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ORIGINAL ARTICLE

Paleoethnobotanical identification criteria for bulbs of the North American Northwest

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Abstract
Paleoethnobotanical assemblages from the Northwestern region of North America often yield geophyte subterranean organs, but these carbonized remains are difficult to identify to species or genus level. We examine 11 species (8 genera) of the most ethnographically prevalent Northwest geophyte foods for macro- and micro-morphologic geophyte features, with a focus on bulbs from the Asparagales and Liliales orders. In this contribution, we discuss ethnographic practices which may affect archaeological material and provide digital photographic and quantitative references for both fresh and carbonized geophytes. We determine that pavement epidermal cells are the most diagnostic criteria for identifying bulbs in paleoethnobotanical assemblages. These identification standards provide researchers with comparative material to address questions of plant use, preparation, and stewardship across the greater Northwest Coast and Columbia-Fraser Plateau cultural and geographic regions.

Keywords Geophytes · Pacific Northwest · Bulbs · Archaeobotany

Introduction

Paleoethnobotany in the Northwest region of North America is a small but growing subfield of archaeological and paleoecological research into past human relationships with plants. Extensive ethnographic work indicates geophytes or underground storage organs (USO's) were among the most important food resources for Northwest peoples (Hunn 1981; Turner and Kuhnlein 1982, 1983; Turner 1995, 2007; Deur and Turner 2005), and were critical in other technological, functional, and symbolic elements of life (Turner 1998). Geophytes, as classified by the Raunkiaerian life-form system, are herbaceous plants with underground storage organs protected by the soil, typically found in climates with pronounced seasons (Mueller-Dombois and Ellenberg 1965; Shimwell 1971). Northwest geophytes are often called root foods collectively, and anywhere from eight to 40 species are named within Northwest Indigenous languages (Turner 2014a, p 282). While our understanding of past diets and human-plant relationships within the Northwest past is growing, there are several challenges to Northwest paleoethnobotany.

The greater Northwest region of North American is a geographic region spanning Canada and the United States, bounded by the Pacific Ocean to the west and the Rocky Mountains and Continental Divide to the east (Fig. 1). This area is vast and encompasses a broad array of landscapes and ecosystems including coniferous forests, rainforests, broad-leaved deciduous trees, subalpine meadows, wetlands, grasslands, and shrub-steppes. Across the Northwest, summers are typically dry from high atmospheric pressure, with most precipitation falling during winter. This greater area encompasses two geographic subregions: the Pacific Northwest Coast and Cascade Mountains and the Columbia-Fraser Plateau, also known as the Interior or Inland Northwest. The

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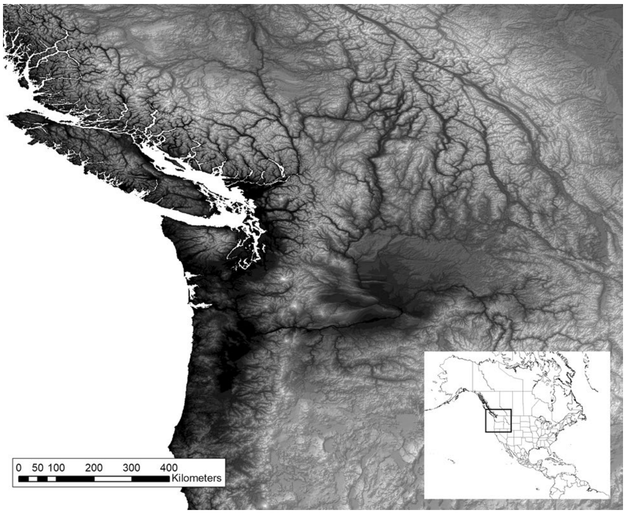

Fig. 1 Relief map of the greater North American Northwest, including both Northwest Coast and Columbia-Fraser Plateau regions

Pacific Ocean moderates the climate of the Coastal Region, giving the area relatively cool summers and warm, wet winters. The Columbia-Fraser Plateau, situated in the rain shadow of the Cascade Mountains, has a continental climate with greater temperature extremes and in general, sees less precipitation than the coast. These subregions largely correspond to cultural areas delineated by the Smithsonian Institution's Handbook of the North American Indians, *Northwest Coast* (Suttles 1990) and *Plateau* (Walker 1998) (see Turner 2014a, pp 5–7).

One of these challenges has been identifying the charred plant tissues frequently encountered in Northwest paleoethnobotanical assemblages (Lepofsky and Lertzman 2008). Plant storage organs often have unlignified parenchymatous tissue, or have limited lignified primary xylem, phloem, and cortical elements (Kasapligil 1961) and are thus less durable than other commonly recovered Northwest macroremains such as seeds, charcoal, or needles. Recovered archaeological plant tissues are fragmentary from pre- or post-depositional taphonomic effects, including both natural diagenetic processes and human usage. There are also several paleoethnobotanical challenges specific to the Northwest (Lepofsky and Peacock 2004; Lepofsky and Lyons 2013). The majority of Northwest paleoethnobotanical work takes place during cultural resource management testing or mitigation projects across provincial, state, and international boundaries. Sample sizes and recovery techniques are not standardized across these modern boundaries and analyzed paleoethnobotanical data are often reported within difficult to access "grey literature." Reference collections are time consuming to create and costly to maintain, and there are few digital resources (though see Northwest Plants Database 2018 for starch reference images). Furthermore, reports, papers, and theses do not always include descriptions of their identification criteria or photographs of identified taxa. Thus, when archaeological, fragmentary plant tissues are recovered in paleoethnobotanical assemblages in the absence of complete organs, they are often not identifiable to family, genus, or species levels.

While grain, cereal crops, maize, and squash domestication processes are relatively well understood, we know little about domestication and management pathways in root or geophyte crops (Denham et al. 2020). Blake (2015, p 20) attributes this scientific knowledge gap to an archaeological prioritization of Eurasian crops and research agendas aimed at understanding population growth and the development of social and political complexity. Significant contributions have been made in identifying archaeological tubers and centers of tuber domestication in Central and South America (e.g. Hastorf 1993; Pearsall 2008; Hather 2016), and more recently, geophytes have featured prominently in the paleoethnobotany of southern California (Anderson 2005; Gill 2014). Some experimental work for identifying the archaeological remains of Northwest geophytes does exist (Spurgeon 1996; Weiser 2006; Wollstonecroft and Baptitse 2016); however, these works have not yet been synthesized into a definitive guide for aiding paleoethnobotanical identifications.

This study represents the first in a series dedicated to systematic descriptions specifically designed to address these challenges and establish identification criteria for paleoethnobotanists working with storage organs within this region and beyond. This paper primarily focuses on the bulbs common to Northwest diets (Table 1) (Turner 1995, 2007). We photographed 11 species, 8 genera, of modern culturally relevant geophyte foods. Of those 11 species, 8 were also experimentally charred to provide paleoethnobotanists with comparative size and weight data. For three species we were unable to collect significant numbers of the geophytes themselves and relied on herbarium data. In this paper, we discuss the cultural activities which may affect geophyte morphology in the archaeological record as well as key identification features for these species. We also present a simple key along with additional photographic digital comparative material (Fig. 2; Online Supplementary Materials 1–8), as well as an online digital database with ethnobotanical summaries (Carney and Tushingham 2019 https://cdsc-wsu.org/nwnativeplants/). We hope these identification criteria, future studies, and digital comparative collection will be useful in a making taxonomic assignments for the bulbs, corms, and tubers which occur in northwest paleoethnobotanical assemblages.

