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The use of underground storage organs in the Early Neolithic (Linearbandkeramik and Blicquy/Villeneuve-Saint-Germain) in the Paris Basin: the contribution of starch grain analyses

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Introduction

- 1 Underground storage organs (USOs hereafter) —which include, rhizomes, roots, bulbs, and tubers— are “remains of low archaeological visibility (Hillman 1989: 209), and their recovery is usually hampered by two main factors: preservation and dedicated methods of analysis and identification. If we consider the first factor, the recovery of vegetative storage parenchyma is difficult as the way it is prepared needs to be considered, for example the way they are consumed (fresh, cooked or thermally treated) and whether some processing is required (grinding, soaking, pounding, parching, removing toxins). Second, it is fragile and therefore has lower chances of being preserved compared to denser plant remains such as seeds, nutshells, and wood (Kubiak-Martens 2016, Pearsall 2015). In some special cases, however, parenchyma does preserve, for example in waterlogged, carbonized, or desiccated contexts (Kubiak-Martens 1996, Ugent *et al.* 1986), especially if the tissues are desiccated prior to carbonization (Celant *et al.* 2015).

- 2 Damage to these fragile remains can also occur during their excavation, flotation, but also in the laboratory (Kubiak-Martens 2016). Even if these fragments are recovered, identifying them may be difficult, as sometimes they are too small, or the morphology is damaged (especially when charred) (Hather 2016). Mason *et al.* (1994: 5) note that “Parenchymatous tissues... can superficially be confused with poorly preserved wood charcoal, as can fragments of processed plant tissues. It is likely that such remains occur fairly frequently in archaeobotanical assemblages, but are usually dismissed as unidentifiable.” Moreover, differentiating between different taxa on the basis of this vegetal tissue is not straightforward, although the use of Scanning Electron Microscope (SEM) techniques has been an important contribution to the field of archaeobotany (Hather 1991, Mason *et al.* 1994).
- 3 While exceptions exist of 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 (5200-4700 BC) sites in the Paris Basin, which spans from Hesbaye in Belgium to Normandy in France. The exact reasons are likely multiple, and include the fact that a good amount of data can be obtained from the study of seeds and other macroremains (plant elements visible to the naked eye). Based on the recovery and study of macroremains, it has been possible to determine that Early Neolithic populations in the Paris Basin were cereal-based economies, consuming hulled wheats (einkorn, *Triticum monococcum* and emmer, *Triticum turgidum* subsp. *dicoccon*, but also relying on pulses (peas, *Pisum sativus*, and lentils, *Lens culinaris*) as well as flax (*Linum usitatissimum*) which provided fibers for textiles but could have also been used for its oil (Bakels 1999, Diestch-Sellami 2004, Salavert 2011, Berrio 2011). Starch grain analysis has also provided additional support indicating the importance of cereals and pulses (Hamon *et al.* 2021, Chevalier & Bosquet 2017).
- 4 Given that USOs are theorized to have been important in hominin evolution (Laden & Wrangham 2005, Wrangham *et al.* 2009), and much more recent evidence from Mesolithic and other Neolithic populations indicate the use of USOs in the diet (see for example Kubiak-Martens 2016 and discussion below), it is important to understand whether this is true also for the Linearbandkeramik and Blicquy-Villeneuve-Saint-Germain populations (LBK/BVSG hereafter). Besides the study of parenchymatous tissue, another way to address this gap is to consider starch grain analysis, which allows the recovery of starch grains, found in different plant organs, but especially numerous in storage organs such as USOs. Starch grains are microscopic (ranging from 1 to 100 μm) and composed of glucose chains of amylopectin and amylose. Although morphological similarities exist between and within species, in some cases, starch grains can be highly diagnostic to a particular plant taxon. Identification of the starch grains is based on their morphology, size, and other important features that 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 *et al.* 2006). Starch grains have been recovered from a wide array of contexts, and therefore can provide information not only on the species present at a specific time period, but also the function of certain tools and objects (Piperno *et al.* 2004, Cagnato & Ponce 2017, Duncan *et al.* 2009, Wang *et al.* 2021), and the diet of both humans and animals when dental calculus, gut contents, and paleofeces are studied (Cagnato *et al.* 2021a, Henry *et*

al. 2011, Madella *et al.* 2014, Vinton *et al.* 2009). Starch grains are susceptible to morphological and physical changes if exposed to heat or due to mechanical processes such as grinding and pounding, therefore additional information concerning the manner in which plants were treated prior to consumption can in some cases also be determined (Crowther 2012).

- 5 In this article we present the first detailed results on the use of USOs by LBK and BMSG people living in the Paris Basin between 5200 BC and 4700 BC.

