segetum</i> Neck.	Hemp-nettle	Lamiaceae	MSH Mondes	Seed	N
<i>Galium aparine</i> L.	Cleaver	Rubiaceae	MSH Mondes	Seed	N
<i>Gentiana lutea</i> L.	Great yellow gentian	Gentianaceae	Nursery	USO	Y
<i>Glyceria maxima</i> (Hartm.) Holmb.	Greater sweetgrass	Poaceae	MSH Mondes	Seed	N
<i>Iris sibirica</i> L.	Siberian iris	Iridaceae	Laura Longo	USO	Y
<i>Lapsana communis</i> Juss.	Nipplewort	Asteraceae	MSH Mondes	Seed	N
<i>Lotus corniculatus</i> L.	Common bird's-foot trefoil	Fabaceae	MSH Mondes	Seed	N
<i>Lupinus albus</i> L.	White lupin	Fabaceae	MSH Mondes	Seed	N
<i>Malus sylvestris</i> (L.) Mill.	Crabapple	Rosaceae	Market	Fruit	N
<i>Medicago lupulina</i> L.	Black medick	Fabaceae	MSH Mondes	Seed	N
<i>Pastinaca sativa</i> L.	Parsnip	Apiaceae	Market	USO	Y
<i>Phleum pratense</i> L.	Timothy-grass	Poaceae	MNHN UMR 7209	Seed	Y
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	Reed	Poaceae	Nursery	USO	Y
<i>Plantago major</i> L.	Broadleaf plantain	Plantaginaceae	MSH Mondes	Seed	Y
<i>Poa annua</i> L.	Annual meadow grass	Poaceae	MSH Mondes	Seed	Y
<i>Polygonum lapathifolium</i> L.	Pale persicaria	Polygonaceae	MSH Mondes	Seed	Y
<i>Polygonum bistorta</i> Delarbr.	Common bistort	Polygonaceae	MSH Mondes	Seed	Y
<i>Polygonum persicaria</i> Gray	Lady's thumb	Polygonaceae	MSH Mondes	Seed	Y
<i>Prunus spinosa</i> L.	Blackthorn	Rosaceae	Wild	Fruit	N
<i>Quercus ilex</i> L.	Acorn (immature)	Fagaceae	Laura Longo	Fruit	Y
<i>Quercus ilex</i> L.	Acorn (ripe)	Fagaceae	Laura Longo	Fruit	Y
<i>Rumex acetosa</i> L.	Common sorrel	Polygonaceae	MSH Mondes	Seed	Y
<i>Rumex acetosa</i> L.	Common sorrel	Polygonaceae	Nursery	USO	Y
<i>Rumex crispus</i> L.	Curly dock	Polygonaceae	MNHN UMR 7209	Seed	Y
<i>Rumex obtusifolius</i> L.	Bitter dock	Polygonaceae	MSH Mondes	Seed	Y
<i>Sagittaria sagittifolia</i> L.	Arrowhead	Alismataceae	Nursery	USO	Y
<i>Sambucus nigra</i> L.	Black elder	Adoxaceae	MSH Mondes	Fruit	N
<i>Schoenoplectus lacustris</i> (L.) Palla	Common club-rush	Cyperaceae	Nursery	USO	Y
<i>Schoenoplectus lacustris</i> (L.) Palla	Common club-rush	Cyperaceae	MSH Mondes	Seed	Y
<i>Setaria verticillata</i> (L.) P. Beauv.	Bristly foxtail	Poaceae	MSH Mondes	Seed	Y

(Continued)