Bulbs as Underground Storage Organs

Bulbs, corms, tubers, tuberous roots, and rhizomes are underground storage organs (USO's) commonly referred to

Table 1 Species examined in this study, organized by family after Turner (1995, 2007)

Scientific name	Common name	Family	Habitat	Preparation and consumption
Allium acuminatum	Hooker's onion, tapertip onion	Amaryllidaceae	Dry open woods and exposed areas	Raw, dried, or steamed
Allium cernuum	Nodding onion	Amaryllidaceae	Open woods and exposed areas	Raw, dried, or steamed
Camassia leichtlinii	Great camas	Asparagaceae	Meadows and bluffs	Steamed underground, dried, or made into cakes
Camassia quamash	Common camas	Asparagaceae	Perennially wet meadows and bluffs	Steamed underground, dried, or made into cakes
Triteleia grandiflora	Wild hyacinth, largeflower triteleia	Asparagaceae	Grasslands, sagebrush desert, dry woodlands	Raw, boiled, or dried
Calochortus macrocarpus	Mariposa lily, sagebrush lily, desert lily, sweet onions	Liliaceae	Dry hillsides and plains	Raw, dried, or steamed
Erythronium grandiflorum	Glacier lily, yellow avalanche lily	Liliaceae	Upland meadows and open woods	Steamed, roasted, boiled, or dried
Fritillaria affinis	Chocolate or checker lily	Liliaceae	Meadows at all elevations	Boiled or steamed, not stored
Fritillaria pudica	Yellowbells	Liliaceae	Grasslands and open forests	Raw, boiled or steamed, sometimes dried
Lilium columbianum	Columbia or tiger lily	Liliaceae	Damp open woods and meadows	Boiled, steamed, dried, or made into cakes
Toxicoscordion venenosum	Death camas	Melanthiaceae	Dry hillsides	Very poisonous, never consumed

All species are bulbous monocots

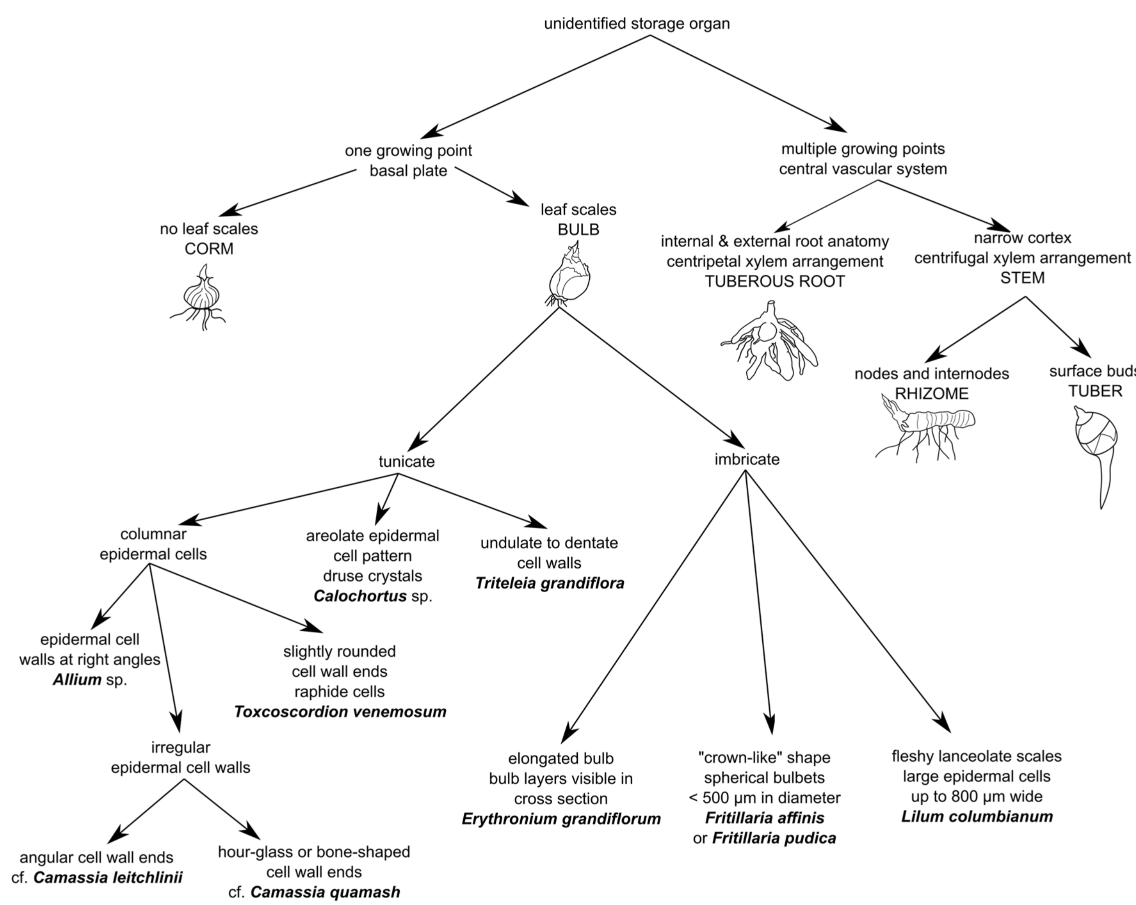

Fig. 2 Diagrammatic flow chart for identifying the genera and species within the text

as root vegetables, although they comprise a much more morphologically diverse group. These species all evolved storage organs to survive through dormancy during drought and temperature extremes (Bryan and Griffiths 1995), common features of the cool, wet winters and dry summers of the Northwest Coast and Columbia-Fraser Plateau. In the following section, we summarize the necessary characteristics for identifying bulbous vegetative organs often found in Northwest paleoethnobotanical assemblages.

Bulbs are round to ovate geophytes, have only one growing point or meristem, and are marked by the presence of a basal plate or base from which adventitious roots grow (Bryan and Griffiths 1995; Brecht 2003). Bulbs are leaf bases, with buds that are enclosed by fleshy scales or modified leaves. Each scale is a swollen modified leaf or leaf base in which energy is stored. These geophytes may be either tunicate and imbricate bulbs (Bryan and Griffiths 1995). A tunicate bulb, i.e., onions, is enclosed by a protective, paper-like tunic or bulb covering of retained, dead epidermal tissue. Imbricate bulbs, such as lilies, do not have the tunic to protect the fleshy scales and are more susceptible to drying out. Bulbs often have several layers of modified leaves, and each leaf is protected by a single-cell layer of epidermal tissue. The epidermal tissue usually consists of elongated cells parallel to the long axis of the organ (Esau 1977, p 84). Although Glover (2000, p 498) notes that these unspecialized or pavement epidermal cells are traditionally considered insignificant, below we provide evidence for cell shapes that are diagnostic to genus. Bulbs reproduce both sexually by seed, often following biennial to multi-year cycles, and asexually by producing daughter bulbs, referred to as bulblets.

Here we focus on the bulbs that are and were commonly consumed throughout the Northwest (Table 1). Many of the species listed within Table 1 are classified either to the Liliales or Asparagales orders of the Lilioid monocots (Chase and Reveal 2009). Genera within the Asparagales order include the native onions (*Allium* spp.), camas (*Camassia* spp.) and triteleia (*Triteleia grandiflora*). We include key characteristics of death camas, *Toxicoscordion veneosum*, Liliales order, as the foliage and bulb shape resemble true camas. We also provide criteria below for other Liliales, including mariposa lily (*Calochortus macrocarpus*), glacier lily (*Erythronium grandiflorum*), the fritillarias (*Fritillaria* spp.), and Columbia lily (*Lilium columbianum*). In future iterations of this work, we plan on providing identification criteria for both morphology and interior root or stem anatomy for other culturally important USO's including tuberous roots such as the lomatiums (*Lomatium* spp.), bitterroot (*Lewisia redivia*), corms such as spring beauty (*Claytonia lanceolata*), and rhizomes such as cattail (*Typha latifolia*).