USOs in the Archaeological Record

- 6 Middle Palaeolithic sites in South Africa have revealed evidence of USO consumption based on the recovery of rhizome and tuber parenchyma dated to 120,000 years ago from Klasies (Larbey *et al.* 2019), and charred rhizomes (*Hypoxis* sp.) from Border Cave dated to 170,000 years ago (Wadley *et al.* 2020). In the Middle Paleolithic (Mousterian, ca. 50,000 BP) levels at Kebara Cave in Israel, although direct evidence of USO use is not available, seeds from three taxa that produce edible USOs are reported: wild radish (*Raphanus raphanistrum*), nut-grass (cf. *Cyperus*) and bulbous barley (*Hordeum spontaneum*) (Lev *et al.* 2005). At Wadi Kubbaniya, an 18,000-year-old site located in what is now Egypt, tubers of wild nut-grass (*Cyperus rotundus*) were found to dominate the samples (Hillman 1989). For the Early Natufian, over 50,000 club-rush tubers are reported from Shubayqa 1 in northeastern Jordan (Arranz-Otaegui *et al.* 2018).
- 7 In China, the processing of roots and seeds is documented from around 20,000 years ago, along the banks of the middle Yellow River (Liu *et al.* 2013). In Southeast Asia (Papua New Guinea, northern Borneo and the Philippines), Late Pleistocene and Early Holocene sites have shown that subsistence strategies included the intensive exploitation of tubers (see references in Barker & Richards 2013). Remains indicate a plant-based diet 65,000 years ago at Madjedbebe in northern Australia, with USO tissues also recovered (Florin *et al.* 2020).
- 8 Finally, in the Americas, the earliest documentation for the processing of roots and tubers comes from the presence of arrowroot (*Maranta* sp.) at 10,000 BP in Colombia. Other tubers are reported from southwestern Ecuador, with leren (*Calathea allouia*) as early as 9320 BP and achira (*Canna edulis*) around 5500 BP (Iriarte 2007). For Southwestern Amazonia, the earliest use of USOs is now well-documented through the presence of phytoliths belonging to manioc, leren, and *Heliconia* during the early Holocene (ca. 10,400-9,400 cal year BP) (Lombardo *et al.* 2020, Watling *et al.* 2018). Sites along the coast of Peru, dated to 4250 BP, have also yielded evidence of USOs such as sweet potatoes (*Ipomoea batatas*), achira, and potatoes (*Solanum tuberosum*) (Ugent *et al.* 1981). In Central America, manioc (*Manihot esculenta*), arrowroot (*Maranta arundinaceae*), and yams (*Dioscorea* sp.) are reported from Panama between 7000-5000 BP (Piperno *et al.* 2000). Further south, evidence of yams is reported by Scheel-Ybert (2001) from southern Brazil dating to 5500-1400 BP. In the Caribbean, a range of USO's, identified through starch grain analysis, are reported to have been consumed or processed during the Late Archaic period (c. 5000 BC), notably sweet potato, manioc, achira, and cocoyam (*Xanthosoma* sp.) (Pagan-Jimenez & Mickleburgh 2023).

- 9 While clearly not an exhaustive list of USO use in the archaeological record around the world, it demonstrates that such resources have played an important role in the diet of ancient populations.

USOs in the European Archaeological Record

- 10 For the Upper Paleolithic, starch grains recovered from dental calculus of Neanderthal individuals from Spy I and II (Belgium, ca. 37 kya) and Shanidar III (Iraq, ca. 50 kya) already showed the presence of USOs (Henry *et al.* 2011). 30,000-year-old grinding stones from Bilancino II (Italy), Pavlov VI (Czech Republic), and Kostenki 16-Uglyanka (Russia) were interpreted as indicating the intentional transformation of a broad variety of starchy plants that primarily include cattail (*Typha cf. angustifolia*) rhizomes and roots of the moonwort fern (*Botrychium* sp.) (Aranguren *et al.* 2007, Revedin *et al.* 2010). Additional data from Russian and Moldovan sites (e.g., Brinzeni 1, Kamennaya Balka II; Kostenki 16-Uglyanka) reveal that USOs belonging to *Arundo donax*, *Phragmites* sp., cattail, and water lily (*Nelumbo* sp.) were processed on grinding stones (Longo *et al.* 2021, Skakun *et al.* 2020). At Dolní Věstonice, in the Czech Republic, large quantities of parenchyma, possibly belonging to Asteraceae roots, have been reported from a hearth dated to 26,000 BP (Mason *et al.* 1994).
- 11 Data on the use of USOs comes from a range of European Late Mesolithic sites in Poland, the Netherlands, and Scotland, where techniques have made it possible to identify parenchyma (Kubiak-Martens *et al.* 2015, Kubiak-Martens 2016, Raemaekers *et al.* 2013). 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* were also recovered. Cattail reed (*Typha* sp.) tubers are also reported in Mesolithic contexts from northern Netherlands and Poland (Kubiak-Martens 1999, Perry 1999). Finally, Late Mesolithic datasets (c. 5th 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*) tubers (Kubiak-Martens 1999, 2002).
- 12 Tubers of lesser celandine (*Ficaria verna*) 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*) is noted as having been consumed by the Neolithic populations living near the Châlain Lake in the Jura, France (Dommelier *et al.* 1998 citing Petréquin & Petréquin 1988). A turnip (*Brassica rapa* v. *rapa*) seed or tuber has been reported from waterlogged contexts (4400-2400 cal BC) in Central Europe (Colledge & Connolly 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 *et al.* 2019), and tuber oat-grass bulbs (*Arrhenatherum elatius* subsp. *bulbosum*) from the Middle Neolithic in northern France (San Juan & Dron 1997) and Late Neolithic Germany (3500-2800 cal BC) (Kirleis *et al.* 2012). 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); stem bases, nutlets (achenes) and the tubers can be consumed (Kubiak-Martens 1999). Finally, seeds of waterlilies (*Nuphar* and *Nymphaea*) have been reported from Mesolithic and Neolithic contexts, indicating they were probably consumed (Bouby *et al.* 2018, Raemakers *et al.* 2013, Dietsch 1996, Kirleis *et al.* 2012, Kubiak-Martens 2002, 2016: 128-129). However, it is known that waterlily rhizomes are also edible, and their consumption is widely attested in the ethnographic record (Kubiak-Martens 2016).