Table 1: Continued

Binomial name	Common name	Family	Source	Plant part tested	Starch present
<i>Setaria viridis</i> (L.) P. Beauv.	Green foxtail millet	Poaceae	MNHN UMR 7209	Seed	Y
<i>Sinapsis arvensis</i> L.	Wild mustard	Brassicaceae	MNHN UMR 7209	Seed	N
<i>Solanum nigrum</i> L.	Black nightshade	Solanaceae	MNHN UMR 7209	Seed	N
<i>Stellaria media</i> (L.) Vill.	Chickweed	Caryophyllaceae	MSH Mondes	Seed	Y
<i>Stipa capillata</i> L.	Very slender feather grass	Poaceae	MSH Mondes	Seed	Y
<i>Symphytum officinale</i> L.	Common comfrey	Boraginaceae	Nursery	USO	Y
<i>Taraxacum</i> sp.	Dandelion	Asteraceae	Market	USO	N
<i>Tetragonolobus purpureus</i> Moench	Winged pea	Fabaceae	MSH Mondes	Seed	N
<i>Trapa natans</i> L.	Water caltrop	Lythraceae	Laura Longo	Fruit	Y
<i>Trifolium dubium</i> Sibth.	Field clover	Fabaceae	MSH Mondes	Seed	N
<i>Typha domingensis</i> Pers.	Cattail reed	Typhaceae	MNHN UMR 7209	Seed	N
<i>Typha latifolia</i> L.	Broadleaf cattail	Typhaceae	Nursery	USO	Y
<i>Urtica dioica</i> L.	Stinging nettle	Urticaceae	MNHN UMR 7209	Seed	N
<i>Vicia hirsuta</i> (L.) Gray	Hairy vetch	Fabaceae	MSH Mondes	Seed	Y
<i>Vicia tetrasperma</i> agg.	Four-seeded vetch	Fabaceae	MSH Mondes	Seed	Y
<i>Veronica hederifolia</i> agg.	Ivy-leaved speedwell	Plantaginaceae	MSH Mondes	Seed	N

To date, we have collected and tested 99 species that cover 35 families (Table 1). Out of those, we tested fruits ($n = 11$), seeds ($n = 69$), underground storage organs ($n = 22$), and stems ($n = 2$). For three taxa (*Daucus carota*, *Rumex acetosa*, and *Schoenoplectus lacustris*), we tested both the seeds and the USOs, while we also tested acorns at different stages of maturity. Thus, we have a total of 103 samples. Besides those obtained from the herbaria, most of the plants were either purchased from local markets (turnip, chestnut, bulbous chervil) or nurseries (e.g., lesser celandine, common comfrey). A small percentage of the taxa were directly gathered from the wild (e.g., dandelion, wild carrot, wild garlic).

3.2 Processing the Modern Plant Samples and Recording the Starch Grains

Fresh plant material was first cleaned and peeled (when dealing with tubers, roots, and fruits). Otherwise, material from herbaria or already dried was directly processed. The sample (seed, fruit, USO) was then gently crushed using a mortar and pestle. To avoid damaging the starch grains in an extremely hard seed (e.g., cereals) they were placed for 1–2 h in distilled water, before cutting off a small piece with a clean scalpel and then gently rubbing it against a clean microscope slide (using a clean toothpick when necessary). A drop of 1:1 glycerine:water solution was added before covering with a coverslip. The glycerine solution allows for the starch grains to be more easily rotated and viewed in both cross-polarized and transmitted light. Although the sample will eventually dry, it can be re-hydrated before observation using this afore-mentioned solution. The reference slides were then examined at 600× magnification using a Nikon E600 POL microscope and starch grains were measured using NIS Elements software, which provided statistical data including the mean, standard deviation, and range of sizes. The number of grains counted by different specialists when establishing their reference collection varies greatly, from at least 50 grains (Hart, 2014; Li, Pagán-Jiménez, Tsoraki, Yao, & Van Gijn, 2020; Musaubach, Plos, & Babot, 2013; Piperno, Weiss, Holst, & Nadel, 2004), to at least 300 (Mercader *et al.*, 2018b). We measured 50 simple starch grains whenever possible, and these were randomly chosen on the slide. Photographs were taken under transmitted and cross-polarized light, and attributes such as the shape of the grain, the type and

position of the hilum as well as the presence or absence of facets and fissures, were described (see Supplementary materials for photos and descriptions). Whenever possible, we kept materials (stored separately) in case new slides need to be prepared. Some species in our reference collection (e.g., *Trapa natans*, *Iris sibirica*) were obtained from Dr Laura Longo (Università Ca' Foscari), who prepared ultrapure starch pellets extracted using a sequential water/ethanol protocol.¹¹ In this case, a small amount of the resulting powder was placed on slides, where a drop of 1:1 glycerine:water solution was then added, before adding a coverslip.