These identification criteria are necessary as paleoethnobotanical data can help with initiatives to strengthen cultural identity (Turner et al. 2003; Turner and Turner 2008; Turner and Spalding 2013), improve human health and well-being (Kuhnlein et al. 2007; Isaac et al. 2018), and inform modern restoration ecology and land management decisions (DeAloia 2004; Nicholas et al. 2016). It is well established that Northwest Indigenous people were and continue to be active managers of their plant resources (Turner et al. 1980; Peacock 1998; Marshall 1999; Peacock and Turner 2002; Turner 2007; Turner 2014b; Ignace and Ignace 2016). Many First Nations and Native American nations and other land management agencies are working to supplement and expand traditional ecological knowledge through archaeology and incorporate traditional land-use strategies into modern land management practices (Ignace et al. 2016; Nicholas et al. 2016). Paleoethnobotany can contribute to these efforts by confirming the antiquity of ethnobotanical practices and revitalizing and renewing traditional land management techniques.

Methods

For each of the 11 species discussed below, we conducted an anthropological and biological literature review. We reviewed journals from the field of systematics in botany and monographs, which provided detailed descriptions of geophyte morphology, function, and life history. We also sought ethnographic works for plant management practices or food preparation methods, as both behaviors have the potential to physically alter morphological structure or the associated archaeobotanical assemblage. We focus primarily on features and ethnobotanical evidence which may affect the plant remains themselves and urge readers to review the sources cited here for additional details. For a complete summary of Northwest ethnobotanical uses, cooking practices, discussions of plant management practices, and the associated proxy evidence which may support such behaviors, readers are referred to Turner (1995; 2007; 2014a, b), Peacock (1998), Turner and Peacock (2005), Thoms (2009), and Black and Thoms (2014).

We collected reference plants and plant tissue from native nurseries, the Washington State University Herbarium, and collected specimens from unmanaged populations in several locations to account for both controlled and uncontrolled growth settings (Table 1; see Online Resources 1–8 for additional information and provenance). All reference geophytes were photographed using a Nikon D3200 digital camera and an Olympus SZX7 light stereoscope microscope. For all tunicate bulbs, epidermal tissue was subsampled from bulbs and placed on a slide with pure glycerin, covered, and photographed using an BX53 Olympus light binocular microscope.

We also measured, weighed, and experimentally charred 13 of these most common species to provide paleoethnobotanists with detailed data on geophyte size, shape, and taphonomic changes. Whenever possible, bulbs and corms were measured at the longest point between stem connector point and bulb base, at the broadest portion of the bulb, and perpendicular to this measurement to approximate bulb diameter.

Extensive experimental carbonization research has demonstrated the situational complexities of seed and wood charcoal taphonomic processes (e.g. Wright 2003; Braadbaart and Poole 2008; Gallagher 2015, p 27; Castillo 2018, Table 1). Roots, rhizomes, bulbs, and corms have seen somewhat less attention in the paleoethnobotanical literature. To our knowledge, *Sagittaria latifolia* is the only northwest geophyte with systematic experimental data on the effects of charring and preservation (Spurgeon 1996). In the present study, we primarily follow Spurgeon's (1996) and Hather's (2016) suggestions for creating carbonized reference material from vegetative tissue with minimal ashing or morphological distortion.

Modern comparative material was wrapped in aluminum foil and charred in an anaerobic environment at 300 °C in a muffle oven at both UCSD and WSU. Charring times varied as we were interested in completely charring the reference samples of varying sizes and densities and averaged between 15 min for smaller bulbs and corms to 1 + hours for larger bulbs and rhizomes. While we recognize that these conditions do not necessarily reflect the charring conditions present in the past or in ethnographic depictions of food processing or earth ovens, we maintain that these conditions provide an idealized carbonized reference for paleoethnobotanical comparisons (Hather 1991, p 663; Pearsall 2015, p 129). Future work is necessary to understand how common Northwest plant food processing techniques such as boiling, steaming, and drying may alter plant tissues and cell walls (Wollstonecroft et al. 2008).

After charring, all specimen dimensions were again weighed and measured, where applicable. Reference material was again photographed at multiple scales, with epidermal and cross-sections of each species selected for scanning electron microscopy imaging (SEM). Samples were imaged on the FEI Quanta 600 SEM at the University of California at San Diego Materials Research Center and the FEI Quanta 200 SEM at the Washington State University Francesci Microscopy Imaging Center. Charred samples were placed in a desiccator and left at full vacuum overnight to stabilize and remove any residual water. Samples were then placed in the SEM on carbon coated stubs. As the electron beam occasionally damaged some of the fragile charred plant material, we varied chamber pressure, beam voltage, and current. These values are reflected in the photographs in the online supplemental materials (Online Resources 1–8). In general, we used lower accelerating voltage (kV) to reduce sample damage, electron buildup and charging. We recommend working with microscopy technicians to find the right combination of settings for both the SEM machine and the archaeobotanical specimens. While destructive, gold or carbon coating of specimens reduces surface charging and may be used to capture clearer images.

Results and discussion

Below we briefly describe the native habitats and ecologies for each bulbous species before describing ethnographic methods of food preparation and management. We then explain key characteristics of each species, beginning with macroscopic features and moving to micro-features visible with microscopy. The discussion is ordered alphabetically by genus and species. Additional digital reference images and all provenance, geophyte size, and experimental charring data are located in the online supplemental materials (1–8). Additional photographs of all species may found at the Northwest Plants website (Carney and Tushingham 2019) and additional digital reference materials are listed at the end of this article.

When trying to narrow down the identification of a Northwest geophyte, we recommend first identifying whether the specimen is a bulb, corm, tuber, tuberous root, or rhizome (Fig. 2). Both bulbs and corms are round to ovate storage organs with basal plates and one growing point; bulbs have distinct layers of leaves while corm interiors will include all stem anatomical features (Bryan and Griffiths 1995). Tuberous roots are swollen roots and will have root internal and external physiological adaptations (Brecht 2003). Rhizomes are modified stems with nodes and internodes, and exteriors are often covered in the remnants of leaf bases. Tubers, which develop from rhizomes, may vary in shape but are more or less round, with typical stem anatomy, and will have an arrangement of buds over its surface (Brecht 2003). While we focus on bulbs below, future articles will cover the corms, rhizomes, tubers, and tuberous roots of the Pacific Northwest. Figure 2 is a visual key to the genera and species mentioned below and should be followed when working with unidentified storage organs, primarily bulb-like tissues.

***Allium* spp.**

Several *Allium* species were commonly consumed throughout the northwest; here we discuss two of the most prolific species. All *Allium* species have diagnostic tunics and unspecialized interior columnar epidermal cells, and these features may be the most diagnostic criteria for paleoethnobotanists (Khorasani et al. 2018). Additional *Allium* reference photographs as well as qualitative and quantitative measurements can be found in Choi and Cota-Sanchez (2010), Choi et al. (2011) and Weiser (2006). For both *Allium* species, we recommend examining epidermal cells and bulb morphology when making identifications.

Allium acuminatum Hook., commonly known as Hooker's or tapertip onion, is a perennial herb found west of the Rocky Mountains in dry, open, rocky meadows at low to mid-elevations. Hooker's onions were less commonly consumed than nodding onion (*Allium cernuum*) but were prepared similarly (see below) (Turner 1995, p 41; 2007, p 61; Ross 2011, p 338).