The Paris Basin during the Early Neolithic: Materials and Methods

- 13 A total of 9 sites across the Paris Basin were considered in the study (Figure 1), with forty grinding implements, including grinders and querns tested (Figure 2). Among these sites, 5 occupations are attributed to LBK and 5 to BQ/VSG. The first farming populations that colonized the Paris Basin around 5100 BC, brought with them a full package of cultivated plants, breeding stocks, and new technologies including ceramics for storage and preparation, as well as grinding tools for daily food processing. LBK as well as BQ/VSG hamlets were composed of several domestic units, including typical long tripartite houses made of timber and daub with lateral detritic pits; their organization seems highly dependent on the social structure and economic pattern. With the emergence of the Blicquy-Villeneuve-Saint-Germain culture between 4900 and 4700 BC, a strong regionalization process emerged, together with the colonization of new territories such as plateaus. Technical innovations were introduced, such as the production of schist bracelets, and a reorganization of exchange networks was visible (Hamon & Manen 2021). From an archaeobotanical point of view, it seems that the BQ/VSG saw the generalization of naked wheat, perhaps under Mediterranean influences. In these contexts, plant gathering (fruits, nuts), cultivation (cereals, legumes) and processing was a major activity, as suggested by the important number of macrobotanical remains and grinding tools recovered (Hamon *et al.* 2019).
- 14 The methods on the extraction and subsequent analysis of the starch grains are fully reported in Hamon *et al.* (2021). The reference collection, how it was established and with descriptions of the starch grains, has already been presented in detail (Cagnato *et al.* 2021b). Since then, some additional plants have been added to the collection, notably USOs of *Lilium martagon*, *Polygonum bistorta*, and *Calla palustris*. Our current USO reference collection consists of 35 species, both wild (*Arctium lappa*, *Erythronium dens-canis*, *Gentiana lutea*) and domesticated (*Brassica rapa* var. *rapa*, *Pastinaca sativa*, *Raphanus raphanistrum* subsp. *sativus*) plants. In many cases these have been reported in the archaeological record, while in others they are known to be consumed today and/or also used medicinally.
- 15 There are some limitations and considerations that need to be considered. The data are skewed towards the USOs that produce starch grains on the larger end of the spectrum. Those taxa that produce small grains (below 10 μm) will not be easy to see or even identify when using an optical microscope (x 600). Taxa that fit this category include: *Arundo donax*, *Calla palustris*, *Pastinaca sativa*, *Rumex acetosa*, *Schoenoplectus lacustris*, and *Typha angustifolia*. Moreover, there are the taxa that do not produce starch grains in their USOs; these include *Allium ursinum*, *Daucus carota*, *Taraxacum* sp., *Campanula*