4 Results and Discussion

We tested 103 different plant parts, but since we tested immature and mature acorns, our calculations are based on a total of 102 different taxa. Out of these, we found that 69 produced starch grains (68%), with a large majority of USOs producing starch grains (77%), followed by seeds (68%). There is a 50/50 chance of recovering starch from fruits or stems, but this probability may well vary if we tested a wider number of stems. It is immediately clear that compared to Hart (2014), who found that only 10 out of 64 species present across Southwest Asia produced starch grains, we found a much greater number of species that do produce these microbotanical remains. This is of course a positive outcome, but we must also keep in mind that even when starch is produced, not all starch grains are diagnostic to genus and even less to species. Moreover, some species will produce exceedingly small grains that will be hard to effectively see using a stereomicroscope. When the grains produced are below 5 µm, these are difficult to characterize with a light microscope, even at 600×. This is the case for species included in our collection such as sea beet, goosefoot, chickweed, as well as some taxa in the grass family (*Festuca*, *Poa*). In this case, additional higher resolution microscopy such as that obtained by SEM may help to further identify these starch grains (Jane, Kasemsuwan, Leas, Zobel, & Robyt, 1994).

The fruits we investigated for most part did not contain starch, except for acorns, water caltrop, chestnut, and horse chestnut. It has been reported that unripe fruits will contain more starch than ripe fruits, as these will convert the starch to sugar as the fruit ripens (Gott et al., 2006). We tested both green and mature acorns, and while our results do not suggest that there is a significant difference, more tests involving other taxa are necessary.

We also found that the presence of starch in seeds is variable. Cereals, notably those in the Triticeae tribe (e.g., wheat and barley), have a bimodal distribution (grains come in two sizes), and produce abundant quantities of starch grains, with the larger ones being lenticular in shape. The morphology of some wild grasses has also been explored in depth (Hart, 2014; Piperno et al., 2004; see Yang & Perry, 2013 for a specific focus on species found in China). We found starch grains in all the grass seeds we collected, except for greater sweetgrass. The smallest grains were produced by cocksbur, stipa, timothy-grass, and *Poa*, followed by *Digitaria* and *Setaria*; with barren brome seeds producing the largest starch grains among the wild grasses sampled.

The Fabaceae family produces very recognizable starch grains with a distinct longitudinal cleft. We extracted starch from all the domesticated taxa tested (peas, lentils, beans grass pea, and bitter vetch), and from both wild *Vicia* species. We discovered that not all members of this family produce starch grains, this was the case for species of *Lotus*, *Medicago*, and *Lupinus*.

As expected, seeds with high oil/fat content, and used for extracting oil such as opium poppy and hazelnuts, did not contain starch grains. As noted by Gott et al. (2006), in these plants, the main storage is lipid, and therefore, little to no starch will be produced or stored. We did, however, find starch grains in the seeds of flax, but only in the ultrapure pellets prepared by Laura Longo and Elena Badetti. Even then, these starch grains remained very tightly packed within the rest of the seed matrix. For this reason, it may be harder to detect them in the archaeological record if they are simply gently pounded or ground.

¹¹ Carried out at DAIS, Ca' Foscari University, Venice, Italy, with Dr Elena Badetti.