Allium acuminatum bulbs are almost completely spherical to slightly ovate bulbs (Fig. 3a). In our examination of modern bulbs (n = 25), we found that bulbs were on average just 1.5 mm longer than they were wide, averaging 8–15 mm in diameter. Some wild bulbs may appear "egg-shaped" (Pojar and MacKinnon 2014, p 106). Hooker's onion bulbs have a characteristic light brown, reticulate-fibrous, "net-like" tunic or bulb coat (Bryan and Griffiths 1995, p 6). Pavement epidermal cells from the tunic are either hexagonal or nearly cuboidal and range from 300–400 µm in diameter (Fig. 3b). Pavement epidermal cells on inner bulb leaves are unspecialized, rectangular in appearance and similar to most *Allium* species, averaging 150 µm in length (Fig. 3c). According to Jacobsen (1979), the number and arrangement of vascular bundles in the scapes of *A. acuminatum* are diagnostic as well.

Allium cernuum Roth, or nodding onion, is perennial widespread across the Pacific Northwest. It is common in open and somewhat moist areas. Nodding onion grows from oval, tapering, and faintly pink bulbs which are often clustered in the wild (Fig. 3e). Nodding onions were popular dietary items of coastal and interior communities (Turner 1995, 2007). Bulbs could be eaten raw or roasted over an open fire but were usually bundled together and steamed in underground earth ovens overnight (Turner 2007, p 62). They were sometimes interspersed with black tree lichen (*Bryoria* sp.) and camas bulbs (*Camassia* sp.) or other foods (Turner 1977; Turner et al. 1980).

Bulbs are elongate and narrow, tapering into the main stem (Bryan and Griffiths 1995, p 9). The fresh membranous tunics are light pink. *Allium cernuum* bulbs range from 8.3

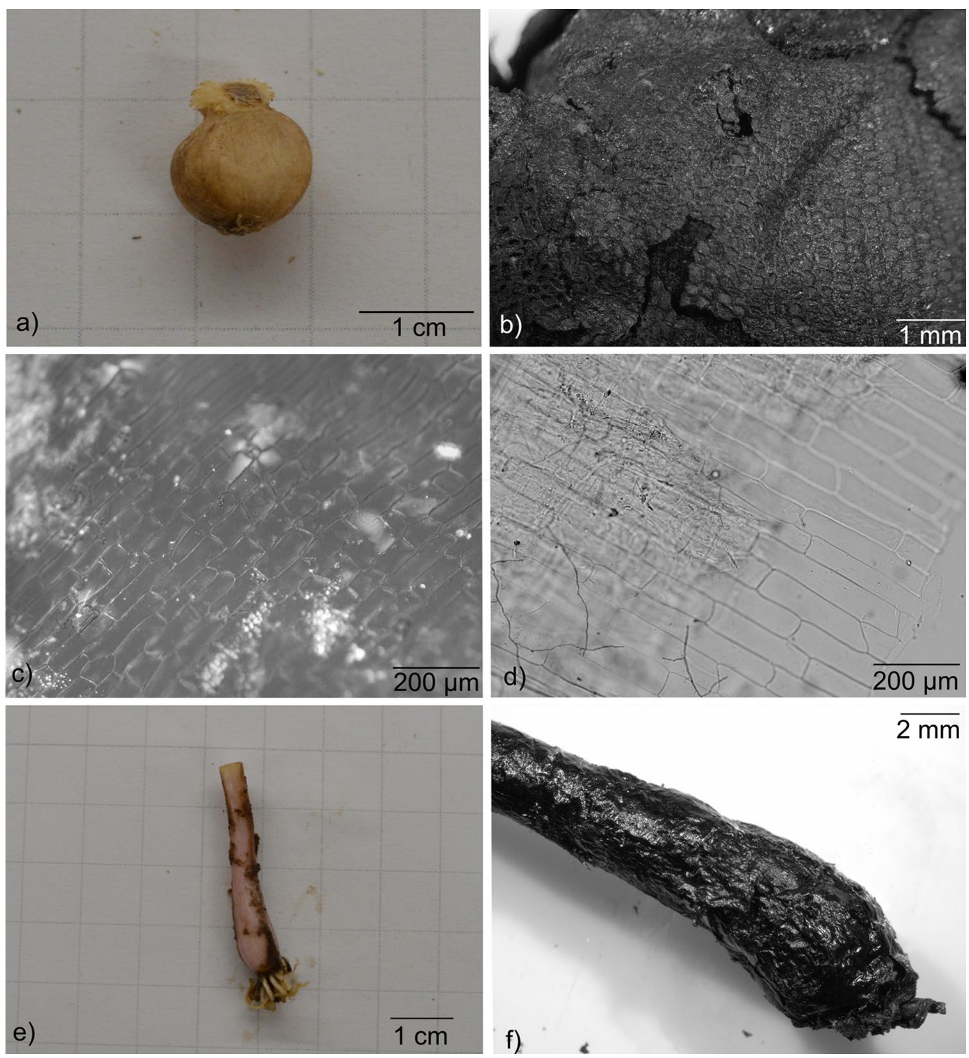

Fig. 3 *Allium* spp. bulb reference images. **a** Whole, fresh *Allium accuminatum* bulb; **b** experimentally charred *Allium accuminatum* bulb showing tunic cells; **c** *Allium accuminatum* epidermal cells; **d** *Allium cernuum* epidermal cells; **e** fresh *Allium cernuum* bulb with light pink tunic; **f** experimentally charred *Allium cernuum* bulb with flakey charred composition

to 22 mm in diameter (Choi and Cota-Sanchez 2010, p 799). Pavement epidermal cells on bulb leaves are unspecialized and rectangular, with perpendicular to slightly angled end walls (Fig. 3d). Cells average 150–200 µm in length and 35 µm in width. Charred specimens tended to be quite flakey, with epidermal cells visible and diagnostic under higher powered microscopy (Fig. 3f).

Calochortus macrocarpus

Calochortus macrocarpus Douglas is a widespread perennial common in dry grasslands and open ponderosa pine forests (Ness 1989). Also known as mariposa lily, sagebrush lily, or desert lily, these bulbs were consumed by all Interior groups and some California groups, but may have been supplemental for most (Mastroguiseppe 2000, p 51; Anderson 2005, p 142; Turner et al. 2007, p 65). We were unable to find any ethnographic references to *Calochortus* spp. consumption for coastal groups. Bulbs are crisp and sweet and were often eaten raw. They could also be steamed or air-dried. Turner (2007, p 65) notes that the Okanagan also sometimes cooked *C. macrocarpus* bulbs as a flavoring with other foods.

Calochortus macrocarpus bulbs are elongated and ovoid, with a membranous tunic (Fig. 4a) (Gerritsen and Parsons 2007). Bulbils often grow from the scapose stem of this plant (Bryan and Griffiths 1995, p 64). Pavement epidermal cells are arranged in an areolate pattern with intercellular air spaces. The most distinguishing characteristic of this bulb are the dense druse crystals which average 50 µm in width (Fig. 4b). Druses are a group of crystals of calcium oxalate and are thought to be an adaptation to prevent herbivory (Webb 1999; Evert 2006, p 56), and *C. macrocarpus* crystals are be visible under both lower powered and higher-powered microscopy. To our knowledge, there are no modern experiments which look at the presence of these druse crystals in mariposa lilies under various food preparation methods, diet proportions, or toxicity.

Camassia spp.

The tunicate bulbs of two members of this genus were commonly consumed across the Northwest (Teit 1928; Gunther 1973; Anastasio 1985; Suttles 2005). *Camassia leichtlinii* (Baker) S. Watson, or great camas, is chiefly distributed west of the Cascades, although there are several populations on the eastern slopes of the Cascade mountains (*Camassia* Lindl. in GBIF Secretariat 2017). *Camassia quamash* (Pursh) Greene, also known as common camas, is frequent throughout both the interior plateau and coastal regions. Both species are bulbous monocots which live in colonies in poorly drained fields or prairies with xeric moisture regimes (Gould 1942, p 712; Turner and Kuhnlein 1983, p 200). The two species are relatively difficult to tell apart; great camas plants and bulbs are generally larger with evenly spaced petals while common camas is somewhat smaller with a bottom petal pointing directly down (Gould 1942, p 720; Turner and Kuhnlein 1983, p 200; Beckwith 2004, p 102) observed that common and great camas were not distinguished in nomenclature among Northwest Coast groups, and we discuss them in tandem here.