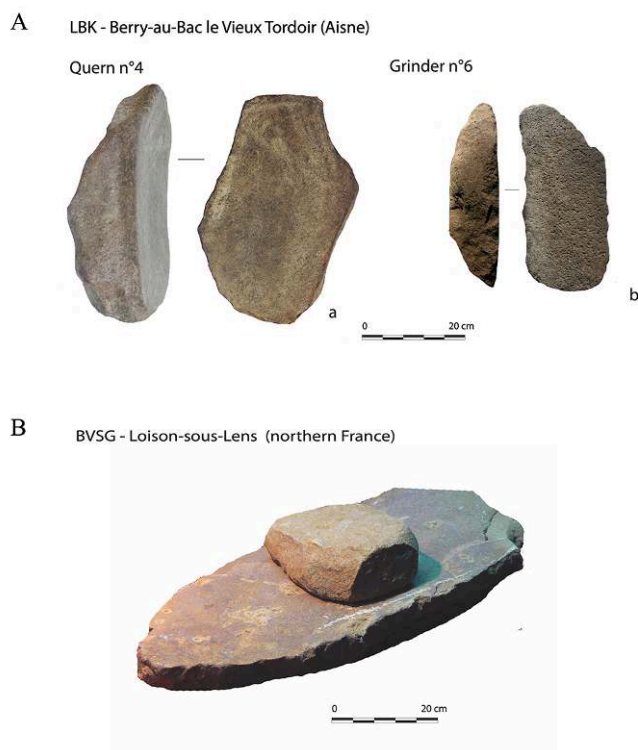
rapunculus, *Apium graveolens* var. *rapaceum*, *Cichorium intybus*, and *Cirsium oleraceum*. Regarding the identifications of the starch grains, we have separated them into different categories (types) based on their morphological attributes (shape, location of hilum, presence or absence of lamellae, and size). Given that in some cases the morphologies overlap between different species, we mention both these taxa in the results section that follows.

Figure 1: A: The Paris Basin, shown in orange, and B: The locations of the archaeological sites considered in this article. Circles indicate LBK sites, stars indicate BVSG sites, while a blue triangle indicates LBK and BVSG sites



Credit: Map modified from Wikipedia Commons

Figure 2: Selection of materials tested. A: Paired quern (a) and grinder (b) from a LBK grinding tool hoard in Berry-au-Bac le Vieux Tordoir (Aisne, France) (Hamon 2020). B: Paired quern and grinder from a BVSG lateral pit in Loisons-sous-Lens (northern France) (Praud *et al.* 2018)



Photos: C. Hamon

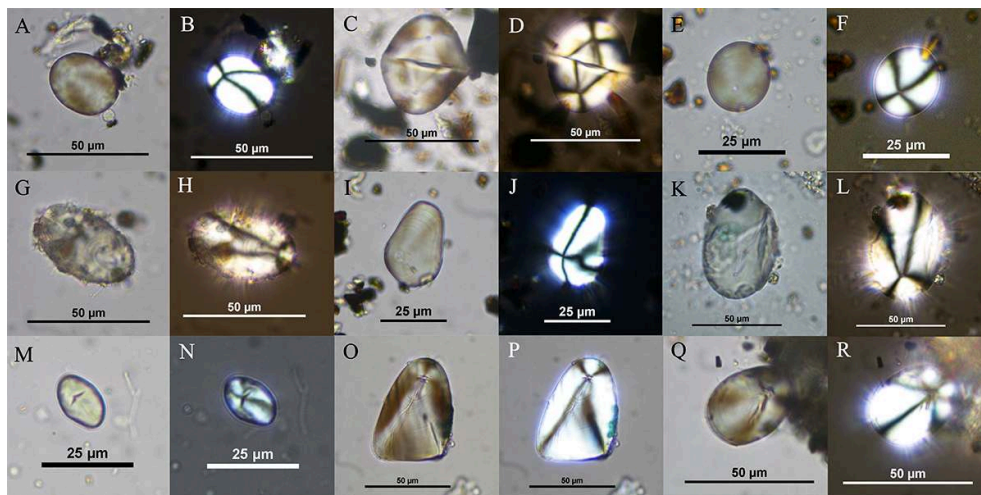
Starch Grain Analysis: Results

- 16 Out of the 40 implements tested, 17 (8 querns, 9 grinders) presented evidence of starch grains attributable to USOs (Table 1). Starch grains belonging to cereals and legumes were for the most part always found on these same tools (for details please refer to Hamon *et al.* 2021). All the sites considered had evidence of tubers, except for Aubechies, but only one tool was tested from this site. A total of 52 starch grains from USOs were identified from these various tools. Based on the data recovered, we were able to classify 34 starch grains (65%) into 5 main types (Figure 3). Some of the starch grains remain unidentified, either due to their damage (n=11, Figure 4) or because they do not resemble any in our current reference collection (n=7, Figure 5). Below we present the types and which species they might belong to.

Table 1: Starch grains recovered from grinding stones from LBK and BVSG sites. See Hamon *et al.* 2021 for details on the individual tools. The starch grain types are described in the text