For this initial reference collection, we focused on seeds and USOs, and set aside the study of the leaves. In the latter, starch grains, known as transient or transitory starch, have been determined to be small (less than 7 μm ; Gott *et al.*, 2006; Haslam, 2004), and therefore probably not diagnostic. However, leaves will have to be included in the future as, more recently, the presence of larger (non-transient) starch grains in the leaves and stems of domesticated and wild plants have been noted (Liu, Wang, & Levin, 2017; Yang *et al.*, 2014). Neolithic populations likely had access to a large range of plants they could have used for their greens (leaves, stems): for example, stinging nettle, wild carrot, dandelion, and dock/sorrel (Mattalia *et al.*, 2013; Simkova & Polesny, 2015). It will be of interest to test these in the future to determine whether the leaves of such species produce diagnostic starch grains. After testing an important number of seeds from wild plants, we found that starch grains were present in a majority of these. However, based on their tendency to be on the smaller side (between 2 and 11 μm), the probability of correctly identifying the ones we recover in the archaeobotanical record is rather slim, unless an SEM is used.

One issue that is clearly at the forefront of starch grain analysis is its utility in identifying underground storage organs in the archaeobotanical record. However, knowing which taxa to include in a reference collection has been problematic when we rely on solely macrobotanical remains. For the Neolithic, few taxa have been reported (but see Klooss *et al.*, 2016; Kubiak-Martens, 2016), yet it is evident that multiple plants could have been gathered by these populations. Hart (2014) already made a similar observation for studies of USOs in Southwest Asia. We believe that our biggest contribution here is to provide a list of putative plants, besides those already found at other sites in the Neolithic, whose USOs may have been consumed by LBK/BVSG populations in Paris Basin. It should be noted that not all USOs contain starch grains, in fact, other reserve carbohydrates can be present (either in place of or in addition). Both monocotyledons and dicotyledons have fructan-containing species, and their families include Poaceae, Campanulaceae, Amariyllidaceae, Iridaceae, Asteraceae, and Liliaceae (Ranwala & Miller, 2008). In our case, we were unable to find starch in the roots of wild garlic (Amariyllidaceae) or dandelion (Asteraceae); however, the Siberian iris (Iridaceae), dogs' tooth-violet (Liliaceae), and the common reed (Poaceae) were all rich in starch. We, therefore, believe that it is important to also test species in these families. Overall, we found that a vast majority of the USOs we collected contained starch grains, for the most part, the grains are typical of USOs: elongated with eccentric hila, but other forms of starch grains exist. Taxa that did not produce starch grains in their USOs include members of the Apiaceae family (wild carrot, wild celery, celeriac), but this is not a fast rule as other members in the same family (bulbous chervil and parsnip) have starch grains (although neither produces particularly diagnostic grains).

Our current work makes it clear that not all taxa will produce diagnostic starch grains and in turn be useful for archaeobotanical studies. If we disregard those that are too small to be clearly visible with a microscope at 600 \times (species which have already been discussed earlier in the text), we can propose the following observations regarding those taxa that are more likely to be diagnostic or identifiable. Cereals such as wheat and barley are easily categorized due to the presence of lenticular starch grains. However, to differentiate between these taxa, is not as straightforward, even when a large reference collection is available (see for example Bocanegra & Sáez, 2012). Moreover, when age and taphonomic factors are added to this mixture, differentiating wheat and barley may be even more problematic. One taxon that could potentially be confused with wheat or barley is *Bromus sterilis*; however, the grains are wider when viewed from the side and the extinction cross is not often bilateral. Oats will likely be identifiable if they are still packed into clusters, but we were unable to distinguish between the two species we tested. When the grains are loosened, these could be mistaken for *Digitaria sanguinalis*. The latter produces slightly more angular grains than those produced by both *A. sativa* and *A. strigosa*. Within the Cyperaceae family, the starch grains in the USOs of both *Cyperus esculentus* and *C. rotundus* are diagnostic. The same cannot be said for the starch grains in the seeds of *Carex hirta* and *Bolboschoenus maritimus*. The grains produced by taxa in the Fabaceae family are extremely diagnostic. Distinguishing between the various species may be possible, with peas, lentils, and *Lathyrus sativus* deemed especially diagnostic. Within the vetches, we found that *V. hirsuta* and *V. tetrasperma* lacked distinct lamellae, which are more visible on *V. sativa* and *V. ervilia*. We did find that several taxa produced small (5–8 μm on average), polyhedral or angular starch grains with a centric hilum. These include seeds of *Echinochloa crus-galli*, *Phleum pratense*, *Bolboschoenus maritimus*, and