Camas was a staple food for many coastal and interior groups and was prepared in a variety of ways, most commonly steam-cooked in a pit for several days (Turner 1995, p 42, 2007, p 67). *Camassia quamash* was often wrapped in skunk cabbage (*Lysichiton americanus*) or bluebunch wheatgrass (*Pseudoregneria spicata)* with lichen (*Bryoria* sp.), wild onion (*Allium* sp.) or yampah (*Periderida gairdneri*) and steam baked in pit ovens for 48–72 h (Turney-High 1941, p 34; Mastroguiseppe 2000, p 47; Ross 2011, p 423). Among coastal groups, ferns (Polypodiopsida) and seaweed (Eukaryota) were often used as liners within steaming pits (Gunther 1973; Turner 1995). After bulbs were thoroughly cooked, they were pounded into a dough and formed into loaves, often steamed a second time before drying (Spinden 1908, p 202). While initial genetic structural work has proven inconclusive (Tomimatsu et al. 2009), ethnographic and archaeological evidence suggests that bulbs were frequently traded throughout the Northwest Coast culture area, and we believe it is likely they were traded within the Interior as well (Turner and Kuhnlein 1983; Lyons and Ritchie 2017).

Camassia spp. bulbs are tear-drop shaped with a medium to dark brown tunic (Fig. 5a). *Camassia quamash* and *C. leichtlinii* bulbs are very similar in appearance,

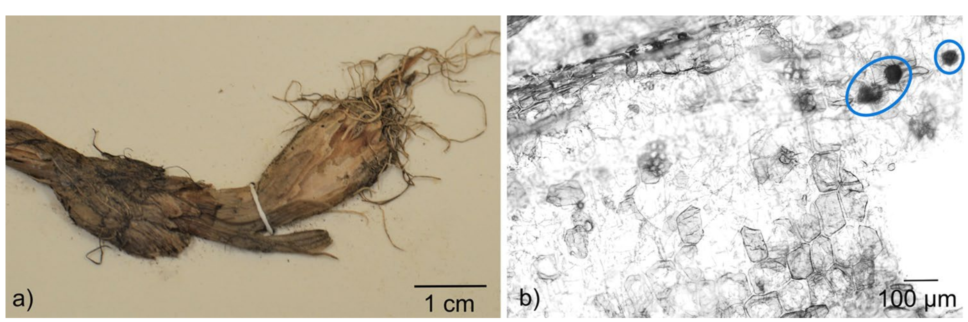

Fig. 4 *Calochortus macrocarpus*. **a** Pressed herbarium specimen; **b** epidermal cells with druse crystals outlined in blue

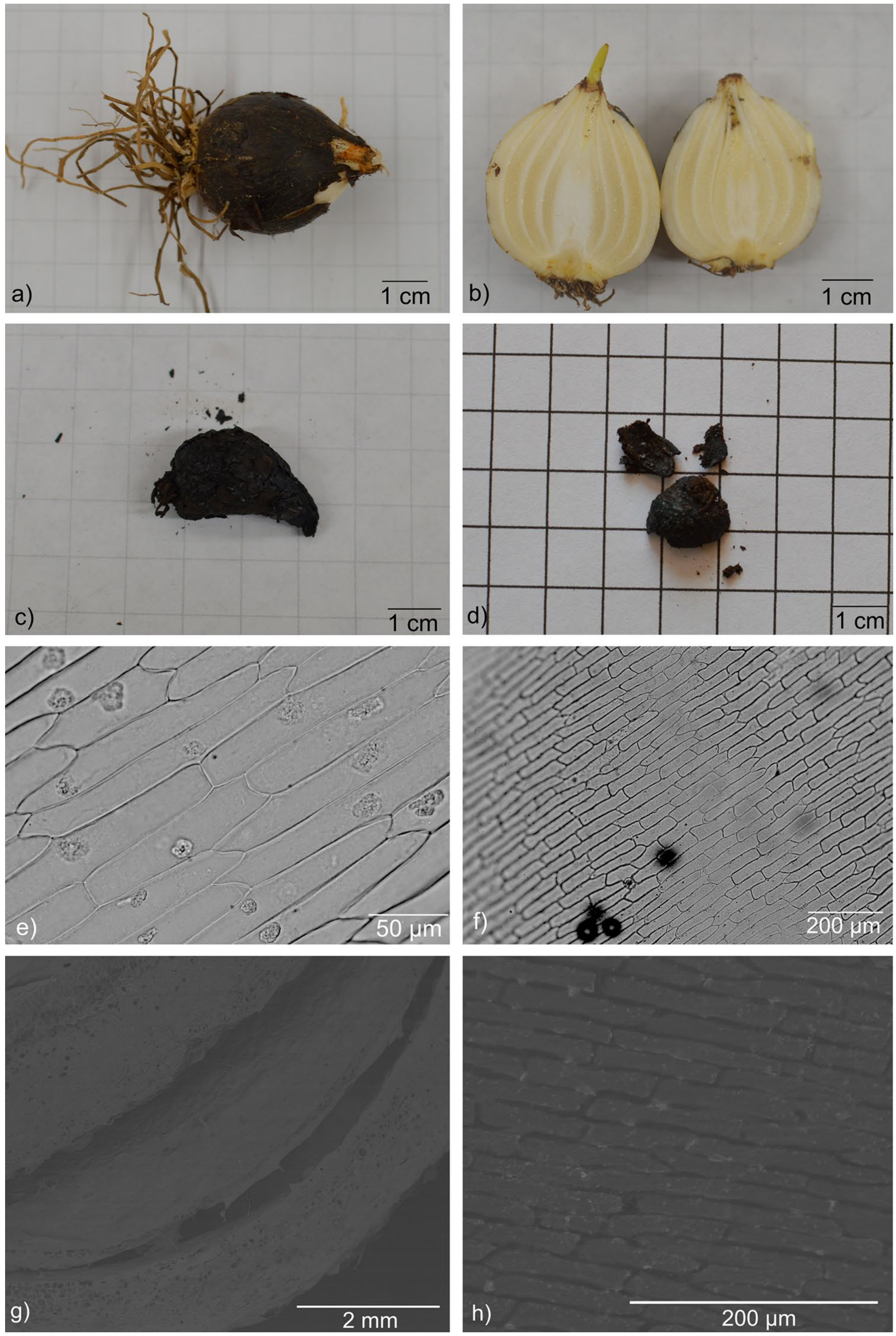

Fig. 5 *Camassia* spp. images. **a** fresh, mature *Camassia leichtlinii* bulb with tunic; **b** fresh, halved *Camassia quamash* bulb showing interior leaf scales; **c** experimentally charred, immature, elongated *Camassia leichtlinii* bulb (about two years of age); **d** experimentally charred Camassia quamash leaflets; leaflet fragments are common in paleoethnobotanical assemblages; epidermal cells with angular; **e** *Camassia leichtlinii* epidermal cells with angular cell walls; **f** *Camassia quamash* epidermal cells with bone or hourglass shape; **g** SEM cross section of experimentally charred *Camassia leichtlinii* bulb showing heat-fused leaf scales; **h** SEM image of experimentally charred *Camassia quamash* epidermal cells

although both young and mature *C. leichtlinii* bulbs are significantly larger than *C. quamash* bulbs (Online Resource 3; Turner and Kuhnlein 1982, p 201). In both species, bulb leaf scales grow in regular layers with 2–3 scales present in bulbs of young (2–3 year-old) plants. More mature bulbs closer to or at sexual maturity will have 4 to 5 or more scales (Fig. 5b) (Online Resource 3; Leffingwell 1930; Thoms 1989, pp 56, 152).