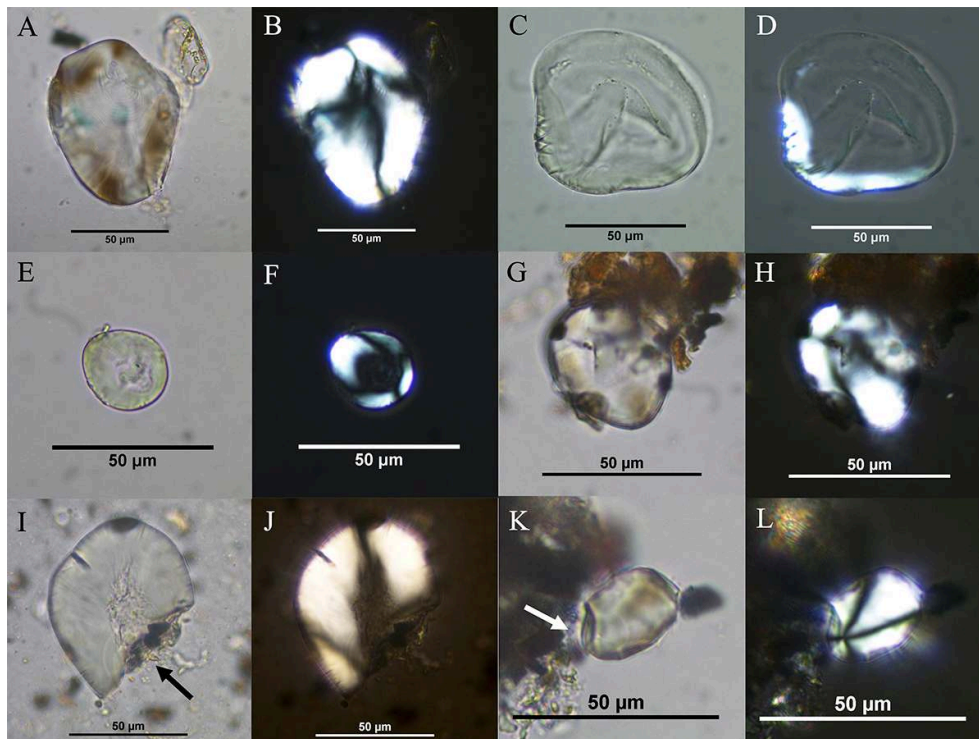
SITE	Cultural attribution	Tool type(s)	Type 1	Type 2	Type 3	Type 4	Type 5	Unidentified	Unidentified (Damaged)	SUB-TOTAL
Menneville Derriere le Village	LBK	Grinder (1)		1					1	2
Remicourt En Bia Flo 2	LBK	Quern (1)	1		1	1				3
Berry-au-Bac le Vieux Tordoir	LBK	Querns (2); Grinders (2)	2	4				2	1	9
Ath	LBK/BVSG	Querns (2)	3							3
Loison sous Lens	BVSG	Grinders (2)							4	4
Tremblay en France	BVSG	Quern(1)							2	2
Verson	BVSG	Grinder(1)	3							3
Villevenard	BVSG	Querns (2); Grinders (3)	9	8			1	5	3	26
			18	13	1	1	1	7	11	52

Figure 3: Starch grains identified. A-F: Type 1; G-L: Type 2; M-N: Type 3; O-P: Type 4; and Q-R: Type 5



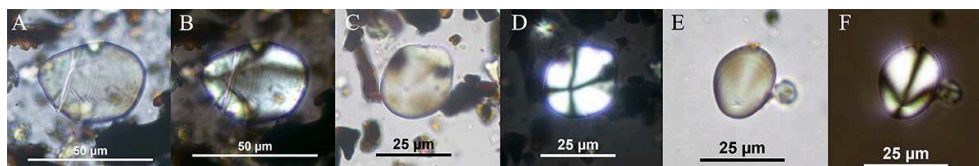
Photos C. Cagnato

Figure 4: Starch grains presenting damage, either from exposure to heat and/or mechanical processing. A-H: Grains probably exposed to heat due to gelatinization at different stages. I-L: Fractured grains (arrows indicate missing parts)



Photos C. Cagnato

Figure 5: A selection of starch grains belonging to probable USOs



Photos C. Cagnato

- 17 **Type 1** is similar to those produced by taxa in the Brassicaceae family, notably the turnip (Figure 3 A-F). A total of 18 starch grains were found belonging to this type. These grains are simple, generally oval in shape. The hilum is eccentric and open, with a linear fissure sometimes emanating from the hilum. The lamellae are very distinct and therefore visible, as is the extinction cross (even when viewed in transmitted light). Less frequently, bell-shaped grains (see Figure 3C-D) can be found. The range of the starch grains of this species is between 18 and 51 microns in length (Cagnato *et al.* 2021b). The presence of turnip would fit with what has been reported from Central Europe (Colledge & Connolly 2014, Tolar *et al.* 2011), although only seeds have been recovered and thus have been interpreted as being used for oil rather than for the root (Zohary *et al.* 2012). Genotyping-by-sequencing has shown that *Brassica rapa* turnips and/or oilseeds were first domesticated in Central Asia around 3,430–5,930 years BP and then diffused east and west to Europe (McAlvay *et al.* 2021). If we consider the earliest date when the domestication could have taken place, this would still be much

later than its use by LBK population in the Paris Basin, and therefore fits with these plants being weedy/wild (Zohary *et al.* 2012).