Table 2: Plant taxa to be considered in the future to test for the presence of starch grains (list not exhaustive)

Binomial name	Common name	Family	Plant part(s)	Comments
<i>Actium lappa</i> L.	Greater burdock	Asteraceae	Root	
<i>Arrhenatherum elatius</i> subsp. <i>bulbosum</i>	Tuber oat-grass	Poaceae	Root	
<i>Arum maculatum</i> L.	Lords-and Ladies	Araceae	Root	
<i>Beta vulgaris</i> ssp. <i>maritima</i>	Sea beet	Amaranthaceae	Root	
<i>Cichorium intybus</i> var. <i>sativum</i>	Root chicory	Asteraceae	Root	
<i>Conopodium majus</i> (Gouan) Loret.	Pignut	Apiaceae	Root	
<i>Elymus repens</i> (L.) Gould	Coach grass	Poaceae	Rhizome	Average measurement of grains given in Juhola, Etu-Sihvola, Näreola, and Ruohonen (2014)
<i>Glyceria fluitans</i> (L.) R.Br.	Flotating sweetgrass	Poaceae	Seed	Average measurement of grains given in Juhola et al. (2014)
<i>Heracleum sphondylium</i> L.	Hogweed	Apiaceae	Root	
<i>Lathyrus cicera</i> L.	Red pea	Fabaceae	Seed	
<i>Lathyrus tuberosus</i> L.	Tuberous pea	Fabaceae	Root	
<i>Lilium</i> sp.	Lily	Liliaceae	Bulb	Photos of American species in Messner (2011)
<i>Nuphar lutea</i> (L.) Sm.	Waterlily	Nymphaeaceae	Seed/Rhizome	Tuber starch grain photos in Henry et al. (2011) and Messner (2011)
<i>Nymphaea</i> sp.	Waterlily	Nymphaeaceae	Seed/Rhizome	<i>N. alba</i> Rhizome starch grain photos in Henry et al. (2011)
<i>Polygonum aviculare</i> L.	Common knotgrass	Polygonaceae	Seed	Starch grain photos in Juhola et al. (2014)
<i>Pteridium aquilinum</i> (L.) Kuhn	Bracken fern	Dennstaedtiaceae	Rhizome	Starch grain photos in Horrocks et al. (2004)
<i>Ruscus aculeatus</i> L.	Butcher's-broom	Asparagaceae	Root	
<i>Salicornia europaea</i> L.	Glasswort	Amaranthaceae	Root	
<i>Typha angustifolia</i> L.	Reed	Typhaceae	Tuber	Starch grain photos in Revedin et al. (2010)

species of *Setaria*. However, the latter, in particular *S. verticillata*, will be likely distinguished by the presence of a distinct continuous double border. USOs of various species, as noted earlier, are more likely to be identified as such given their shape and relatively larger sizes. We propose that *Brassica rapa* var. *rapa*, *Gentiana lutea*, *Erythronium dens-canis*, and *Ficaria verna* could thus be identified in the archaeobotanical record. Finally, fruits of *Aesculus hippocastanum* and *Quercus* are also good candidates for identification.