The columnar epidermal cells are generally visible under SEM, although leaf scales are often fused and may appear glassy. Hather (1991, p 673) indicates that solid glassy carbon may be the result of charring tissues with high sugar content, and we suggest may be the result of charring post-cooking in earth ovens (Fig. 5g). *Camassia leichtilinii* pavement epidermal cells average between 120 and 180 μm long by 20–50 μm wide, with many angular cell walls (Fig. 5e).

Camassia quamash epidermal cells often appear bone-shaped or hour-glass shaped, and are similar in appearance to osteosclereid cells. They average 130–190 μm long and 30–50 μm wide (Figs. 5d, f). As with onions, pavement epidermal size and particularly cell wall shape may be the only way to distinguish between the two species archaeologically. We suggest species level identifications be made conservatively (see also Weiser 2006, pp 190–191).

Erythronium grandiflorum

Erythronium grandiflorum Pursh is a widespread herbaceous subalpine lilaceous perennial with an elongated imbricate bulb (Fig. 6a). Also known as yellow avalanche or glacier lily, this monocot grows anywhere from sagebrush slopes to near timberline in mountains, often found blooming shortly after snow fields melt (Parish et al. 1996, p 303). A significant source of food for both coastal and interior peoples, the deeply buried, sweet bulbs must be steamed, roasted, or boiled for consumption. They were also dried and stored over winter, often reconstituted with water (Turner et al 1980, p 46; Ross 2011, p 337). *Erythronium grandiflorum* bulbs were used most intensively among Interior Salish First Nations groups and for the Secwepemc and Nlaka'pamux were the most important foods (Turner 2007, pp 68–69; Loewen et al. 2016, p 223).

Bulbs commonly have an attached chain of segments of bulb remnants from past annual growth (Loewen et al. 2001). These bulb appendages may act as vegetative propagules when separated from the parent plant and are frequently replanted during bulb harvests (Loewen et al. 2001, p 506, Loewen et al. 2016, p 224). *Erythronium grandiflorum* thrives in disturbed meadows and bulbs in these locations had higher nutrient values within bulb tissue and yielded greater seed production (Tardiff and Stanford 1998). Ethnographic interviews indicate larger bulbs were kept and smaller bulbs replanted (Loewen et al. 2016), and there is potential for this combination of selective harvesting, tillage, and vegetative propagation to be visible within archaeological bulbs.

Sometimes mistaken as a corm, *E. grandiflorum* bulbs have only a few fleshy, nearly fused leaves or scales (Loewen et al. 2016, p 223). These scales are visible in cross-section under low powered and high-powered microscopy (Fig. 6d). Fresh elongated bulbs have a thin, pale brown to tan tunic. In our survey, we found that 4-year-old bulbs ranged from 2–3.5 cm in length. Bulb surface is generally smooth, with rectangular to trapezoidal epidermal cells visible under low-powered microscopy. The epidermis of charred specimens wrinkled, and many experimentally charred bulbs broke horizontally (Fig. 6b). We suggest these bulbs are best identified by a combination of epidermis cellular patterning and the fused leaves visible within a transverse view of the bulb.

Fritillaria spp.

Fritillaria species were widely consumed across the greater region and are often collectively referred to as rice root (Turner and Kuhnlein 1983, p 201; Turner 1995, pp 46–48). Several species were frequently used across both the plateau

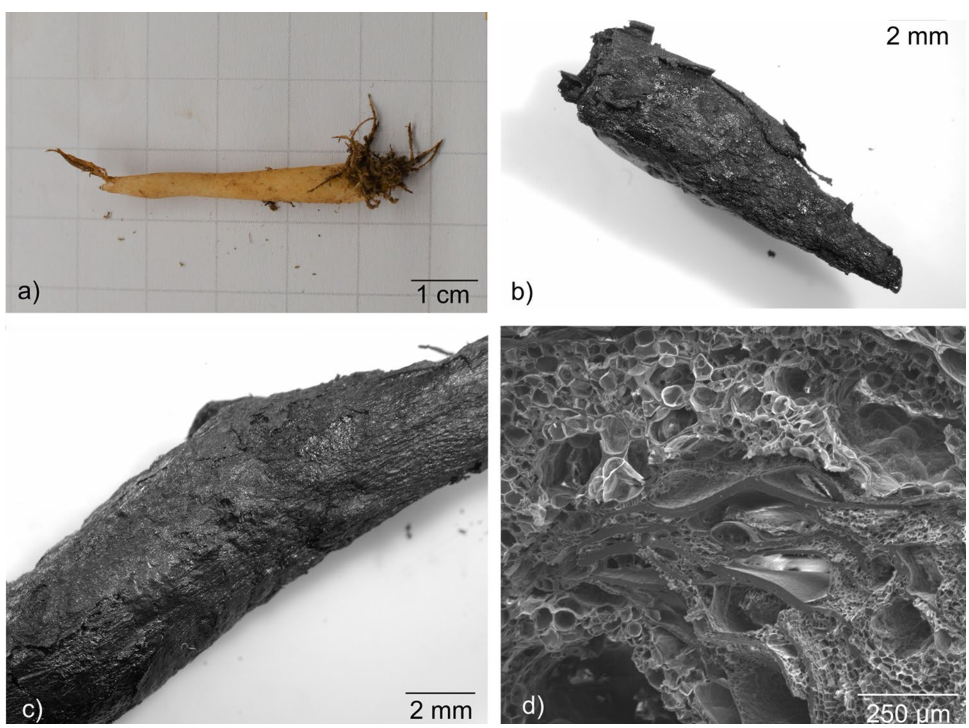

Fig. 6 *Erythronium grandiflorum*. **a** Fresh, whole, mature bulb; **b** experimentally charred whole bulb; **c** higher magnification of charred bulb showing wrinkled epidermis; **d** SEM cross section of experimentally charred *Erythronium grandiflorum* bulb showing fused interior leaf scales

and coastal regions; here we highlight two common species. *Fritillaria affinis* (Schult. & Schult. f.) Sealy (syn. *F. lanceolata*) and *Fritillaria pudica* (Pursh) Spreng. are herbaceous perennials that have white to yellow bell-shaped bulb, usually covered with rice-like bulblets. *Fritillaria affinis*, or checker or chocolate lily, grows on both sides of the Cascade Mountains in open prairies and woodlands. *Fritillaria affinis* is distinguished by its chocolate-brown to dark purple flowers (Fig. 7a). *Fritillaria pudica*, or yellowbells, is shorter, growing only 10–25 cm tall with drooping yellow flowers (Fig. 7b). *Fritillaria pudica* is generally restricted to the Plateau, preferring shrub-steppe to mixed coniferous forests. Bulbs were generally boiled and mashed, though they could also be mixed with grease, or blanched or steamed (Teit 1928, p 56; Turner and Kuhnlein 1983, p 213; Turner 1995, p 47). Turner (2007, pp 71–72) suggests only yellowbell bulbs were stored. Bulbs were harvested throughout the year by different groups, though always after the bulb had produced a shoot (Fig. 7b).