- 18 **Type 2:** These starch grains (n=13) closely resemble two taxa in our collection: those found in the tubers of lesser celandine (*Ficaria verna*) and roots of bistort (*Polygonum bistorta*) (Figure 3 G-L). For the former, the grains are simple, spherical to oblong and conical, with an open, eccentric, and sometimes y-shaped hilum. The lamellae are visible towards the edges of the grains, and they range between 23-57 microns in length. The bistort starch grains are bimodal: the smaller grains measure around 6-7 microns while the larger ones range between 25 to 55 microns in length. The grains are oval, with an open hilum (sometimes y-shaped). The lamellae are present but typically faint.
- 19 Charred tubers of lesser celandine have been reported from European sites dating from the Mesolithic to the Iron Age, with a greater number of tubers reported from Neolithic sites (Klooss *et al.* 2016, Mithen *et al.* 2001). As will all members of the Ranunculaceae family, mild toxins present in the plant can be removed by heating or cooking. Additionally, the tubers can then be ground to produce flour (Klooss *et al.* 2016). The latter species can be consumed raw or cooked (Hardy 2010). To reduce high quantities of tannins in the roots, these can be roasted. They can be used in the preparations of stews, but also in the preparation of a flour to make bread (PFAF 2022). *Polygonum* tuber or root material was reported from a Mesolithic context in Poland (Kubiak-Martens 1996). *P. bistorta* and *P. viviparum* were used by people in Canada and Alaska as well as in Europe and Scandinavia (Kubiak-Martens 1996).
- 20 **Type 3:** One starch grain was found attributed to Type 3 (Figure 3 M-N), which resembles those produced by arrowhead (*Sagittaria sagittifolia*) but also great pignut (*Bunium bulbocastanum*). Arrowhead starch grains are simple, elongated, often wider towards the hilum, and then tapering slightly. The hilum is eccentric, wispy, and open, while the lamellae are not visible. In terms of size, the grains range between 3 and 23 microns. For the great pignut, the grains are simple, spherical-oval, or elliptical, with a hilum that is eccentric with small fissures emanating from them. The lamellae are not visible, and the grains measure between 4 and 15 microns.
- 21 Arrowhead tubers can be consumed raw although they are more frequently cooked (Hardy 2010, Kubiak-Martens 2016) and can also be dried and ground to prepare a gruel or added to other flours (PFAF 2022). Archaeologically, arrowhead has been reported from Mesolithic contexts (Kubiak-Martens 1996). Ethnographic studies show that *S. sagittifolia* and *S. latifolia* (native to the American continent) are consumed by indigenous groups in Russia and Canada respectively, and prepared in different manners: baked in ashes or pits, or boiled (Kubiak-Martens 1996, Messner 2011, Peacock 2008). *Bunium* tubers are consumed in the Western Italian Alps, with two main ways of processing them. The first is to grind the tubers to prepare a dough using salt, milk and flour which is then baked, or the tubers could be roasted (Mattalia *et al.* 2013). In Spain, other *Bunium* species are typically eaten raw as snacks, with one cooked similarly to potatoes (Tardio *et al.* 2006). In the archaeological record there are few mentions of this taxon. Moffett (1991) found tubers of either great pignut or pignut (*Conopodium majus*), both in the Apiaceae family, in a Bronze Age cremation (3520 cal BP).
- 22 **Type 4:** This type resembles those produced by taxa in the Liliaceae family, in our case *Lilium martagon*, but different *Lilium* species are noted as being edible (see for example

Messner 2011; Peacock 2008). One starch grain was found in our Neolithic samples (Figure 3 O-P). This taxon produces starch grains that are oval to pear-shaped, with an eccentric hilum that is often closed, and faint lamellae. In terms of size, the grains range from 20 to 55 µm in length. To consume this starch-rich organ, the bulb is often mentioned as requiring some form of cooking. Bokov *et al.* (2019) note that raw bulbs are consumed, but they are also dried and then ground to produce flour or baked or boiled. To the best of our knowledge, there is no evidence of *Lilium* being used in Western Europe. Beyond this part of the world, *Lilium* starch grains have been reported from the Szeletian Layer of Brînzeni-1 in Moldova (Skakun *et al.* 2020), pastoralist dental calculus in the Altai (Zanina *et al.* 2021), Natufian contexts in Israel (Liu *et al.* 2018), and from Northwest China (Wang *et al.* 2019).