While we were unable to gather all the plants that we had hoped to sample, for example, sea beet, pignut, tuber oat-grass, and tuberous pea¹² (see Table 2), the creation of a reference collection is often a work in progress, and we plan to continue expanding it. We believe our work thus far provides a starting base for starch grain analysis in the region. Besides continuing our search for new plant species that could have been used and present in the region during the Early Neolithic, some additional types of samples need to be considered. For example, we need to collect plants at different stages of maturation but also from different environments, as these factors may affect the size of the starch grains (see references in Gott *et al.*, 2006). Other plant parts could have been utilized, for example, the inner bark tissue of pine and birch, which are starch-rich resources (Gott *et al.*, 2006; Kubiak-Martens, 2016; Sandgathe & Hayden, 2003) and will also need to be considered. Experimental work that comprises mechanical processing (grinding, pounding), as well as thermal exposure (cooking) and fermentation, is essential to gather a broader picture of how starch grains are modified (see for example Cagnato, 2019; Chantran & Cagnato, 2021; Henry, Hudson, & Piperno, 2009; Li *et al.*, 2020; Wang *et al.*, 2017). Preliminary work (Cagnato, Hamon, & Salavert, *in press*) on domesticated species (cereals and pulses) has already been carried out, but we plan to expand this collection with the processing of wild plants, especially tubers and rhizomes, due to their presence in archaeological samples from the Paris Basin (Hamon *et al.*, 2021).

Overall, our work here shows that through starch grain analysis, it may be possible to broaden the spectrum of plants likely consumed by Early Neolithic (and beyond) populations in the Paris Basin, in particular concerning the use of wild plants and specific plant parts, especially underground storage organs. Now that a large selection of starch-rich species has been identified, future research can focus on determining whether it will be possible to clearly differentiate between them. We hope that our research helps guide future scholars in the creation of their own starch grain reference collection as there is the necessity for a solid database, and this across disciplines.

4.1 What Does Starch Grain Analysis Tell Us Thus Far About LBK Food Processing?

To conclude, we provide a brief synthesis of what we know about food transformation to date in the Paris Basin. The application of starch grains has revealed that cereals were not the only foods processed on grinding stones. Notably, 9 LBK grinding stones from Remicourt “En Bia Flo II” in Belgium revealed the presence of wheat, barley, oats, peas, and acorns (Chevalier & Bosquet, 2013, 2017). Our research (Hamon *et al.*, 2021), carried out on a large corpus of grinding stones ($n = 32$) from across LBK and BVSG sites in the Paris Basin, supports the notion that grinding stones were multipurpose as we also found starch grains of wheat, barley, and peas. Cooked (or at least heated) plants were also processed with these stone tools, based on our data. Finally, we also found evidence for the processing of different types of USOs (Hamon *et al.*, 2021; Cagnato, Hamon, Salavert, & Elliott, *in prep.*), thereby proving that starch grain research can be fruitful and provide a new vision of past plant use.

Acknowledgments: We wish to thank Laura Longo for kindly providing pellets of starch extracted from various plant species, as well as Françoise Toulemonde and Charlène Bouchaud for providing some of the species included in this research. Finally, we are grateful to Julien Wiethold for his help with proposing which plants to include in this study.

¹² Some of the plants listed here have been studied by other scholars, and morphological information is available in some cases.

Funding information: The work was financed by a DIM MAP Ile de France postdoctoral fellowship and the ANR Homes grant (ANR-18-CE27-0011).

Author contributions: All authors have accepted responsibility for the entire content of this manuscript and approved its submission. CH, CC, AS, and ME designed the project, and CC prepared the reference collection. CC prepared the manuscript with contributions from all co-authors.

Conflict of interest: Authors state no conflict of interest.

Data availability statement: The datasets generated and analyzed during the current study are available in the collections of UMR 7041 ArScAn, Archéologies environnementales (MSH Mondes, Nanterre), UMR 8215 Trajectoires (9 Rue Malher, Paris), and UMR 7209 Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements (AASPE) (55 Rue Buffon, Paris). Many of the dataset generated is also included in this article in its supplementary information file. Additional photos generated during the current study are available from the corresponding author on reasonable request.

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