Mature bulb morphology is the best factor when identifying the imbricate bulbs of *Fritillaria* species (Figs. 4b, c). Mature bulbs are distinctly bell-shaped with a "crown" at the bulb base (Fig. 7e) (Bryan and Griffiths 1995, p 133). When bulbs sprout, the embryo shoot often splits the bulb into two to three scales, which may appear fused if the bulb was harvested before sprouting (Fig. 7b). This genus is most well-known for the numerous, "rice-like" daughter bulbils which grow from the basal plate (Fig. 7d) (Turrill 1950). These

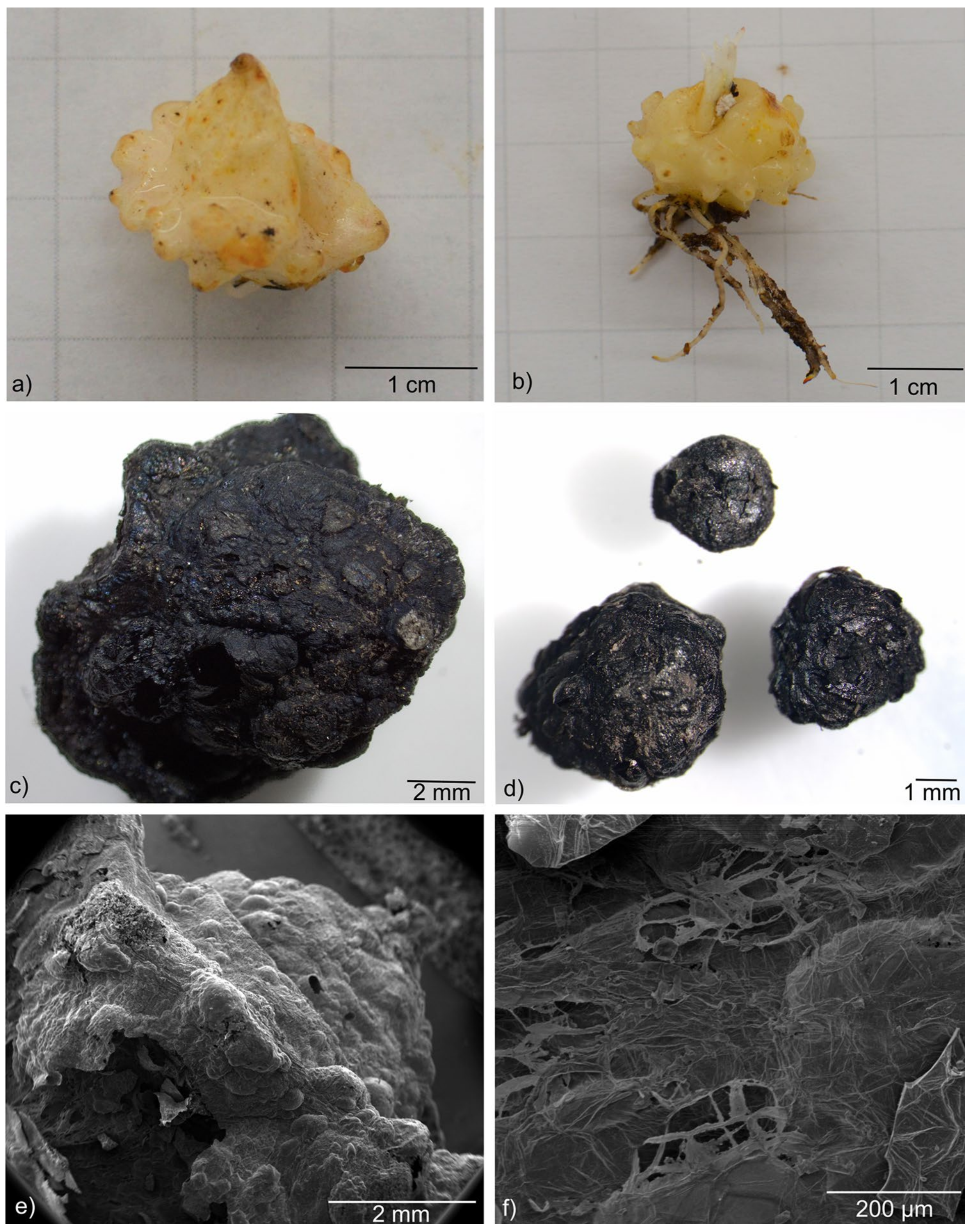

Fig. 7 *Fritillaria* spp. images. **a** *Fritillaria affinis* whole, fresh bulb; **b** *Fritillaria pudica* whole, fresh bulb sprouting, showing leaf scales splitting; **c** experimentally charred *Fritillaria affinis* with bulb basal plate or "crown" at the bottom left of image; **d** experimentally charred *Fritillaria pudica* bulblets; **e** SEM image of experimentally charred *Fritillaria pudica* bulb; **f** higher magnification of experimentally charred *Fritillaria pudica* bulb epidermis

small bulblets may also appear in the archaeological record. We found that general shape was preserved after charring.

Lilium columbianum

Lilium columbianum Leichtlin, also known as Tiger or Columbia Lily, is a tall perennial with a white imbricate bulb somewhat similar in appearance to garlic cloves (Fig. 8a). Tiger Lily grows in damp open woods and meadows at a variety of elevations across the greater Northwest region. Bulbs were usually harvested in the spring, boiled or steamed to temper the bitter taste, sometimes with lichen (*Bryoria* sp.), and occasionally dried in the sun after cooking (Turner 1977, p 468, 2007, p 74). They were also mashed into thin cakes. Harvest time varied across coastal groups; leaves were often buried underground after bulb harvests (Gunther 1973, p 25; Turner 1995, p 49). Teit (1900, p 237) reports that among the Thompson, *L. columbianum* and *Lomatium macrocarpum* were boiled with salmon roe.

The bulbs of *L. columbianum* are concentric, up to 4×4 cm, with fleshy, lanceolate scales or leaves (Fig. 8b) clustered around a central growing point (Bryan and Griffiths 1995, p 231). Four-year-old bulbs in this study averaged 2.5–3 cm in diameter, although Turner (2007, p 74) notes that bulbs 5–7 cm in diameter are possible. Two to 3 mm in diameter, adventitious roots grow from the basal plate. Bulb epidermis cells are rectangular to cuboidal, but much larger than *Camassia* or *Allium* spp., ranging from 300–800 µm wide (Fig. 8c). These distinctive and large cells are also quite visible on charred specimens at low magnification,