- 23 **Type 5:** This last type mirrors starch grains that are produced by *Erythronium dens-canis* bulbs but also the roots of the great yellow gentian (*Gentiana lutea*) (Figure 3 Q-R). In terms of their morphology, the grains of the former are simple, wedge-shaped when viewed from above, cone shaped when viewed in profile. Their distal end often curved, with an eccentric hilum. The lamellae are generally absent but can in some cases be faint. They range between 20 and 51 microns in length. For the great yellow gentian, the grains are simple, rounded to rounded triangular, sometimes irregular. Some semi-compound grains are present. Sideways they are flatter than when viewed from the top. The hilum is eccentric, while the lamellae are not visible. The extinction cross is well-defined, and the grains range between 16 and 51 microns.
- 24 The former can be consumed raw, or cooked (Hardy 2010) and then ground (PFAF 2022). According to Peacock (2008), Interior Salish Peoples regularly consumed bulbs of the yellow avalanche lily (*Erythronium grandiflorum*) after cooking it in pits. Starch grains belonging to a related species (*E. sibiricum*) have been reported from pastoralist dental calculus in the Altai (Zanina *et al.* 2021). The bitter roots of the great yellow gentian are used to prepare a digestive liquor (Abbet *et al.* 2014). To the best of our knowledge, this plant has not been reported in the archaeobotanical record.
- 25 **Damaged grains:** In this category were placed the starch grains (n=11) that presented major morphological alteration, precluding any type of classification. Two major types of damage were identified: the first is gelatinization of the starch grains (an irreversible structural change) which leads to changes in the shape of the starch grain itself and the partial or almost complete loss of the extinction cross (Figure 4A-H). The second type of damage consists of fractures (see Figure 4I-L).

Discussion

Methods of preparation

- 26 Depending on the taxa, the tubers could have been eaten raw or cooked. For those taxa present in our reference collection, the majority can be consumed raw, and therefore would not need additional processing. However, some of the taxa (*Ficaria verna*, *Calla palustris*, and *Lilium martagon*) do require some form of processing to render them edible, achieved by removing toxins and/or oxalate crystals that may be present. The absence of dedicated experimental studies on the changes in starch grains in USOs found across Eurasia does not allow us to go further with fully identifying the manners in which the plants may have been treated. However, the damages observed on some of

the starch grains are in line with those observed in South American tubers (Babot 2003, Babot *et al.* 2014) but also on other experimentally cooked and processed taxa; damage that includes gelatinization, but also fracturing, appearance of fissures, and loss of the extinction cross (Chantran & Cagnato 2021, Cagnato *et al.* 2021c, Henry *et al.* 2009, Ma *et al.* 2019).

- 27 Besides the removal of toxins, the nutritional value can also be increased by processing. Wollenstonecroft *et al.* (2008) showed that pulverising was necessary to effectively process tubers of sea club-rush (*Bolboschoenus maritimus*), as cooking alone did not soften them. The mechanical processing leads to the rupturing of plant tissues, and in turn increases bioaccessibility- “the fraction of a nutrient that is released from a food matrix during digestion and is therefore potentially available for absorption in the gastrointestinal tract” (Wollenstonecroft *et al.* 2008: S20). Certain USOs, rich in inulin, a polysaccharide composed of fructose molecules, must undergo hydrolysis, which allows the fructose to be liberated and in turn readily digested by the gut (Thoms 2009). In the case of North America, camas (*Camassia* sp.), balsamroot (*Balsamorhiza sagittata*), and Drummond's onion (*Allium drummondii*) cooked in pits (earth ovens), served to convert complex carbohydrates into simple ones, making the roots sweeter and more palatable (Leach & Sobolik 2010, Peacock 2008, Thoms 2009). Returning to Europe, early evidence of cook-stone features is reported from the Aurignacian site of Abri Pataud but also from the late Pleistocene site of Pincevent in Central France (Thoms 2009). According to Straus (2006, cited by Thoms 2009), fire-cracked rock concentrations have been reported across Western Europe until the Mesolithic (see also Mithen *et al.* 2001). It remains unclear whether similar features would have been used by Early Neolithic populations to process their USOs, especially those rich in inulin, which is the case of several taxa in the Asteraceae family (burdock, dandelion, chicory) but also for example wild garlic (*Allium ursinum*). Alternatively, USOs could have been roasted in open-air hearths (Mallol *et al.* 2007, Stahl 1989).
- 28 Another reason to grind these organs may have been to prepare flour. As has been noted for lesser celandine for example “after cooking or roasting and grinding, the produced flour can be used, especially after the addition of gluten-containing flour from cereals that improves the baking properties of the tuber flour” (Oschatz 1848, cited by Kloos *et al.* 2016: 28). We know that even pre-Neolithic bread-like products were produced, for example *Bolboschoenus glaucus* tubers were used to produce flat bread-like products at the Natufian hunter-gatherer site in northeastern Jordan (Arranz-Otaegui *et al.* 2018), and at Çatalhöyük in Turkey, tubers of this same species were found inside charred food fragments (Gonzalez Carretero *et al.* 2017). For the Neolithic, Heiss *et al.* (2017) report on “bread-like” products found at a site in Switzerland, although no tubers were reportedly used as ingredients. Further afield, in China, starch grains of snakegourd (*Trichosanthes kirilowii*), a root known to require mechanical processing before it could be consumed was reported from grinding stones (Liu *et al.* 2013). In our case, various tubers are ethnographically ground to prepare flours, notably *Arundo donax*, *Erythronium dens-canis*, *Phragmites australis*, *Schoenoplectus lacustris*, and *Typha angustifolia* and *T. latifolia*.