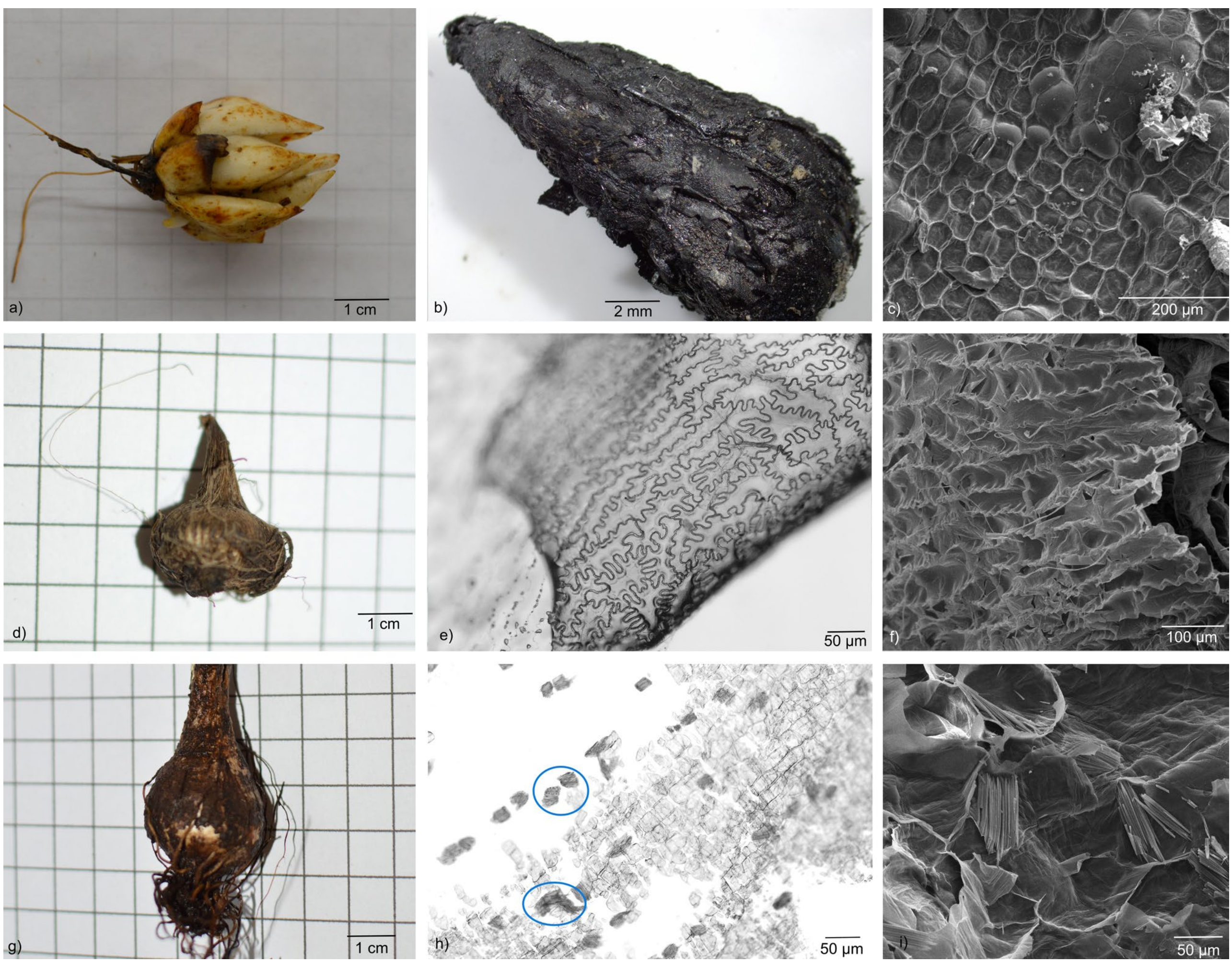

Fig. 8 Composite of *Lilium columbianum, Triteleia grandiflora*, and *Toxcoscordion venemosum.* **a** whole, fresh *Lilium columbianum* bulb; **b** experimentally charred *Lilium columbianum* leaflet; **c** SEM of charred *Lilium columbianum* epidermis; **d** whole, fresh *Triteleia grandiflora* bulb with reticulate fibrous tunic; **e** *Triteleia grandiflora* epidermal cells; **f** SEM image of experimentally charred *Triteleia grandiflora* epidermal cells; **g** whole, fresh, *Toxcoscordion venemosum* bulb with brown tunic; **h** epidermal cells of *Toxcoscordion venemosum* with raphide crystals outlined in blue; **i** SEM image of experimentally charred *Toxcoscordion venemosum* highlighting diagnostic raphide crystals

and along with macro bulb morphology, should make identification straightforward. We did not note any morphologic changes to the bulb or leaf scales after charring.

Triteleia grandiflora

Triteleia grandiflora (Lindl.), syn. *Brodiaea douglasii* Piper, is a common monocot growing among prairies, grasslands, and forest openings in seasonally dry interior and coastal northwest habitats (Lesica 2012, p 729). Also known as Wild Hyacinth or largeflower triteleia, these tunicate bulbs were harvested early in the spring and eaten raw or boiled and dried (Turner 2007, p 64). Several ethnographic and ethnobotanical sources mention wild hyacinth were a part of Indigenous diets, including Marshall (1977, p 51), Teit (1900, p 232), and Mastroguiseppe (2000, p 51), although there is little information about their preparation. These bulbs were likely prepared similarly to camas. Bulbs were harvested in April at about the same time as yellowbell bulbs (*Fritillaria pudica*).

Triteleia grandiflora grows from straw-colored slightly ovate bulbs with a reticulate-fibrous tunic (Fig. 8g) (Bryan and Griffiths 1995,p 325). Bulbs are slightly longer than they are wide, ranging from 0.9 to 2 + cm in length. The diagnostic pavement epidermal cells are columnar with undulate or dentate cell walls and are easily recognized in charred specimens at 3 × magnification under light microscopy and SEM (Figs. 8e, f). The jigsaw puzzle shape of these epidermal cells may add mechanical strength to these organs (Glover 2000).

Toxicoscordion venenosum

Toxicoscordion venenosum (S. Watson), syn. *Zigadenus venenosum* (Brasher 2009), is not an edible geophyte, but rather an extremely poisonous perennial herb. *Toxicoscordion venenosum* is colloquially called death-camas for its close resemblance to the other *Camassia* species (Turner 2007, p 181). It is common throughout the Northwest, frequently found in vernally wet places and often in close proximity to *Camassia* spp. Bryce et al. (2019) noted that death camas was annually rotated through camas plots in coastal areas as a means of marking harvesting ground ownership, and thus may be found in archaeological assemblages. Turner et al. (1980) report that the Okanagan and St'at'imc used the mashed bulbs as an arrow poison. Russel (2001, p 211) hypothesizes that death camas may have been much more abundant throughout the Northwest if it were not for millennia of active removal by Indigenous populations.

Death camas bulbs are very similar in appearance to other Interior Northwest bulbs, ranging from 1.5 to 2.5 cm in length and 0.75–1 cm in width (Fig. 8g). These bulbs have dark brown to black tunics and may only be distinguished by epidermal cell structure (Weiser 2006, p 191). Epidermal cells are rectangular to cuboidal, with slightly rounded corners (Fig. 8h). The most distinguishing characteristic for this species is the presence of idioblasts containing raphides (Fig. 8i). Raphides are needle-shaped crystals of calcium oxalate and are adaptations against plant predators (Webb 1999; Evert 2006, p 56). These cells average 120–150 μm in length and 70–100 μm in width, and are visible using both lower powered and higher powered microscopy on charred specimens.

Conclusion

Definitive criteria for northwest edible geophytes are necessary to address contemporary archaeological research questions. However, identification steps and procedures are not often mentioned within studies, are relatively difficult to access in grey literature or theses, or must be adapted from highly technical plant systematic studies. Here, we have consolidated much of the available literature on Pacific Northwest bulbs as well as taphonomic considerations into an easily accessible format specifically for paleoethnobotanists. We suggest that for bulbs, epidermal cells are the key diagnostic feature. In this study we also present high-quality digital reference images, a simple key flow chart (Fig. 2), reference measurements for charred and uncharred plants (Online Resources 1–8), and our insights into identifying archaeological bulbs, with a focus on carbonized remains. These resources, references, and materials were specifically chosen to assist both archaeologists and Native American and First Nations descendent communities seeking information on past plant use, preparation, stewardship, and food sovereignty, but should also be useful to a variety of disciplines. We encourage future Northwest paleoethnobotanical studies to include identification steps and images of identified species whenever possible to assist future work.

Through this combination of ethnobiological, systematic, and experimental data, we hope the criteria outlined here will provide the tools to conduct archaeological, paleoecological, and interdisciplinary research. We also share links to additional digital resources in the electronic supplementary material that may be useful in identifying archaeological and modern vegetative storage organs" and are continuously updated with additional images and information. We hope these resources as well as the identification methods established in this study will not only contribute to future archaeological and interdisciplinary investigations, but also knowledge of human-plant relationships both in the past and in the future.

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