New perspectives on Neolithic diets

- 29 Due to the way that many USOs can be consumed raw, it is very likely that an even wider range of USOs were in fact consumed by Early Neolithic populations. Even if these other tubers may be invisible due to their preparation style (consumed raw, not ground, or pounded), our data clearly indicate the use of USOs by Neolithic communities in the Paris Basin.
- 30 While the data at hand cannot determine the frequency with which tubers were consumed, it has been suggested, in the case of Neolithic Çatalhöyük that such resources could have “balanced the shortage of carbohydrates from crops” (Santiago-Marrero *et al.* 2021: 21). In many cases USOs are mentioned in the ethnographic record as being famine foods or as being used when there were food shortages (Hardy 2010, Fahmy 2005, Airaksinen *et al.* 1986, Simkova & Polesny 2015). However, based on the utility of tubers today (for example manioc, potatoes, yams), and the ever-growing number of ethnographic and archaeological studies presenting them as valuable source of food (e.g., Peacock 2008, Zanina *et al.* 2021), we must perhaps reconsider how we interpret these when they are discovered in the archaeological record. Based on the data available, we are unable to determine how LBK populations viewed USOs but finding evidence of their use on 43% of the total corpus studied is of interest and needs to be further studied. What is clear is that they were used, probably as sources of food, although medicinal purposes should not be excluded (see Santiago-Marrero *et al.* 2021). Some of the taxa in our reference collection are known for their medicinal properties, notably lily of the valley and cyclamen, while others have multiple uses, for example lesser celandine, Liliaceae bulbs, and *Gentiana lutea* (PFAF 2022).
- 31 Several taxa included in our reference collection can be ground and added to cereal flours to prepare doughs and breads. This may have well been a similar practice undertaken by Neolithic people, who clearly consumed important quantities of cereals and used grinding stones to process them (Hamon *et al.* 2021).
- 32 Finally, we would like to note that if in fact our identification of certain starch grains belonging to the Brassicaceae family is correct, this would indicate an even longer and more complex history for the use of turnips and radishes, vegetables still commonly consumed today in Europe. More data are clearly necessary to develop this theme further and determine whether Early Neolithic populations in the Paris Basin were also consuming weedy or wild turnips/radishes.

Conclusion

- 33 Based on the data recovered to date from sites in the Paris Basin, it is evident that USOs were utilized by the populations of the LBK and BVSG. People who practice agriculture, with probably a more restricted mobility at least during some part of the year, clearly also utilized wild plants to supplement their diet, or even for medicinal purposes. We therefore agree with the idea that “root plants should hardly be considered in isolation from the more general spectrum of food plants utilized by any group at a particular time.” (Griffin-Kremer 2014: 245). Considering the long history of human consumption of USOs this may not seem surprising, however, this is the first time that USO use has been documented so extensively for this period in Western Europe. Future studies that consider the study of parenchyma remains recovered from contexts in the Paris Basin,

together with microbotanical analyses, including those carried out on ceramics (results which are forthcoming) and experimental studies, will undoubtedly provide additional information on the use of these resources. By doing so, it will be possible to establish the actual spectrum of plant use in the past. The study of starch grains could highlight the cultivation and consumption of indigenous plants, whose place in the plant economy of Neolithic societies is probably largely underestimated.

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ABSTRACTS

Underground storage organs are poorly preserved in the archaeological record, and as a result their contribution to the diet of ancient societies is poorly understood. Starch grain analysis is a well-established methodology used in archaeology to reveal the use of various plants, including tubers, rhizomes, and roots. This paper presents the results of a study of starch grains recovered from millstones from various archaeological sites located in the Paris Basin. Our results highlight the use of tubers by these first agricultural populations at the beginning of the Neolithic (Linearbandkeramik and Blicquy-Villeneuve-Saint-Germain; 5200-4700 BC), providing new data on their contribution to the diet of agro-pastoral societies.

Les organes souterrains de stockage sont mal conservés dans les archives archéologiques et, par conséquent, leur contribution au régime alimentaire des sociétés anciennes est mal comprise.

L'analyse des grains d'amidon est une méthodologie bien établie en archéologie pour révéler l'utilisation de diverses plantes, y compris les tubercules, les rhizomes et les racines. Cet article présente les résultats d'une étude des grains d'amidon prélevés sur des meules provenant de différents sites archéologiques du Bassin parisien. Nos résultats mettent en évidence l'utilisation des tubercules par les premières populations agricoles au début du Néolithique (Linearbandkeramik et Blicquy-Villeneuve-Saint-Germain ; 5200-4700 av. J.-C.), apportant de nouvelles données sur leur contribution au régime alimentaire des sociétés agro-pastorales.

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